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PRIMARY RESEARCH PAPER

Artificial ponds: a substitute for natural Beaver ponds in a Central European Highland (Eifel, Germany)?

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Abstract The European Beaver (*Castor fiber*), once widely distributed across Europe, was almost completely eradicated in the 19th Century. In the meantime it has recovered large parts of its distribution range and has increasingly resettled the valleys of the Central European Highlands. In the past, in these same valleys, countless man-made fish and fire-fighting ponds, with a water regime similar in size and location to those of the Beaver, were created

In order to assess how near-natural the amphibian communities of the artificial weir ponds are, we studied 21 artificial and 22 Beaver ponds in the Eifel, a typical Central European Highland in Germany, by means of personal observation and the use of funnel traps. In general man-made and Beaver ponds supported the same eight amphibian species; whereby the Beaver ponds had on average a larger number of species (4.82 species as opposed to 3.57).

The average population size of the two dominant Urodela species, determined by a mark-recapture method, was higher than the norm in both types of water bodies (*Triturus alpestris*: Beaver: 267; weir pond: 159 individuals; *Triturus helveticus* Beaver: 816; weir pond: 418 individuals), whereby the influence of the factor Beaver/artificial pond proved to be either neutral (*Triturus alpestris*) or positive (*Triturus helveticus*). The decisive factor for the activity density of both species in the ponds studied was the presence of fish. At least for the majority of woodland species in large areas of Central Europe, artificial weir ponds probably provide an important substitute for the once common Beaver ponds.

This leads to the following conclusions:

(1) The destruction or renaturation of weir ponds in line with the EU Water Framework Directive needs to be critically called into question in order to prevent avoidable damage to biodiversity.

(2) Beaver ponds open undreamt-of opportunities for amphibian conservation in Europe. The Beaver should therefore be allocated special consideration and considered a key species for the preservation of biodiversity when preparing relevant EU programmes.

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Introduction

The countryside of Central Europe has a considerable history of change, above all because of increasingly intensive land management; but also through the annihilation of key species since the last Ice Age (Gerlach, 2005; Meurers-Balke & Kalis, 2005; Bosinski, 2006). In the past 100 to 200 years in particular, the technical development of waterways, mechanization of farming and forestry management, together with urbanisation have led to a dramatic reduction of natural and semi-natural dynamic landscapes (Bender et al., 2005). This is particularly true of regions with a long history of human settlement and high population density, which is applicable to almost all of West and Central Europe.

Water bodies in particular are affected by changes in the countryside through drainage, sinking of the water table and wide scale destruction of small water bodies and natural water meadows (Krone, 2003). This has in particular had a negative effect on animal species tied to water bodies and with complex habitat requirements (Denoël & Ficetola, 2007). Amphibians are among the animal species which, because of their way of life, are both dependent on suitable bodies of water for reproduction as well as on suitable upland habitats. They are therefore particularly affected by habitat destruction and habitat fragmentation (Cushman, 2006; Arens et al., 2007; Becker et al., 2007; Johansson et al., 2007). At the same time, either intentionally or by accident, humans create new bodies of water in the modern countryside, which can be used as an alternative habitat (Krone, 2003; Denoël & Ficetola, 2007).

The Central European Highlands, including the Rhenish Slate Mountains, support few natural standing water bodies because of their steep topography (Drews & Ziemek, 1995; Krone, 2003), whereas artificial ponds are widely distributed. Weir ponds, which were created by the damming of small streams in smaller V-formed (notched) valleys as fire-fighting or fish ponds, are characteristic of the Central European Highland landscape. These ponds often represent the only standing water of any size in the countryside and are commonly populated by amphibians (Bitz et al., 1996). They therefore have a great significance for the maintenance of aquatic biodiversity, as already verified for small water bodies on farmland (Robson & Clay, 2005; Declerck et al., 2006; Céréghino et al., 2008).

Nonetheless, there is increasing doubt as to whether this poverty in biodiversity on larger standing water bodies really corresponds to the natural situation, as this does not take account of the Beaver (*Castor fiber*) (Dalbeck et al., 2007). As in Europe, the Beaver was widely eradicated worldwide due to intensive persecution, and the remaining populations survived mainly in lowland sections of larger rivers such as the Elbe, where hardly any ponds are constructed (Heidecke & Klenner-Frings, 1992). Only after the resettlement of the Beaver in the 20th Century, and the start of its spread into smaller wooded parts of the lower mountain ranges, did it become clear that the ponds created by damming of running water was part of the natural water body scheme in these parts of the countryside(Elmeros et al., 2003; Dalbeck, et al. 2007).

As the artificial weir ponds are frequently located where the Beaver also settles and builds its ponds, it can be assumed that over the past centuries the weir ponds have substituted for the Beaver ponds and therefore, despite the eradication of the Beaver, the continuity of dammed ponds has been maintained. This raises the question as to how near-natural these water bodies are, and how effective weir ponds have been in providing an alternative habitat for amphibians formerly associated with Beaver-created ponds.

In the course of the renaturation of flowing water, artificial barriers which interrupt the flow of water for water-dependent organisms have been regarded with increasing criticism for a number of years. This includes artificial ponds which have been created by damming of streams in the Central European Highlands.

As a result of the Water Framework Directive 2000/60/EG (WFD) an administrative, binding framework has in the meantime been created for all EU member states, which lays down regulations for dealing with ground and surface water and water bodies. In order to achieve the desired ‘good ecological status’, the unhindered passage of water must be maintained or restored. This means that barriers which interfere with the migration of aquatic organisms should be removed (Annex V, WFD).

At EU level, and therefore in all of its 27 European states, the aim is to removal water barriers, including small weir ponds such as those in the Rhenish Slate Mountains.
Against the background of the acute threat to numerous amphibian species in large parts of Europe (and beyond), the imminent implementation of the WFD in EU member states and the welcome expansion of the Beaver in Central Europe, we believe that it is imperative to obtain more information on the significance of artificial and Beaver ponds for amphibian fauna. We are convinced that this is crucial if unwanted developments leading to further impairment of species guilds, already highly endangered, are to be avoided.

In the present study we have therefore examined the amphibian communities of Beaver and artificial ponds in the Eifel, a typical cross-section of the Rhenish Slate Mountains in Germany.
In addition to a qualitative comparison of the amphibian species make up of both types of water bodies, we concentrated on the settlement density and population size of the newts of the sub-family Pleurodelinae (Genus Triturus).

