Amphibia-Reptilia 35 (2014): 321-329

Beavers (*Castor fiber*) increase habitat availability, heterogeneity and connectivity for common frogs (*Rana temporaria*)

Lutz Dalbeck[1,*], Joyce Janssen[1,2], Sophie Luise Völsgen[3]

Abstract. Beavers (*Castor fiber*), as typical ecosystem engineers, alter living conditions especially for amphibians through the building of dams and felling of trees, thereby changing the hydroperiod and substantially affecting forest succession stages. In this study we quantify the effects of beavers on the availability of amphibian breeding waters in the Hürtgenwald, a woodland area in the Central European Rhenish Massif, its colonisation by common frogs (*Rana temporaria*) and the effects of age and succession stage of beaver ponds on ovipositional site selection. In 2013, beaver ponds comprised about half (49%) of all lentic water bodies but contained 82.5% of all common frog egg masses. Mature beaver ponds (>6 years old) harboured approximately half of the egg masses ($n = 775$), but new beaver ponds (1-3 years old) can also be home to large breeding aggregations. Abandoned beaver ponds are of minor importance as ovipositional sites for common frogs. High egg mass counts were also found in artificially-dammed ponds ($n = 216$). We believe that common frogs prefer occupied beaver ponds as ovipositional sites because of high insolation and a permanent hydroperiod, which lead to rapid tadpole emergence. Beaver ponds are generally located in close proximity to each other, facilitating movement and rapid colonisation by common frogs. Our research provides additional evidence to show that beavers enhance habitat availability, heterogeneity and connectivity, thereby fostering amphibian populations at a landscape level. As natural elements of small streams, beaver ponds must be taken into account in the context of the EU Water Framework Directive.

Keywords: ecosystem engineer, egg masses, EU Water Framework Directive, lentic water bodies, Rhenish Massif.

Introduction

Ecosystem engineers are organisms that alter, maintain or create their habitat while regulating the availability of biotic and abiotic resources for themselves and other species (Jones, Lawton and Shachak, 1994; Rosell et al., 2005). By creating dams and ponds, beavers (*Castor fiber* and *C. canadensis*) change not only the geomorphology, but also hydrology of water bodies, and create entire new landscapes. In addition, beavers have substantial direct effects on forest succession stages in the floodplains of streams by the felling of trees (Naimann, Melillo and Hobbie, 1986; John and Klein, 2003; Rosell et al., 2005).

Castor fiber was originally common throughout Europe, but was almost entirely eradicated at the end of the 19th century. As a result of comprehensive conservation measures the beaver has been reintroduced in almost all European countries, and the population is increasing substantially (Zahner, Schmidtbauer and Schwab, 2005). Whereas beavers occur in larger rivers of lowland areas, they also massively invade the headwaters and small streams of upland areas, subsisting only by creating ponds (Naimann, Melillo and Hobbie, 1986).

Amphibians are good indicators of the landscape impact of beavers, as their occurrence depends on the availability of both water and suitable upland habitat (Denoël and Ficetola, 2008). Amphibians in general are globally under threat and even common species are decreasing at a worrying rate (Blaustein and Wake, 1990; Wake and Vredenburg, 2008).

In North America, amphibians profit markedly from beaver impounding activities. For instance, in Alberta three anuran species occurred solely in streams dammed by beavers

1 - Biological Institute of Nature Conservation Düren, Zerkaller Strasse 5, 52385 Nideggen, Germany
2 - Resource Ecology Group, Wageningen University, Droevendaalsesteeg 3a, 6708 PB Wageningen, The Netherlands
3 - University Bonn, Institute of Zoology, Meckenheimer Allee 169, 53115 Bonn, Germany
*Corresponding author; e-mail: L_Dalbeck@yahoo.com

 DOI:10.1163/15685381-00002956

(Stevens, Paszkowski and Foote, 2007). In New York and Maine various ranid frog species prefer beaver ponds to unimpounded streams or vernal pools (Cunningham, Calhoun and Glanz, 2007; Karraker and Gibbs, 2009; Popescu and Gibbs, 2009). An overall positive effect on abundance and diversity of amphibians cannot however be assumed, in particular in respect to the response of urodelans in North America to beaver impoundments (Russell et al., 1999; Metts, Lanham and Russell, 2001).

Studies from temperate Europe show a general increase of amphibian species richness – including urodelans – in beaver ponds compared to unimpounded streams (Balčiauskas, Balčiauskienė and Trakimas, 2001; Dalbeck, Lüscher and Ohlhoff, 2007; Dalbeck and Weinberg, 2009) and an increase of abundance of common frog (*Rana temporaria*) in particular (Elmeros, Madsen and Berthelsen, 2003; Dalbeck, Lüscher and Ohlhoff, 2007; Bashinskyi, 2012).