These newts form a typical guild of the Central European amphibian community(Denoël et al, 2007). The genus *Triturus* in Central Europe north of the Alps comprises 4 species, three of which occur in the study area. During the reproduction period in spring, they remain in the spawning grounds which are mostly in standing water, For the rest of the year they live in the surrounding uplands, up to several hundred mertres distant from the waqter bodies, whereby two species (*T. alpestris* in particular but also *T. helveticus*) prefer a woodland and habitat and the third occurring species (*T. vulgaris*) extensively used open countryside (Schlüpman et al., 1996; Denoël & Ficetola 2007; 2007b).

In respect of the significance for amphibians of Beaver ponds in Europe there are some initial study results (Elmeros et al., 2003; Dalbeck, et al. 2007), whereby up to now quantative data was only available for the European Common Frog (*Rana temporaria*). In contrast little is known about the significance of Beaver ponds for the Urodela in Europe. Urodela must however be considered as one of the dominant guilds of the numerous amphibian communities in Central Europe and it should not therefore be neglected if the role of Beaver ponds for pond breeding amphibians is to be understood. As it is relatively easy to monitor newts in the spawning grounds using funnel traps, it was logical to include newts in the comparative study of artificial weir ponds and Beaver ponds in the relatively near-natural wooded low mountain countryside.

The aim of the studies was to clarify whether:

(1) there is a general difference between the amphibian communities inhabiting artificial weir and Beaver ponds, in particular the newt guilds of the genus *Triturus*
(2) if such differences exist, what habitat factors are responsible and
(3) what conclusions can be drawn for dealing with artificial ponds in the temperate zone of the Central European Highlands?

Methods

General description of the study area

The study was conducted in two large woodland areas, Hürtgenwald and Kermeter, in the north of the Eifel region in Western Germany and in the catchment area of the River Rur, a tributary of the Maas. These closely adjacent woodland areas belonging to the same macrochore and represent a typical cross-section of the Rhenish Slate Mountains, a highland area characteristic of large parts of Central and West Europe from Northern France, via Belgium and the south of the Netherlands, into Germany. Typical of this countryside are extensive plateaus scored with 100 – 200 m deeply notched and steep valleys with narrow meadows alongside the streams. In the study area the plateaux, the slopes of the valleys, and the 30 – 60 m wide meadows are mostly wooded and therefore in a comparatively near-natural state.

Because of the distinctive topography, natural as well as artificial water bodies are mainly restricted to the valleys, and are mostly small and widely separated (Dalbeck et al., 2007), whereby the valleys with near-natural meadow water bodies and ponds are approximately 2 km apart (Fig. 1). The standing water bodies naturally suited for amphibians are mainly small springs, tree roof plates or small oxbow lakes along the course of the stream. Artificial water bodies in addition to the weir ponds include a few large reservoirs, water-filled ruts on forest tracks and isolated bomb craters from WW II which, in the meadows along the streams, are in part filled with water.Apart from the reservoirs (with occurrences of *Rana lessonae*/“*esculenta*“ and *Bufo bufo*), the man-made weir ponds and the Beaver ponds, the amphibian populations of the natural and man-made water bodies are small, not least because of the former’s small size. (Dalbeck et al., 2007).

The study area climate is temperatesub-Atlantic with mild winters and cool summers and average temperatures of some 7°C to 8.5°C (MURL, 1989). The altitude a.s.l. is between 220 m to 550 m. Our study included a total of 21 artificial and 22 Beaver ponds (Fig. 1, Tab. 1). The Beaver ponds are located in four valleys, each of which is settled by one to two Beaver colonies. In these valleys the Beavers, part of a reintroduction project, built between four and 22 ponds respectively in the course of the past two to a maximum of 20 years, These were created by the building of dams some 4 m to 45 m in length and up to 2.5 m in height.

The 21 artificial ponds are distributed between a total of ten valleys, with one to five ponds per valley, and created by the damming of small streams. They were built in the first instance as fire-fighting or fish ponds but are, with one exception, no longer in use. The man-made ponds, ranging from at least 50 to 100 years in age, are distinctly older than the Beaver ponds.
At the moment the resettled Beaver populations in the study area are in a phase of exponential growth (Schadewinkel, 2006), whereby the Beaver is increasingly penetrating into the wooded valleys of the Eifel region. Here they frequently settle in the man-made weir ponds to begin with. In order to clearly differentiate between and compare the two groups, we took care to select for the study only artificial ponds that were not yet settled by Beavers,, because the Beaver, through tree felling and transportation of coarse woody debris in the water, markedly alter the character of the artificial ponds. In addition, the selected artificial ponds were located in forested valleys comparable to those where the Beaver had settled in terms of relief, geology, vegetation, the type and flow of the streams, and with a generally similar amphibian population in the surrounding environment. This is known from previous comprehensive amphibian monitoring projects. As woodland cover can be of great importance for the species richness of amphibian communities (Hecnar & M’Closkey, 1998; Cushman, 2006; Denoël et al, 2007), all water bodies studied were either in extensive coherent woodland, or lie at least within a radius of <150 m from large wooded areas in wooded corridors at least 40 m wide connected directly to woodland. The non-wooded areas in the surrounding countryside were characterised by little-used pasture, which ensures that the influence of land use on vegetation and water body structure is minimal (Declerck et al., 2007). All water bodies studied, including those in the surrounding land habitats, were therefore subject to similar conditions, in particular for the Uroleda species which are considered to be less mobile (Smith & Green, 2005). This applies particularly to the newt species studied (Denoël & Ficetola, 2007b).

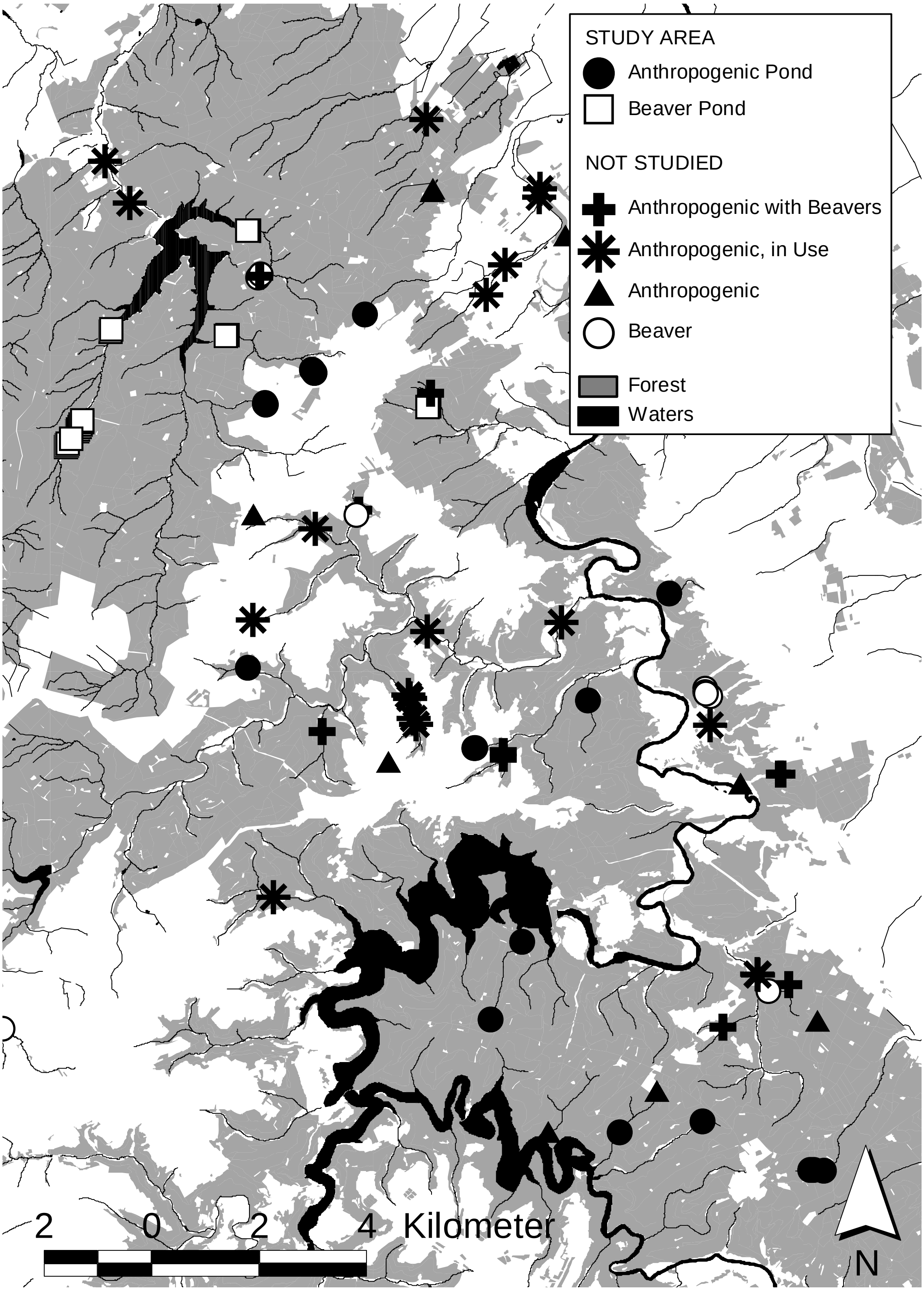

Fig. 1 Study area in the North of the Eifel region, Germany

Tab. 1. In-pond characteristics of 21 artificial and 22 Beaver ponds in a Central European Highland

TYPE [a)]	SIZE [b)] m² (SD)	DEP [c)] m (range)	SILT [d)] % (SD)	CWD [e)] (range)	Ma [f)] (SD)	Lh [g)] (SD)	Fish *n* spp. [h)] (SD)
Artificial	378	1.5 – 2.0	7.9	1	1.06	1.86	0.24
(*n* = 21)	397	> 0 – 3.0	11.5	0 – 3	1.45	1.82	0.54
Beaver	642	1.0 – 1,5	66.6	3	0.87	2.40	0.82
(*n* = 22)	521	> 0 – 3.0	29.1	2 – 5	1.52	2.31	0.96

[a)] Type of water body: Beaver pond/artificial pond; [b)] Size of water body; [c)] Water depth (median); [d)] Silted-up areas; [e)] Coarse woody debris: 1: none or very little, 2: moderate, 3: large to very large amounts in water (median); [f)] *Triturus alpestris*, CPUE values (Absolute: Beaver: 3118; artificial: 2088); [g)] *Triturus helveticus* CPUE values (absolute: Beaver: 7899; artificial:3729); [h)] No. of fish species

Recording of data

We recorded the occurrence of newts between 12 March and 14 May 2007, i.e. during their main phase of activity and examined Beaver and weir ponds synchronologically in order to avoid a bias arising from different examination times. Trapping was done using some 101 funnel traps (Ortmann et al., 2006 for details). Depending on the size of the pond we set five to 26 traps for a period of four days. We checked the traps every 48 hours, classified the trapped newts and all other amphibians (including larvae) and any fish caught, marked the newts by toe-clipping, and subsequently released them back into the centre of the ponds. With the exception of two Water Shrews Neomys fodiens found dead in a trap, we recorded no other trap mortalities. In cases where no newts, or very few were caught, the trapping effort was extended for up to 12 days.

In order to gain a first impression of the absolute magnitude of newt occurrence in the individual water bodies, we used a mark-recapture method and used the Lincoln-Peterson Index (Henle, 2000) to calculate the numbers of the two common newt species, Alpine and Palmate Newts. Because of the very different capture or recapture numbers (e. g. T. helveticus catch: 0 – 1302; recapture 0 – 248 (0 – 65 %); *T. alpestris*: catch: 0 – 1151; recapture: 0 – 244 (0 – 59 %), the standard error of the Lincoln Index, especially for the water bodies with only few newts, was very high and was therefore not suitable for use in the GLM. For the GLM models we therefore used the Catch per Unit of Effort (CPUE) value as a measure of the newt population density in the ponds as the number of newts per trap in a 24 hour period.

In order to record the complete amphibian, and where possible the complete fish species spectrum, we also carried out a daily sweep with hand nets and a nightly search with flashlights at each pond. Altogether the water bodies were therefore inspected on at least 4 separate days. We considered a species to be present when we could prove the presence of one of the possible life stages (adult, larvae, eggs) or when breeding calls were heard. We did not differentiate between the species of the Rana lessonae /"esculenta"/ridibunda complexes. Nonetheless we did not hear any of the characteristic calls of the Marsh Frog (Rana ridibunda).We therefore consider that a population of Rana lesonae/"esculenta" exists. Water bodies in which neither observed nor captured fish or were considered to be fish free.

We have no information on to what extent the occurrence of the species proven as present were stable vital stock (sources) or not (sinks). Nonetheless the absolute numbers of capture newts indicate that both strong source as also sink stocks occur in the water bodies studied (Fig. 2). We could also not definitely rule out that, despite the intensive survey conducted, individual species were not registered. Nevertheless, the settlement densities of such species are certainly very low and one can assume that the habitat conditions are not optimal in such cases. These occurrences should therefore be considered as sink or transient habitat (Denoël & Ficetola 2007; 2007b). During one of the last daily sweeps we recorded the habitat parameters used in the models.