The aim of this study is to evaluate the impact of beaver activity on habitat availability and abundance of the common frog at a landscape level. The specific study objectives are:

(i) To quantify the extent of beaver impoundments in a Central European upland woodland.
(ii) To evaluate the use of beaver ponds as ovipositional sites by the common frog relative to other lentic water bodies.
(iii) To examine the possible effect of age and succession stage of beaver ponds on ovipositional site selection by the common frog.

Our study was conducted in 2013, but we have included our findings on egg mass abundance in the context of several other studies conducted between 2007 and 2012, using the same techniques and focused on the same area (Dalbeck, Lüscher and Ohlhoff, 2007). Based on our findings, we discuss implications for habitat and species protection and provide recommendations on beaver management and protection in the context of the European Natura 2000 protected areas network and implementation of the EU Water Framework Directive.

Materials and methods

Study area

The Hürtgenwald (coordinates: 50°43′N, 6°20′E) is characteristic of the Central European Rhenish Massif and is located at the northern edge of the Eifel region. The study area in the Hürtgenwald comprises some 24.28 km^2 of a large, contiguous forest. The Rhenish Massif covers a large area stretching from France, through Belgium (Ardennes) and Luxembourg, the southern part of The Netherlands and well into Germany. This upland is covered with a finely branched, dense network of streams, which are formed by relatively high rainfall and steep terrain. Characteristic for large parts of the Rhenish Massif is a peneplain with many steep and narrow valleys. In the Hürtgenwald, these valleys are narrow (some 10 to 120 m wide) with steep wooded slopes. The study area is drained by four stream systems that flow into a drinking water reservoir. The water bodies include numerous small springs and 1st to 3rd order streams, but relatively few permanent and predominantly man-made lentic water bodies (table 1). The climate in the Hürtgenwald is sub-Atlantic with mild winters and cool summers; average temperatures range between 7.5 and 8°C and annual precipitation between 850 and 1000 l/m^2 (MURL, 1989); elevations range from 240 to 450 m a.s.l.

Beavers (*Castor fiber*) were re-introduced in the 1980s (Naumann, 1991) and subsequently spread out in the area and well beyond. Because of the shallowness of streams, beavers can only subside in the study area by building dams and creating ponds. The width of such beaver ponds is determined by the width of the riparian floodplains and ranges from ∼5 m in the small 1st order streams to ∼45 m in the main valleys.

Table 1. Physical and biotic data on the presence of beaver ponds and water bodies not created by beavers in the 24.3 km^2 study area in 2013 (*Rt* = *Rana temporaria*).

	Beaver	Other
Lentic waters		
All lentic waters	149	157[1)]
Permanent waters (%)	149 (100%)	54 (34%)
Lentic waters/km^2	6.1	6.5
Average size/pond m^2	117.6	20.3
Biotic data		
$\sum Rt$ egg masses	1713	364[2)]
n (%) waters with *Rt*	54 (36%)	25 (16%)
Egg masses/water body	11.5	2.3
Egg masses/inhabited water	31.7	14.6
Egg masses/km^2	70.6	15.0

[1)] 121 (77.1%) of these water bodies were artificial.
[2)] 216 of these egg masses were found in 10 artificially-dammed ponds.

Recording the water bodies

Our survey recorded lentic water bodies only, including dammed ponds and floodplain waters, since flowing water is not used for oviposition by the common frog (Schlüpmann, Geiger and Weddeling, 2011). In 2013 all water bodies potentially suitable for amphibians, including all beaver ponds, were recorded by systematic inspections of the study area. Between 2008 and 2012, a subset of beaver ponds was recorded annually. The majority of water bodies not created by beavers are man-made and were either constructed as fish, fire or settling ponds or were shaped by heavy forestry machinery. Currently, none of the fish and settling ponds are used by humans. In addition, a number of WW II bomb craters have been identified. Most of the natural water bodies are situated in the floodplains of the four largest streams in the area.

Beaver ponds are markedly different from the aforementioned water bodies and had not previously been considered in the amphibian survey of North-Rhine Westphalia (NRW). The Hürtgenwald beaver ponds were divided into the following categories, based on their age and succession stage:

I: New pond: One to three years old, numerous trees still standing, high amounts of fresh dead wood and leaf mould, as yet no aquatic vegetation. As tree felling has just begun, new ponds are moderately sunlit, or in some cases shady in the first year.

II: Young pond: Three to six years old, initial succession of aquatic vegetation and surrounding clear-cut areas, for the greater part without vegetation and successive silting-up of the pond, usually starting at the mouth of the brook; due to the felling of trees more or less sunlit or partially shaded (∼50%).

III: Mature pond: More than six years old, banks and surroundings of the pond mainly cleared of trees and therefore sunlit (or lightly shaded), mostly silted-up with mud, characteristic submersed vegetation, large amounts of rotted and fresh dead wood. Banks are well-structured with numerous collapsed lodges and bays, channels and beaver meadows.

IV: Newly abandoned pond: Less than two years abandoned, water levels markedly reduced as result of (possibly temporary) abandonment but retaining pond character as the dam is still functional. Shallow, mudflats, quite sunny.