Habitat characterisation

We recorded 11 habitat factors for use in the model. As multivariate analyses react sensitively to collinearity, it was necessary to reduce the number of factors. Therefore, we used the following six factors in the models: area (SIZE, m²), water depth, (DEP, categories), Coarse Woody Debris (CWD, categories), proportion of silted-up area (SILT, %), type of pond (TYPE, Beaver: Yes/No) and the presence or absence of fish (FISH).

We recorded the size of the water bodies with the assistance of orthophotos and property maps (1:5,000) on which, in the field, we marked in prominent landmarks such as large trees, Beaver dams and tracks. Where necessary we also used a tape measure to measure distances on the ground. Size was then calculated with the help of GIS (ArcView). Area was included because both artificial as well as Beaver ponds varied remarkably in size (Beaver: average 642 m², range 52 m²–2000 m², artificial: 378 m²/ 21 m²–1750 m²; Tab. 1). Moreover, pond area can, but need not, play a major role for the settlement and density of amphibians (Oertli et al., 2002; Tockner et al. 2006). In addition, water depth is known to be an important factor(Hecnar & M'Closkey 1998), especially for the newt species in focus (Denoël & Ficetola, 2007), and CWD seems to play a pivotal role for amphibians by providing food and shelter for larvae as well as adults (Tockner et al., 2006). CWD is a typical feature of Beaver ponds (and Beaver inhabited weirponds) as Beavers actively import large amounts of wood, twigs and wood chips to the ponds (Rolauffs et. al. 2001). As CWD consisted of very different materials, and was often arranged in three dimensions (e.g. whole tree crowns in the water, wood chips in layers of differing thickness, 10 m long Beaver dams as part of the banks), we did not consider it sensible to quantify the CWD factor and regarede this variable as a category.Beaver ponds differ markedly in other factors, for which it is known that they can play an fundamental role in the suitability of water bodies for amphibians (Hecknar & M'Closkey 1998; Denoël & Ficetola 2007b), e.g. vegetation structure (more silted-up areas and floating vegetation are found in Beaver ponds because of a larger proportion of shallow, but permanently flooded areas, and a higher degree of isolation) pond perimeter (perimeters of Beaver ponds are markedly longer because of small islands and bays in the shallow reaches), or the shoreline gradient (Beaver pond banks are generally less steep).

These factors differ between the individual water bodies in a complex manner and are therefore difficult to quantify. We therefore preferred to apply the factor 'proportion of silted-up area', which was based on the shallow bur mainly permanent dammed-up areas of the ponds, which usually occurs as a result of silting-up. The factor 'silted-up area' correlates with the factors 'submerged vegetation' ($r = 0.57$) and 'length of the shoreline'($r = 0.69$). Therefore the 'silted-up area' is a measure of the amount of microhabitat available, including emergent vegetation, and shoreline.

Fish, as predators, have a considerable significance for amphibians in general and the newts in the study in particular (Hehmann & Zucchi, 1985; Breuer, 1992; Wegner & McPeek, 1994; Aronsson & Stenson, 1995; Hecnar & M'Closkey, 1997; 1998; Denoël & Ficetola, 2007), whereby larger predatory species are able to forage on adults and larvae and small species on eggs and larvae (Denoël & Ficetola, 2007). The shoreline area of all Beaver ponds studied were either partly or completely open and sunny up to a distance of some 20 m due to tree felling; the shorelines of all man-made water bodies were in contrast wooded. This factor correlates therefore completely with the factor 'Beaver Pond Yes/No' and was therefore not taken into account. The factor 'Beaver Pond Yes/No' was applied to all models.

The factors 'canopy cover' and 'altitude a.s.l.' were not included in the GLM analyses. Although, because the most similar ponds were selected, the vegetation in the surrounding >20 m did not markedly differ, the altitude a.s.l. and amount of sunlight are assumed to play only a subordinate role in terms of population by the dominant newt species. Beaver ponds are more sunlit because of tree felling by the Beavers. The two dominant newt species, Alpine Newt (*T. alpestris*) and Palmate Newt (*T. helveticus*), are greatly attached to woodland which is their principal terrestrial habitat, but are less selective in respect of the canopy cover of the reproduction ponds in Belgium (Denoël & Ficetola, 2007b). This fact was also established as a result of studies in the region (Dalbeck et al., 1997; Zehlius et al., 2001).

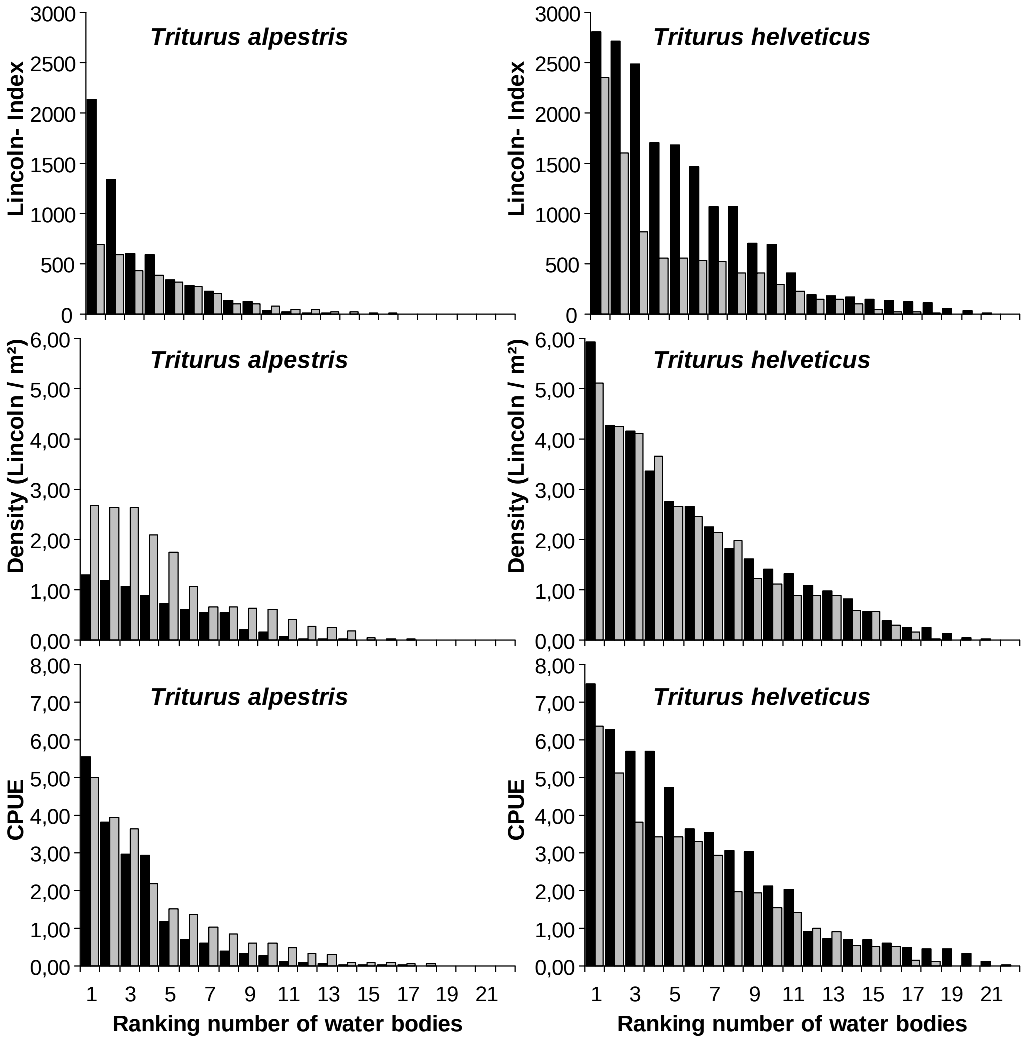

Fig. 2 Absolute number (calculated using the Lincoln–Peterson Index), densities (absolute number/ pond area m2) and activity densities (CPUE: individuals per trap and 48 h) of Alpine and Palmate Newts in Beaver ponds (n = 22, black) compared to artificial ponds (n = 21, grey). Ponds are arranged according to densities/numbers of newts. Average numbers [median] were *T. alpestris* artificial pond: 159.3 [45.6]; Beaver pond: 267.0 [15.8]; *T. helveticus*: artificial pond: 418.2 [221.9] and Beaver pond: 815.9 [298.8]

Data analysis

We used General Linear Models (GLM) in order to test which of the six independent parameters best explain settlement by the two most common newts, Alpine and Palmate Newt. The dependent variables, the CPUE values for Alpine and Palmate Newt, were log-transformed in order to achieve a normal distribution (Kolgomorow-Smirnow of the residue Log10-CPUE: *T. alpestris* K = 0.776; p = 0.584; n = 43; *T. helveticus*: K = 0.892; p = 0.404; n = 43). As no newts were caught in some of the ponds and the logarithm for zero values is not defined we used, instead of a zero value, half of the smallest recorded value > 0 for the respective independent variable (Berry, 1987).

We regarded the individual ponds as sufficiently independent units for the study, as both the species composition and the population density of the amphibian species studied were often extremely different in immediately adjacent ponds even when arranged in a cascade fashion. Because of the structure of the countryside it can be generally assumed that the amphibian occurrences studied belonged to coherent populations in Hürtgenwald and in Kermeter respectively (in the sense of a patchy population – see Smith & Green, 2005).

We employed Akaike's Information Criterion (AICc) for small random sampling and Akaike's differences (Δi) and Akaike weights (ωi), in order to find the most likely (most parsomonious) set of independent variables that best explained the population density of Alpine and Palmate Newts (Mazerolle, 2006).

Δi values between 0 and 2 served as orientation for the selection of the best model. As models with Δi values > 10 are very unlikely (Mazerolle 2006), only the first three models are presented.
We used the Man-Whitney U-Test in order to check whether the number of recorded amphibian species differed between Beaver and artificial ponds. We used the SPSS 10.0 Windows programme for all calculations.

Results

Composition of the amphibian species communities

In terms of recorded amphibian species, the artificial and Beaver ponds did not greatly differ from one another. Altogether, in both types of pond, we recorded the same four Anura and four Urodela species. Nonetheless, the mean number of species in Beaver ponds (3 to 7 species; mean 4.82 ±1.18; n = 22) were significantly higher (U = 347.5; p = 0.004; n = 43; DF = 1) than in the artificial ponds under study (0 to 6 species; Mean: 3.57 ±1.33; n = 21). Whereas four species were markedly more regularly found in the Beaver ponds, only one species was more common in artificial ponds. Three species appeared with an equally great degree of probability in both Beaver and artificial ponds (Tab. 2). Although man-made and Beaver ponds are markedly different in size (Tab. 1), the number of amphibian species was independent of the size of the respective water body type (Spearman: Beaver r= –0.12, p= 0.586, n= 22; artificial r= –0.40, p= 0.862, n= 21).

Population density of the recorded species

Whereas the Smooth Newt was too uncommon to enable a comparison of population densities (absolute figures: Beaver ponds - 23 from 8,946 *Triturus* individuals [0.26 %]; man-made ponds - 3 from 4,303 individuals [0.07 %], the Alpine and Palmate Newts were by far the most common Urodela species in the study area (Tab. 2).

If one considers the absolute size of Alpine Newt occurrence calculated using the Lincoln-Petersen Index, this is on average larger for the Beaver ponds. Nevertheless the mean for the Beaver ponds is smaller than that of the man-made ponds (Fig. 2). In relation to the water surface (Lincoln-Index / m²) the occurrence in the Beaver ponds is markedly lower than that of the artificial weir ponds. The activity density (CPUE) of the Alpine Newt in Beaver ponds is also lower compared with that of the man-made ponds, although the difference is markedly lower than the Lincoln density values (Fig. 2). In contrast, the occurrence of the Palmate Newt in Beaver ponds, calculated using the Lincoln-Petersen Index, is markedly higher than in the man-made ponds. The CPUE activity density is higher in the Beaver ponds, although it is somewhat similar if one considers the density values (Fig. 2). The generally higher absolute values for Beaver ponds derive from their considerably greater water surface area (Tab. 1).