V: Abandoned pond: More than two years abandoned, long and narrow due to further decreased water levels, with reduced current flow compared to the undammed stream, with lentic conditions still persisting in some areas.

VI: Dam remnants in complete lotic condition only. In comparison to undammed streams reduced current, relatively fine substrate, more sunlight due to beaver tree-felling.

We recorded the size of the water bodies with the assistance of orthophotos and property maps (1:5000) marked with prominent landmarks, performed on location. Where necessary we also used a tape measure. We used the ELWAS-database to quantify the total length of flowing water bodies in the study area (MKULNV, 2013).

Survey of the common frog

In 2008 we initiated an amphibian monitoring programme of a subset of the beaver ponds with standardised methods (day and night surveys, counting of egg masses, funnel traps for urodelans and anuran larvae) between March and August each year. As the common frog is the only available amphibian species suitable for comparatively accurately recording, we focused on this European widespread species in this study. The common frog is a typical woodland species in large areas of Europe using a wide range of water bodies for reproduction (Schlüpmann and Günther, 1996) and is the most common amphibian species in NRW (Schlüpmann, Geiger and Weddeling, 2011). In addition to inhabiting different forms of woodland, the common frog also uses wet grassland as upland habitat. As a result, in the Rhenish Massif, its distribution is not limited by upland habitat. The females in the region usually breed at three years of age (Schmidt et al., 2006). The common frog is regarded as a philopatric species, with the adults regularly returning to their natal pond to breed. Nonetheless the spontaneous settlement of new water bodies is not uncommon in the first breeding season (Schlüpmann and Günther, 1996). The adult breeding dispersal (adults changing their breeding pond between different seasons) is around 10% and the natal dispersal of the juveniles (frogs that breed in a pond other than their natal pond) 17% (Weddeling et al., 2006). Distinct shifts of breeding sites do occur and are related to significant changes in the availability of water bodies and to the colonisation by predators (e.g. fish; Gollmann et al., 2002). Common frogs are early breeders that occupy water bodies for only a few days between February and April, depending on weather conditions (Schlüpmann and Günther, 1996).

In 2013 all water bodies of the study area were surveyed for the presence of the common frog. We applied the standard method employed by the NRW Amphibian Monitoring programme for this species, by counting egg masses (see Schlüpmann, Geiger and Weddeling, 2011). The common frog prefers to breed communally in shallow water (Dalbeck, Lüscher and Ohlhoff, 2007; Schlüpmann, Geiger and Weddeling, 2011), often leading to large and easily detectable aggregations of egg masses at the shallow margins of water bodies. Visually counting of egg masses results in a realistic estimate of masses, but may underestimate abundance in larger water bodies, i.e. beaver ponds and artificially-dammed ponds. As however all water bodies were comparatively small, and the total water surface of every water body was surveyed, the probability of a significant underestimation is negligible.

As a rule, each egg mass represents a reproducing female (Schlüpmann, Geiger and Weddeling, 2011). Because of the long breaks in the breeding process due to cold spells in 2011-2013, two, or in some cases three counts were necessary (Schlüpmann, Geiger and Weddeling, 2011). In case of very large egg mass aggregations, where several square metres of shallow water are covered by egg masses, preventing determination of individual egg masses, we measured the area covered by the complete egg mass and multiplied the m^2 covered by egg masses by 75. Representative counts have shown that some 75 egg masses/m^2 can be calculated (Schlüpmann, Geiger and Weddeling, 2011).

In order to compare the number of egg masses between the different pond types in the Hürtgenwald, an Analysis of Variance (One-Way ANOVA) with a Bonferroni post hoc test was carried out with SPSS (17.0) on the 2013 data.

Results

The influence of beavers on the density of lentic water bodies

In 2013 the Hürtgenwald study area counted a total of 306 lentic water bodies of which about half (48.7%) were beaver ponds (table 1). Twelve occupied colonies encompassed a total of 149 ponds including 112 intact ponds (Type I-IV: mean 12.4 ± 10.4 ponds/colony). The size of individual ponds varied from only a few m^2 to ~1200 m^2 (table 2A) and covered a total surface area of 17 662 m^2, representing 727 m^2 of beaver pond per/km^2. As a rule, beaver ponds are permanent, and dry up only in exceptional circumstances such as extreme, dam-breaking floods (Dalbeck and Weinberg, 2009).

The distribution of pond types is related to the age of the colony (table 3), although even old colonies have new ponds (Type I). Beavers build new ponds either upstream or downstream of existing ponds, resulting in new ponds often situated directly adjacent to mature ponds (Type III). The mean distance (± SD) of ponds from the nearest neighbouring colony is on average 420 m (± 332 m), and 1460 m (± 413 m) to the nearest colony in another stream system.

The mean number of intact beaver ponds (Type I-IV) per stream km was 3.9 (0-30.0) ponds with an average of 1.9 (0.5-4.1) ponds/km in the 19.3 km of 1st order streams, 10.1 (1.9-15.9) ponds in the 7.4 km of 2nd order streams. No ponds occurred in the 0.6 km of 3rd order streams in the study area.