Tab. 2 Relative proportions (number of occupied / total number of ponds) of the recorded amphibian species and fish in the 22 Beaver ponds and 21 artificial ponds studied and the proportion of water bodies where the presence of fish of several trophic guilds was recorded

Pond type / trophic guild	Beaver	Artificial
Triturus alpestris	81.8	85.7
Triturus helveticus	100.0	85.7
Triturus vulgaris	22.7	9.5
Fish [a)]	50.0	19.1
Ominvorous [b)]	31.8	14.3
Insectivorous [c)]	18.2	9.5
Insectiv./piscivorous [d)]	27.3	4.8

[1)] Preference for sunlit waters (Dalbeck et al. 1997) ++ very high; +: high; 0: none; –: prefers shaded water; [a))] Presence/absence of fish, including [b)] *Ctenypharyngodon idella*, *Rutilus rutilus*, *Scardinius erythrophthalmus*, *Tinca tinca* [c)] *Cottus rhenanus*, *Gasterosteus aculeatus*, *Gobio gobio*; [d)] *Perca fluviatilis*, *Samlo trutta*

Habitat preferences of Alpine and Palmate Newt

The best respective GLM models selected by means of AICc for Alpine and Palmate Newt have ωi values, which are so large that all other models are considered as less probable. The 'best' models for both Alpine Newt and Palmate Newt (Tab. 3) contain the same factors namely TYPE (pond type: Beaver/artificial) and FISH (Fish present/absent), and explain 47 % of the variance of the CPUE values for the Alpine Newt ($P < 0.001$) and 30 % for the Palmate Newt ($P < 0.001$).

As far as the Alpine Newt is concerned, in all models where the FISH factor only is present, this is significant with $P < 0.001$, so that ultimately all such models represent one model (Tab. 5). In all Palmate Newt models containing FISH, this factor is also significant ($P \leq 0.001$), whereby in some models TYPE, especially those selected by AICc, is significant as a second factor (Tab. 6).

The population density of the Alpine Newt can therefore be explained with the help of one of the tested factors, namely FISH. The population densities of the Palmate Newt are, compared to the Alpine Newt, markedly less dependent on the number of fish species. The pond type plays an additional role here (Fig. 3). None of the other factors tested helps to explain the variation.

Fish

We recorded altogether nine fish species (Tab. 2), five in the man-made ponds (Perca fluviatilis, Gasterosteus aculeatus, Gobio gobio, Rutilus rutilus, Ctenypharyngodon idella - on average 0.24 species per pond) and five in the Beaver ponds (*Salmo trutta, Cottus gobio, Rutilus rutilus, Scardinius erythrophthalmus, Tinca tinca*; 0.82 species per pond). Tab.These fish were evidently present either before the streams were dammed (*Salmo trutta, Cottus rhenanus*), came from standing water bodies in the vicinity - above or below the Beaver ponds (*Rutilus rutilus, Scardinius erythrophthalmus, Tinca tinca*), or were clearly introduced by man (other species), particularly in the artificial ponds.

Tab. 3 Candidate models for Alpine Newt and Palmate Newt population activity densities (catch per unit of effort) in Beaver and artificial ponds in the North Eifel region of Germany, weighted in accordance with the Akaike Information Criterion for small random samples (AICc).

Rank	Candidate Models	Alpine Newt	*K*	AICc	Δ_i	ω_i
1	TYPE, FISH		3	-21.8	0.00	0.99
2	TYPE, FISH, TYPE*FISH [a)]		4	-13.1	8.60	0.01
3	TYPE, DEP		3	-7.01	14.76	0.00
Rank	Candidate Models	Palmate Newt	*K*	AICc	Δ_i	ω_i
1	TYPE, FISH		3	-27.0	0.00	0.98
2	TYPE, FISH, TYPE*FISH a)		4	-18,7	8.29	0.02
3	TYPE, DEP		3	-13,1	13,80	0.00

K: No. of factors in model. Δ_i is the difference between the highest ranked model and the candidate model, Akaike weights (ω_i) sum to 1. For definitions of the factors see Tab. 1

[a)] Interaction term Type of water body*presence of fish

Discussion

Beaver ponds as habitat for amphibians

The significance of Beaver ponds for amphibians has been the theme of various studies in North America and, to a lesser extent, in Europe (Rosell et al., 2005). Studies show that the effects appear to be markedly dependent on the respective countryside and amphibian guilds, and are not easily transferable to the landscape of other climatic zones let alone continents. Amphibians generally occur more or less frequently in Beaver ponds in North America, Europe and also in Eastern Asia (Safonov & Safeljev, 1992). The effects of Beaver activities on the number of amphibian species appear however to have a regional character. Whereas Metts et al. (2001) in the South-eastern USA found little diversity in Beaver habitats in comparison to rivers not influenced by Beavers, the opposite was true of one of the valleys in the study area, where Beaver ponds were compared to natural and semi-natural waters (Dalbeck et al., 2007). In the meantime it has become increasingly clear that factors such as the age of the Beaver pond play a major role (Stevens et al., 2006) and that different species react differently; such as frogs (Ranidae) in Maine, USA (Cunningham et al., 2007) or in this present study the very similar – in their choice of habitat – Urodela species Alpine and Palmate Newt.

In any event it is clear that Beaver ponds in the whole of the Holarctic ecozone play a role and, in respect of the history and ecology of amphibians and amphibian guilds, must not be ignored.

Amphibian species richness of artificial and Beaver ponds

At a regional level Beaver and man-made ponds are similar in terms of the amphibian species make up, which highlights the importance of unused man-made weir ponds for woodland-dwelling amphibians in Central Europe. This similarity is essentially due to the very similar location of the water bodies studied in the wooded notched valleys of the European low mountain ranges, in which, before the arrival of the Beaver, in addition to the large reservoirs and numerous streams, were dominated by shady water bodies without a high degree of dynamics. This explains the dominance of species with a broad habitat amplitude and species tied to woodland, and the absence to date of species dependent on spawning waters with a higher degree of dynamics. However, Beaver ponds have on average a remarkably higher number of amphibian species, and are therefore the water bodies richest in species in the small, wooded and near-natural valleys of the study area. Numbers not only greatly exceed those of artificially dammed ponds (Tab. 2), but also those of the natural meadow waterways where Dalbeck et al. (2007), in one of the Beaver valleys studied in this paper, recorded 4.1 species in Beaver ponds, but only 1.2 in stream meadows not settled by Beavers.

The artificial ponds studied were smaller than the Beaver ponds (Tab. 1), and therefore the pond area can play an essential role in terms of amphibian species richness, which has been proved for invertebrate communities of farm ponds in France (Céréghino et al, 2008). We did not establish such a relationship for either the weir or the Beaver ponds. This agrees with the results of studies in other wetland habitats where, for example in the highly dynamic natural riverine habitat of the River Tagliamento in NE Italy (Tockner et al, 2006) or water bodies in Switzerland (Oertli et al, 2002), no relationship was found either between water body size and number of amphibian species. It therefore appears that the reasons for the difference in species variety are to be found in other factors, where Beaver and man-made ponds differ in general respects. The amount of sunlight on the water or the surrounding environment evidently plays a significant role (Tab. 2), as the weir ponds are shaded by a dense canopy. Nonetheless, other biotic factors, related to canopy cover (Skelly et al., 2002), can restrict the settlement possibilities of a significant number of amphibian species.