The size of water bodies not created by beavers varies according to type. The majority (66%) of the smaller water bodies dry up in the course of the year (table 1). Due to a dry spring in 2013 a large number of the shallower water bodies, together with their common frog egg masses, dried up already in April.

Common frog abundance

A total of 2077 common frog egg masses were counted in the study area in 2013, equal to 85.6 egg masses/km^2 of woodland area or 0.10 egg masses/m^2 area of ponds. Of these, 82.5% were found in beaver ponds (table 1). In 2013, mature beaver ponds (Type III: mean 24.2 ± 46.3; table 2A) and artificial (fish, fire and settling) ponds (mean 21.6 ± 35.7) had the highest mean numbers of common frog egg masses.

Within the beaver ponds, the number of egg masses was highest in mature ponds which was significantly more [One-Way ANOVA, Bonferroni: $F_{(5,144)} = 2.931$, $P = 0.032$] compared to abandoned ponds (mean 1.1 ± 3.2; fig. 1, table 2A). New ponds had the second highest number of egg masses (mean 14.1 ± 21.0). In the surveys carried out between 2008 and 2012 (table 2B), high numbers of egg masses (mean 123.6 egg masses from 28 < 1 year-old ponds) were found in new ponds created in late summer/autumn of the previous year.

Since the start of annual surveys, a marked decline in the common frog population has occurred. 2013 was an extreme year for common frogs in the Hürtgenwald with exceptionally low egg mass counts. In 2013 the mean number of egg masses in beaver ponds was only 15% of the mean value for the period 2008 to 2012.

Discussion

Influence of beavers on the density of lentic water bodies

The density of beaver ponds in the study area is comparable to the density of all other lentic water bodies not created by beavers in the Hürtgenwald (table 1). The density of beaver ponds/km^2 is also comparable to the density of all lentic water bodies of other large forest ar-

Table 2. Common frog egg mass counts of (A) all beaver ponds in the Hürtgenwald in 2013 (±SD), and (B) subsets in 2008-2012 (±SD).

(A)	Beaver pond type	No. of ponds	Average size in m^2	Mean no. of egg masses	$\sum$ no. of egg masses
I	new	36	106 (±113)	14.1 (±21.0)	493
II	young	18	101 (±169)	12.1 (±35.7)	218
III	mature	32	294 (±339)	24.2 (±46.3)	775
IV	newly abandoned	26	62 (±89)	7.5 (±16.7)	196
V	abandoned	25	34 (±96)	1.1 (±3.2)	28
VI	nearly stream	12	11 (±8)	0.3 (±0.9)	3
$\sum$		149	118 (±207)	11.5 (±28.5)	1713

(B)	2008		2009		2010		2011		2012	
Beaver pond type	Mean no. of egg masses	No. of ponds	Mean no. of egg masses	No. of ponds	Mean no. of egg masses	No. of ponds	Mean no. of egg masses	No. of ponds	Mean no. of egg masses	No. of ponds
I	440.2 (±779.6)	5	106.2 (±195.4)	5	55.0 (±110.0)	4	24.8 (±38.5)	12	25.9 (±47.4)	23
II	0	1			160.0 (±226.3)	2	100.0 (±115.8)	4	20.5 (±36.8)	11
III	160.0 (±281.4)	4					123.6 (±153.3)	2	68.1 (±118.5)	14
IV	150.0	1	275.0	1			130.0 (±14.1)	2	145.3 (±239.5)	4
V	0	1	152.5 (±46.0)	2	1.0	1			9.0 (±14.8)	5
VI			0	1	0	1	0	1	0	4
$\sum$	249.3 (±523.7)	12	123.4 (±156.6)	9	67.6 (±127.7)	8	77.2 (±111.7)	30	39.4 (±90.7)	61

Table 3. Proportion of pond types among beaver ponds in differently aged colonies in the Hürtgenwald in 2013 (% ±SD). The oldest colony is 28 years old.

Age of the colony	1-3 years	4-7 years	>7 years	$\sum$
No. of colonies	3	4	5	12
Mean no. of ponds	8.0 (±6.2)	8.3 (±5.0)	18.6 (±13.4)	12.4 (±10.4)
% Type I	67.4 (±49.9)	25.3 (±23.6)	13.4 (±11.5)	36 [24.2%]
% Type II	10.0 (±17.3)	20.0 (±28.3)	4.5 (±6.8)	18 [12.1%]
% Type III	0	6.3 (±12.5)	30.9 (±12.9)	32 [21.5%]
% Type IV	13.3 (±23.1)	5.6 (±11.1)	23.8 (±10.7)	26 [17.5%]
% Type V-VI	9.2 (±10.1)	42.9 (±37.0)	27.4 (±18.3)	37 [24.8%]

eas of the Rhenish Massif: 3.4 in the Siebengebirge (Hachtel and Dalbeck, 2006), 5.6 in the Leuscheid (L. Dalbeck and M. Hachtel pers. comm., 2003) and 6.4 in the Kottenforst (Dalbeck et al., 1997). If the beaver population is permitted to expand further, a doubling of the number of lentic water bodies created by beavers can be expected across large areas of the Rhenish Massif. In the absence of the numerous artificial water bodies (table 1), beaver ponds would probably be the numerically dominating lentic water body type and therefore the main amphibian breeding site.