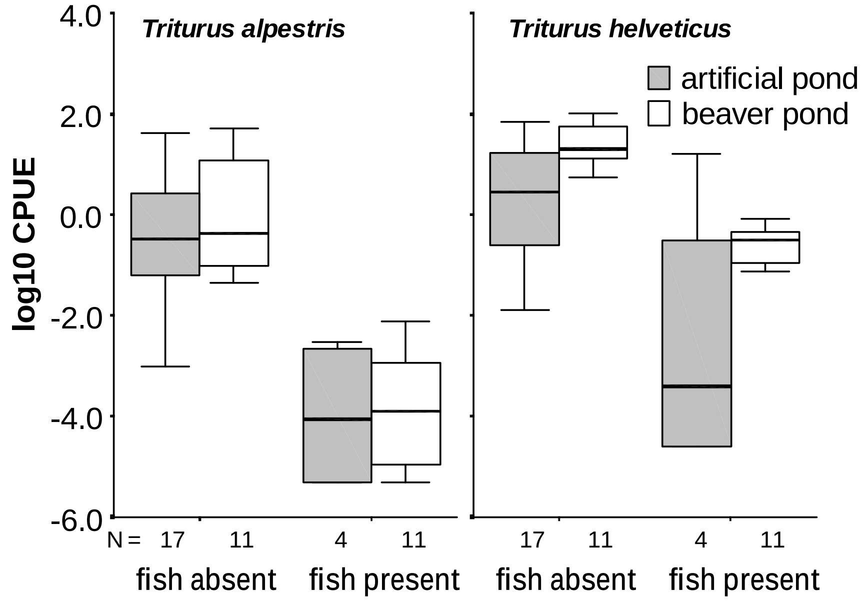

Fig. 3 Box plot of activity densities (as Log CPUE values) of Alpine and Palmate Newts in relation to type of pond and presence of fish

The results of the study provide first indications that the differences in the species diversity between artificial and Beaver ponds derives in no small degree from the requirements of the species in the region in regard to the amount of sunlight on the water or the surrounding environment. Species which are more strongly dependent on sunlit water, especially the Smooth Newt, Pool Frog (R*ana lessonae*/"*esculenta*") – but also the Common Toad (*B. bufo*) and the Midwife Toad (*Alytes obstetricans*) which require sunny land habitat near water – frequently settle the Beaver ponds, which receive more sunlight because of the Beaver's large scale tree-felling activities around the ponds. Only the Fire Salamander (*Salamandra salamandra*) which prefers shaded waters, was much more commonly recorded in the man-made ponds (Tab. 2).

The higher number of species in the Beaver ponds is also above all remarkable, as Beaver ponds are populated on average to a greater extent by fish (Tab. 1), although fish from very different families (e.g. Salmonidae, Cyprinidae, Percidae, Tab. 2) are known to be very efficient predators of Central European amphibians (except for *B. bufo*, Jakobus, 1986; Breuer, 1992; Bronmark & Edelham, 1994, Denoël & Ficetola, 2007). The shallow, structure-rich Beaver ponds are evidently better suited to amphibians than unused artificial ponds and are more likely to permit coexistence of amphibians and fish. Artificial ponds with extensive shallow water zones have proved to be better for population by more amphibian species as those without such zones (Breuer, 1992).

On the basis of the present results, it is already clear that the artificial ponds are capable of substituting for the Beaver ponds as spawning waters, at least in a residual function. If one considers that of the 15 amphibian species occurring in the study area as a whole, only four occur in lowlands well under the altitude of the study area (*Bufo viridis*; *R. dalmatina*; *Pelobates fuscus*, each very noticeably < 200 m a.s.l.), a maximum of only four species are potentially missing from the Beaver ponds studied (*Bufo,calamita; Hyla arborea; Bombina variegata; Triturus cristatus*).

All in all the Beaver ponds are of markedly higher quality for amphibians than the artificial weir ponds in the woodlands of the Rhenish Slate Mountains and the species richness of the Beaver ponds (eight species) compares well with the more or less dynamic and near-natural riverine habitats of larger rivers in Central Europe such as the Tagliamento, Danube or the Rhone (seven to 10 species, Tockner et al., 2006).

The relatively high numbers of species in the Beaver ponds does not necessarily mean that Beaver ponds are generally better than man-made ponds, especially against the background that the typical amphibian species of man-made water bodies in the modern countryside were absent in the Beaver ponds studied.

Pond age

With the exception of the weir ponds, which are absent in the ‘Beaver valleys’, the woodland and valleys of the study area are generally poor in water bodies suitable for pond breeding amphibians. Source populations available for settlement in ponds of the younger Beaver colonies are therefore relatively distant from one another, although an isolation of the most widely distributed species must not be assumed. The distance bewteen suitable water bodies are often < 2km (Fig. 1) and therefore quite within the expected possible spread parameters for both Anrurans and Urodelans (Smith & Green, 2005).

For this reason we consider that the development of autonomous populations in the new Beaver colonies will take several years for the common (woodland) species and a markedly longer time-frame for rarer species (e.g. species of sunnier water bodies) to settle the Beaver colonies.

This does not provide evidence as to whether younger ponds have a generally lower species richness as found by Stevens et al. 2006 in Canada, as the age of a colony within which a newly-formed pond is situated is possibly an necessary factor for the number of species and development of the species' communities of the pond. One must therefore make a clear distinction between the age of a colony and the age of the individual pond.

The amphibian species of water bodies with moderate physical disturbances, such as *Bombina variegata* and *Bufo calamita*, are absent in the (younger?) Beaver ponds. This is possibly only because older weir ponds and other man-made or typical natural woodland water bodies of this type do not offer suitable conditions and therefore do not occur in the study area.

Newts in Beaver versus Man-made Ponds

In contrast to the Alpine and Palmate Newt, which are typical woodland species, the Smooth Newt is clearly tied to the open countryside (Denoël & Ficetola 2007; 2007b). This species also dominates in the open countryside of the study area (own data) but is mostly absent in the water bodies studied As water bodies tied to woodland were selected for the szudy, the scarcity of this species appears to be connected to the structure of the land habitat.It is nevertheless remarkable that this species occurred more regularly in the Beaver than in the man-made ponds (Tab. 2). The Beaver ponds are possibly somewhat more suitable due to the open and sunny areas that border direct on the shoreline. To what extent the species is unable to establish itself due to competition with the other two small newt species (Buskirk, 2007) remains open.