Compared with the boreal foothills of Alberta, Canada (Stevens, Paszkowski and Foote, 2007) the densities of beaver ponds/km^2 are similar (Alberta 4.6; Eifel 4.1). The pond sizes in Alberta are however ten times larger (Alberta 8481 m^2/km^2; Hürtgenwald 727 m^2/km^2), which can be explained by the typical topographic relief of the Rhenish Massif with its narrow and relatively steep valleys. In general, a relatively large number of rather small beaver ponds is typical of the Rhenish Massif. As in Canada (Naimann, Melillo and Hobbie, 1986; Stevens, Paszkowski and Foote, 2006) the num-

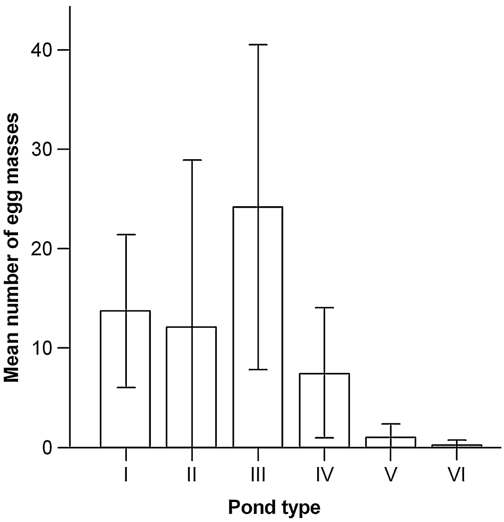

Figure 1. Average number of *R. temporaria* egg masses in beaver ponds in different succession stages in the Hürtgenwald. Error bars display ±2 SE. The number of egg masses differed significantly [One-Way ANOVA: $F_{(5,144)} = 2.931$, $P = 0.015$]. Mature and abandoned ponds differed significantly (Types III and V) [Bonferroni: $P = 0.032$]. I: new ponds; II: young ponds; III: mature ponds; IV: newly abandoned ponds; V: abandoned ponds; VI: abandoned ponds with stream characteristics.

ber of beaver ponds in 1st order streams is markedly less than in 2nd order streams.

Effects of beavers on common frog abundance

Beaver ponds account for 49% of the lentic water bodies in the Hürtgenwald, yet contain 82.5% of common frog egg masses. As a result, common frog abundance (based on number of egg masses/km^2) in the beaver ponds alone (70.6; table 1), was comparable to that of other large forested areas of the Rhenish Massif: 78.9 in the Siebengebirge (Hachtel and Dalbeck, 2006), 117.9 in the Leuscheid (L. Dalbeck and M. Hachtel pers. comm., 2003) and 52.3 in the Kottenforst (Dalbeck et al., 1997). This demonstrates the importance of beaver ponds as habitat fosterers to common frog abundance. Only artificially-dammed ponds, which are similar to beaver ponds in size, structure and their amphibian assemblages (Dalbeck and Weinberg, 2009), contained comparable egg mass numbers (216 egg masses in 10 ponds). In addition to (mature) beaver ponds, these permanent lentic water bodies are specifically suitable for amphibian colonisation (Malkmus, 1983; Schlüpmann and Günther, 1996; Gollmann et al., 2002).

Canopy cover and hydroperiod, both fundamentally altered by beavers (Naimann, Melillo and Hobbie, 1986; Naimann, Johnston and Kelley, 1988), are two of the parameters that fundamentally affect the distribution and composition of amphibian communities in other beaver impounded landscapes (Karraker and Gibbs, 2009). Beaver ponds provide favourable habitat structure for the common frog and other anurans (Skelly and Freidenburg, 2000). The rise in water temperature in beaver ponds, due to a massive increase in insolation, increases the speed of development of common frog eggs and tadpoles (Malkmus, 1983; Schlüpmann and Günther, 1996; Gollmann et al., 2002). In addition, in the Hürtgenwald, especially in dry spring seasons such as in 2013, a large number of common frog eggs and tadpoles in non-beaver water bodies dried up due to the relatively long time of development to metamorphosis of 7 to 12 weeks (Schlüpmann and Günther, 1996). This did not occur in beaver ponds. The beaver's ability to preserve lentic water during droughts (Hood and Bayley, 2008) has a positive effect on the survival of common frog eggs and tadpoles.

In 2006 the 20 beaver ponds formed by two beaver colonies in a valley 2325 m in length contained some 2500 egg masses (Dalbeck, Lüscher and Ohlhoff, 2007). This was considerably more than the numbers recorded in 2013 in all 149 beaver ponds combined (1713 egg masses) and indeed more than in the whole of the 24 km^2 study area (2077 egg masses) in this year. Although a trend of declining egg mass numbers in the Hürtgenwald can be observed, a general decline in the common frog population in the study area cannot be confirmed due to the short time scale (Meyer, Schmidt and Grossenbacher, 1998).

The occupation of beaver ponds by common frogs also benefits from the fact that the beaver ponds in a colony are closely connected.

Even new colonies usually consist of several ponds and, in older colonies, ponds of different ages are immediately adjacent to one another (table 3). The average distance of 420 m between beaver colonies can be covered by the common frog relatively easily, since gene flow still exists in populations separated more than 2000 m (up to 4000 m) from each other (Johansson, Primmer and Merilä, 2007; Safner et al., 2011), and the colonies are linked by stream corridors allowing rapid occupation (Cunningham, Calhoun and Glanz, 2007). The distance between colonies in different valley systems in the study area allows rapid colonisation or re-colonisation by the common frog (min. 1100 m, max. 1450 m).

Beaver pond dynamics and succession affect ovipositional site selection

Mature ponds contained significantly more egg masses than abandoned ponds. This may be accounted to the fact that the majority of common frogs is philopatric, returning to their natal ponds when two or three years old. The reason for a population decline in abandoned ponds can be explained by low water levels and the variable hydroperiod. As a result, predation risk for tadpoles increases, most particularly from Brown Trout (*Salmo trutta*), as common frogs are very vulnerable to fish predation (Breuer, 1992; Leu et al., 2010).

After mature ponds (Type III), new beaver ponds (Type I) provided the largest counts of egg masses. This argues in favour of a high colonisation rate, which was also indicated between 2008 and 2012 by high egg mass counts (123.6; ± 347.3) in <1 year-old ponds, which had not existed at all during the previous breeding period. The increasing habitat heterogeneity for common frogs in beaver ponds in the Hürtgenwald, with about a quarter of the ponds $\leqslant 3$ years (Type I), another quarter in an advanced stage of deterioration (Type V-VI) and about half between these two extremes (table 3), makes dispersal a necessity in an area characterised by beaver ponds.

Conclusions

Central European upland landscapes, due to their topography, generally are dominated by flowing water with only few lentic water bodies. Taking the influence of beavers on water bodies into account, it can be concluded that the density of lentic water bodies, under natural conditions and without man-made additions is reasonably high (e.g. Hürtgenwald: 6.1 beaver ponds/km^2 or 727 m^2 pond surface/km^2).

Beaver ponds, with their special characteristics, restore a natural, very dynamic, structurally rich and often fully sunlit type of water body to the countryside, considerably different to typical woodland waters. The importance of beavers as constructor of breeding habitats for the common frog in the Central European uplands can scarcely be overestimated. Mature beaver ponds in particular are favoured as ovipositional sites. Beavers can increase common frog abundance manifold, so that even in years of low breeding rates, abundances in beaver ponds alone can reach a level typical of common frog populations in woodlands without beavers. Beavers thereby enhance landscape connectivity for amphibians and can contribute significantly to the stabilisation of populations of common species (Dalbeck and Weinberg, 2009) whose importance in functional ecosystem relationships depend on their abundance (Denoël et al., 2013), e.g. common frogs and common newt species (e.g. palmate newt, *Lissotriton helveticus* and alpine newt, *Ichthyosaura alpestris*). Even rare and endangered species, such as the common midwife toad (*Alytes obstetricans*), benefit from pond construction and the removal of trees by beavers (Dalbeck, Lüscher and Ohlhoff, 2007).

Management implications

As beavers themselves care for and maintain the landscapes they create, their effects on conservation of biodiversity are not only sustainable but also cost-effective. The beaver can thereby play a major role as a management instrument for habitat and species protection (Naimann, Melillo and Hobbie, 1986; Törnblom et al., 2011). The precondition however is the acceptance by the general public of the beaver's presence.

It is of importance to acknowledge the beaver as an integral part of the European countryside, and to this end we make the following recommendations:

1. Integration of beaver activities and their effects in the EU Water Framework Directive (Törnblom et al., 2011). The acknowledgement of beaver ponds as natural elements in small streams is essential, as they can promote improvement in the ecological state of surface waters.
2. Development and implementation of projects that employ beavers specifically as an instrument for habitat and species protection, by ensuring ample allocation of the necessary space for beaver activity on small water bodies, with as little disturbance as possible.
3. Taking account of the impact of the beaver in all water body plans and projects – including regions where the beaver does not at present, but might in the near future occur.
4. Public relations work, disseminating the ecosystem services that the beaver can offer, both in terms of biodiversity, and also in flood water retention (Nyssen, Pontzeele and Billi, 2011), to the general public.

Acknowledgements. We are grateful to the Hürtgenwald Forestry Office and the countryside authorities in the Rural District of Düren for their support of the studies. We would like to thank Karin Quanten for her help and two anonymous referees for helpful comments on an earlier version of the manuscript.