The results of the mark-recapture analyses of the Alpine and Palmate Newt, which commonly co-occur in the Rhenish Slate Mountains, show that both water body types offer suitable conditions for settlement. Allerdings ergibt sich ein A differentiated picture however results, in that the Palmate Newt has achieved markedly higher population size and densities, which are equally large or indeed larger in the Beaver ponds. This is not the case with the Alpine Newt (Fig. 2). The GLM- Analyses for these two species, which are indifferent to the sunlight factor (Tab. 2; Denoël & Ficetola, 2007) show that on the other hand fish, as well as the factor type of pond are of critical importance for the Palmate Newt (Fig. 3). Differences in behaviour between the species, especially that of the larvae, obviously play a significant role here, as the larvae of the Palmate Newt react to the presence of predators with an avoidance strategy (Buskirk & Schmidt, 2000). In the presence of predators, Palmate Newt larvae become markedly cryptic in their behaviour and conceal themselves in the substratum, whereas Alpine Newt larvae do not alter their behaviour and remain on the water surface where they are vulnerable to predators. Because of their great structural diversity, Beaver ponds appear to offer the Palmate Newt or its larvae better opportunities for concealment.

Nevertheless, the mean absolute quantities of both newt species in Beaver ponds are markedly higher than in artificial ponds (Fig. 2), which can be attributed to the generally greater size of the Beaver ponds. These are on average some 70 % greater in area than artificial ponds (Tab. 1). Independent of the population density in the ponds, the absolute size of the occurrence could be of great importance, above all in respect of the genetic make up of the populations, their expansion potential, and also the population densities of the amphibians in the surrounding land habitats. This can have an effect on other species, for example amphibian predators.

If one compares the Alpine and Palmate Newt population size with references in the relevant literature, it is demonstrated that the populations of both types of water bodies wer above average in size. Feldmann & Belz (1981) found in 68 % of almost 800 water bodies of the Westphalian mountain region, which is part of the Rhenish Slate Mountains, less than 20 Alpine Newts and only 8 % of the water bodies had >100 individuals. In comparison we calculated <20 individuals in 55 % and >100 individuals in 41 % of the Beaver ponds. The man-made ponds also lie clearly above the values for the Westphalian mountains (38 % <20 and 43 % >100 individuals, n=21), even when the mean values of the latter are smaller (Fig. 2). The densities of the Palmate Newt in the Beaver ponds are very high compared with the average of 901 ponds in the German low mountain regions (Schlüpman et al., 1996), where 80 % of the population <20 and only 3 % >100 individuals were recorded (Beaver ponds 9 % <20 and 82 % >100 individuals). The values for the man-made ponds also lie markedly well above the average (24 % <20 and 62 % >100 individuals, n=21, Fig. 2). The Beaver ponds in the Central and West European woodland therefore evidently possess an extraordinarily high potential for woodland-dwelling newts and other amphibian species, but the man-made ponds also appear to be of great importance for both newt species in question.

In Europe, Beaver ponds are natural habitats and the Beaver has existed in the Rhenish Slate Mountains for at least 600,000 years during the ice-free periods (Bosinski, 2006). Correspondingly, the symbioses in the water bodies can be considered as adapted to the activities of the Beaver. Because of their semi-permeability, Beaver ponds do not permanently influence the passage of running water in the sense of the WFD. In Europe’s modern countryside the dam-building Beaver in particular deserves sufficient room to exist Conflicts between the Beaver and the aims of nature protection or conservation can only then occur when far from natural conditions caused by human activity dominate (e.g. in canalised streams or riverine woodland on straightened stretches of rivers where, apart from isolated trees, the habitat is destroyed).

Conclusions

Extensively used or unused weir ponds and Beaver ponds differ markedly in respect of their settlement by amphibians in general, and the order of Urodela in particular. Nevertheless, at least 2/3 of the amphibian species of the Beaver ponds were represented in the artificial ponds. As the majority of the species occurring are dependent on standing water, and are either absent or only occur in small populations in the majority of the small natural standing and flowing waters of the highlands (Dalbeck et al., 1997), artificial ponds which are either unused or extensively managed play a key role in the survival of the characteristic amphibian species assemblages in this type of countryside. They belong to the category of standing water in which human activity has promoted amphibian diversity (Krone, 2003; Denoël & Ficetola, 2007). The existence of these artificial water bodies, which have characterised the highlands for hundreds of years, has therefore probably bridged the gap for the amphibians following the loss of the Beaver ponds as a result of the eradication of the Beaver population. The existence of these artificial ponds have probably contributed in a significant degree to the survival of the characteristic species communities, in vital and little fragmented populations, until the present day. This leads to the following conclusions:

(1) The promotion by the EU of the destruction or renaturation of man-made weir ponds in areas of the Central European Highlands close to the water sources, in the context of WFD implementation must be critically reviewed, at least in terms of amphibian conservation.. Such measures are frequently applied to unused waters in particular, as ponds used for fish farming are normally not accessible. It is our view that amphibian conservation must be given urgent consideration in this respect. In general, small artificial water bodies, in particular those that are unused or little used, are extremely important for aquatic biodiversity and should be protected from interference (Céréghino et al., 2008). This is clearly also valid for artificial weir ponds in Central European woodland.. Until today, Beaver ponds played only a selective role in the Central European low mountain ranges, and several decades will pass before the Beaver is again widespread. The renaturation of man-made ponds, with their remarkable above average importance for some amphibian species, should be delayed at least until the former are replaced by Beaver ponds, thus avoiding damage to the woodland amphibian communities.

(2) It is clear that the Beaver pond can be of considerable significance for amphibian conservation. Mid and long term planning, and implementation of measures to promote the Beaver in the Central European Highlands, are therefore of great importance. Against the background of the mostly minor economic value of such valleys for forestry and agricultural management, exellent opportunities exist for nature and species protection on a European level. A special EU programme to preserve (e.g. by priority purchase) and prepare the areas in the valleys of the Central European Highlands for Beaver settlement makes particular sense. The Beaver, as a key species, should be granted special significance in the preparation of EU programmes for preservation of biodiversity in Europe.

(3) The results presented in this paper are intended as a contribution to the understanding of the importance of the Beaver for amphibian communities. There is a requirement for further research in terms of a causal analysis of the significance of the Beaver for other species and in other regions of Europe.

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