References

Balčiauskas, L., Balčiauskienė, L., Trakimas, G. (2001): Beaver influence on amphibian breeding in the agro-landscape. In: The European Beaver in a New Millennium, p. 105-112. Cech, A., Schwab, G., Eds, Krakow.

Bashinskiy, I.V. (2012): The main factors of beaver's impact on amphibians in small river valleys – 6th International Beaver Symposium 17-20 September 2012, Ivanić-Grad, Croatia: Book of Abstracts: p. 47. http://www.beaver.sumfak.hr/PDF/6thIBS_abstract%20book.pdf, date of last access: 23.01.2014.

Blaustein, A.R., Wake, D.B. (1990): Declining amphibian populations: a global phenomenon? Tree **5**: 203-204.

Breuer, P. (1992): Amphibien und Fische – Ergebnisse experimenteller Freilanduntersuchungen. Fauna Flora Rheinland-Pfalz **6**: 117-133.

Cunningham, J.M., Calhoun, A.J.K., Glanz, W.E. (2007): Pond-breeding amphibian species richness and habitat selection in a beaver-modified landscape. J. Wildl. Manage. **71**: 2517-2526.

Dalbeck, L., Weinberg, K. (2009): Artificial ponds: a substitute for natural beaver ponds in a Central European Highland (Eifel, Germany)? Hydrobiologia **630**: 49-62.

Dalbeck, L., Lüscher, B., Ohlhoff, D. (2007): Beaver ponds as habitat of amphibian communities in a Central European highland. Amphibia-Reptilia **28**: 493-501.

Dalbeck, L., Hachtel, M., Heyd, A., Schäfer, K., Schäfer, M., Weddeling, K. (1997): Amphibien im Rhein-Sieg-Kreis und in der Stadt Bonn: Verbreitung. Gewässerpräferenzen. Vergesellschaftung und Gefährdung. Decheniana **150**: 235-292.

Denoël, M., Ficetola, G.F. (2008): Conservation of newt guilds in an agricultural landscape of Belgium: the importance of aquatic and terrestrial habitats. Aquatic Conserv.: Mar. Freshw. Ecosyst. **18**: 714-728.

Denoël, M., Perez, A., Cornet, Y., Ficetola, G.F. (2013): Similar local and landscape processes affect both a common and a rare newt species. PLoS ONE **8**(5): e62727. DOI:10.1371/journal.pone.0062727.

Elmeros, M., Madsen, A.B., Berthelsen, P. (2003): Monitoring of reintroduced beavers (*Castor fiber*) in Denmark. Lutra **46**: 153-162.

Gollmann, G., Gollmann, B., Baumgartner, C., Waringer-Lötschenkohl, A. (2002): Spawning site shifts by *Rana dalmatina* and *Rana temporaria* in response to habitat change. Biota **3**: 35-41.

Hachtel, M., Dalbeck, L. (2006): Amphibien und ihre Lebensräume im Siebengebirge. In: Naturschutz im Siebengebirge – Tagungsband: 100 Jahre Rheinischer Verein für Denkmalpflege, p. 57-68.

Hood, G.A., Bayley, S.E. (2008): Beaver (*Castor canadensis*) mitigate the effects of climate on the area of open water in boreal wetlands in western Canada. Biol. Conserv. **141**: 556-567.

Johansson, M., Primmer, C.R., Merilä, J. (2007): Does habitat fragmentation reduce fitness and adaptability? A case study of the common frog (*Rana temporaria*). Mol. Ecol. **16**: 2693-2700.

John, S., Klein, A. (2003): Beaver pond development and its hydrogeomorphic and sedimentary impact on the Jossa floodplain in Germany. Lutra **46**: 183-188.

Jones, C.G., Lawton, J.H., Shachak, M. (1994): Organisms as ecosystem engineers. Oikos **69**: 373-386.

Karraker, N.E., Gibbs, J.P. (2009): Amphibian production in forested landscapes in relation to wetland hydroperiod: a case study of vernal pools and beaver ponds. Biol. Conserv. **142**: 2293-2302.

Leu, T., Lüscher, B., Zumbach, S., Schmidt, B.R. (2010): Small fish (*Leucaspius delineatus*) that are often released into garden ponds and amphibian breeding sites prey on eggs and tadpoles of the common frog (*Rana temporaria*). Amphibia-Reptilia **30**: 290-293.

Malkmus, R. (1983): Soziale Thermoregulation bei Larven des Grasfrosches (*Rana temporaria*). Abh. Naturhistorischen Vereins Würzburg **23/24**: 109-118.

Metts, B.S., Lanham, J.D., Russell, K.R. (2001): Evaluation of herpetofaunal communities on upland streams and beaver-impounded streams in the upper Piedmont of South Carolina. Am. Midl. Nat. **145**: 54-65.

Meyer, A., Schmidt, B.R., Grossenbacher, K. (1998): Analysis of three amphibian populations with quarter-century long time-series. Proc. R. Soc. Lond. B **265**: 523-528.

MKULNV – Ministerium für Klimaschutz, Umwelt, Landwirtschaft, Natur und Verbraucherschutz des Landes Nordrhein-Westfalen (2013): ELWAS – Elektronisches wasserwirtschaftliches Verbundsystem: http://www.elwasweb.nrw.de, date of last access: 23.01.2014.

MURL – Minister Für Umwelt, Raumordnung Und Landwirtschaft Des Landes Nordrhein-Westfalen (1989): Klima-Atlas von Nordrhein-Westfalen. Düsseldorf.

Naimann, R.J., Johnston, C.A., Kelley, J.C. (1988): Alteration of North American streams by beaver. BioScience **38**: 753-762.

Naimann, R.J., Melillo, J.M., Hobbie, J.E. (1986): Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). Ecology **67**: 1254-1269.

Naumann, G. (1991): Aussetzen von Bibern in der Eifel – Ein Beispiel für die Problematik von Wiedereinbürgerungen. Naturschutz im Rheinland. Rheinischer Verein für Denkmalpflege und Landschaftsschutz. Jahrbuch 1989-1991: 137-150.

Nyssen, J., Pontzeele, J., Billi, K.R. (2011): Effect of beaver dams on the hydrology of small mountain streams: example from the Chevral in the Ourthe Orientale basin, Ardennes, Belgium. J. Hydrol. (Amsterdam, Neth.) **402**: 92-102.

Popescu, V.D., Gibbs, J.P. (2009): Interactions between climate, beaver activity and pond occupancy by the cold-adapted mink frog in New York State, USA. Conserv. Biol. **142**: 2059-2068.

Rosell, F., Bozsér, O., Collen, P., Parker, H. (2005): Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. Mammal Rev. **35**: 248-276.

Russell, K.R., Moorman, C.E., Edwards, J.K., Metts, B.S., Guynn, D.C. (1999): Amphibian and reptilian communities associated with beaver (*Castor canadensis*) ponds in the Piedmont of South Carolina. J. Freshwater Ecol. **14**: 149-158.

Safner, T., Miaud, C., Gaggiotti, O., Decout, S., Rioux, D., Zundel, S., Manel, S. (2011): Combining demography and genetic analysis to assess the population structure of an amphibian in a human-dominated landscape. Conserv. Genet. **12**: 161-173.

Schlüpmann, M., Günther, R. (1996): Grasfrosch – *Rana temporaria* Linnaeus, 1758. In: Die Amphibien und Reptilien Deutschlands, p. 412-454. Günther, R., Ed., Fisher, Jena.

Schlüpmann, M., Geiger, A., Weddeling, K. (2011): Grasfrosch – *Rana temporaria*. In: Handbuch der Amphibien und Reptilien Nordrhein-Westfalens, Vol. 1, Suppl. Zeitschrift für Feldherpetologie. **16**, p. 787-840. Arbeitskreis Amphibien und Reptilien Nordrhein-Westfalen, Ed., Laurenti, Bielefeld.

Schmidt, P., Hachtel, M., Sander, U., Rottscheid, R., Thomas, M., Bosbach, G., Ortmann, D., Tarkhnishvili, D.N. (2006): Masse oder Klasse?: Altersstruktur, Überlebensraten und Rekrutierung. Naturschutz und Biol. Vielfalt **30**: 125-196.

Skelly, D.K., Freidenburg, L.K. (2000): Effects of beaver on the thermal biology of an amphibian. Ecology Letters **3**: 483-486.

Stevens, C.E., Paszkowski, C.A., Foote, A.L. (2007): Beaver (*Castor canadensis*) as a surrogate species for conserving anuran amphibians on boreal streams in Alberta, Canada. Biol. Conser. **134**: 1-13.

Törnblom, J., Angelstam, P., Hartman, G., Henrikson, L., Sjöberg, G. (2011): Toward a research agenda for water policy implementation: knowledge about beaver (*Castor fiber*) as a tool for water management with a catchment perspective. Baltic Forestry **17**: 154-161.

Wake, D.B., Vredenburg, V.T. (2008): Are we in the midst of the sixth mass extinction? A view from the world of amphibians. Proc. Natl. Acad. Sci. USA **105**: 11466-11473.

Weddeling, K., Schmidt, P., Rottscheid, R., Thomas, M., Bosbach, G., Ortmann, D., Tarkhnishvili, D. (2006): Gene auf Wanderschaft: Populationsstruktur und Ausbreitung bei Amphibiendemen im Drachenfelser Ländchen. Naturschutz und Biol. Vielfalt **30**: 197-266.

Zahner, V., Schmidtbauer, M., Schwab, G. (2005): Der Biber – Die Rückkehr der Burgherren. Buch & Kunstverlag Oberpfalz: 136 pp.

Submitted: February 5, 2014. Final revision received: June 5, 2014. Accepted: June 14, 2014.
Associate Editor: Benedikt Schmidt.