Friends or foes? Importance of wild ungulates as ecosystem engineers for amphibian communities

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Abstract. As ecosystem engineers, ungulates can importantly alter the habitats where they live by changing plant cover, soil and water properties through wallowing, rooting, urinating, excreting, grazing and trampling. It is a common belief that wild ungulates, especially wild boar, Sus scrofa, represent a threat to amphibian communities due to disturbance caused while using water pools. On the other hand, ungulates could also create new aquatic habitats suitable for amphibians. So far these effects have been poorly understood. We conducted a pilot study to test whether ungulate engineering action affected amphibians' pool choice comparing amphibian species number in pools created and/or maintained by wild ungulates and pools that were fenced or, for other reasons, not used by ungulates. We observed that amphibians readily used pools also used by ungulates, although amphibian species richness in these pools was generally lower, especially when the pools were smaller. Our results suggest the need for further research and highlight the importance of wild ungulates as ecosystem engineers that create new aquatic habitats, as well as trade-offs connected with the presence of wild ungulate populations for amphibian communities. This has several management and conservation implications and prudent managers could use this understanding to incorporate ungulate management in their conservation programs targeting endangered wildlife that depends on habitats created or modified by these ecosystem engineers.

Key words: ecosystem engineers, ungulates, amphibians, disturbance, habitat modification

Introduction

Ecosystem engineers directly or indirectly modulate the availability of resources for other species by causing physical state changes in biotic or abiotic materials (Jones et al. 1994). Ecosystem engineering can importantly affect biodiversity through habitat modification (Crooks 2002, Wright & Jones 2004). Habitat disturbance can have a negative influence on some species, while others can benefit, for example when modified habitats provide new refuge and breeding sites or improve foraging opportunities (Jones et al. 1997).

Ungulates were often recognized as ecosystem engineers that modify their environment through various activities, including trampling, grazing, urinating, excreting, rooting, and wallowing (Frank & Evans 1997, Mohr et al. 2005, Smit & Putman 2011, Elschot et al. 2015). Wallowing is a widespread behaviour among ungulates used to assist in thermoregulation, prevent dehydration and sunburn, protect from ectoparasites and insect bites, as well as for social interactions (Gossow & Schürholz 1974, McMillan et al. 2000, Bracke 2011). At the same time, wallowing can significantly modify habitats. For example, dust-bathing by American bison, Bison bison, changes vegetation

cover, as well as soil texture and composition (Polley 1986, Truett et al. 2001, Fox et al. 2012), hippo, *Hippopotamus amphibious*, wallows alter local hydrology, geochemistry, and vegetation (Deocampo 2002), and wallowing by red deer, *Cerous elaphus*, changes nutrient concentrations (McDowell 2009). Such changes to water ponds and similar habitats could affect other animals that depend on them. In Europe, especially the wild boar, *Sus scrofa*, is believed to strongly affect water ponds due to their frequent wallowing (Fernández-Llario 2005).

We used amphibians to study the effects that ecosystem engineering by wild ungulate wallowing or trampling can have on freshwater communities. Water ponds represent an essential habitat for amphibians, which often use them as breeding and feeding sites, as well as stepping-stones to disperse and colonize new areas (Russel et al. 2005, Semlitsch 2008, Kolozsvary & Holgerson 2016, Salazar et al. 2016). Nowadays, loss of aquatic habitats is one of the main threats to amphibian life (Cushman 2006, Becker et al. 2007, Todd et al. 2009). Beside negative effects on amphibian communities (e.g. impact on terrestrial habitats: Badillo-Saldaña et al. 2016; on aquatic habitats: Zengel & Conner 2008), ecosystem engineering by ungulates can create or maintain new

humid areas and thus improve habitat suitability for amphibians (Friend & Cellier 1990, Gerlanc & Kaufman 2003, Hartel & von Wehrden 2013, Hartel et. al 2014) and influence both amphibian population demography (Ringler et al. 2015) and species richness (Beck et al. 2010). So far it remains unclear to what degree amphibians use the pools created or maintained by wild ungulates and what are the effects of disturbance caused by wallowing, which could result in direct mortality, drying of pools or excessive muddling of water.

We compared amphibian communities between pools created and/or maintained by wild ungulates and pools that were fenced or, for other reasons, not used by ungulates. This provided us with an opportunity to evaluate the positive and negative effects of ungulates use of water pools on amphibians that depend on such water sources.

Materials and methods

Study areas, pools and study species

The study took place in Emilia-Romagna in Italy, specifically in four areas between Parma and Bologna: The Amphibian Centre and its surroundings in Pianoro, Bologna (AC); the Natural Reserve of Contrafforte Pliocenico and its surroundings, Bologna (CP); the Regional Park of Suviana and Brasimone lakes and its surroundings, Bologna (SB); and the WWF Nature Reserve of Ghirardi and its surroundings, Parma (GH). The region is characterised by the Mediterranean sub-oceanic to Mediterranean subcontinental climate (Costantini et al. 2013). The elevation of the sampled areas varies between 160 and 780 m a.s.l. The annual average temperature in the region is approximately 13° C and annual precipitation around 700-850 mm. The soil is predominately rich in clay and loam, so the water often remains on the surface. Sampled pools were located in open fields dominated by graminoids, common hazel, Corylus avellana, European hop-hornbeam, Ostrya carpinifolia, silver poplar, Populus alba, black poplar, Populus nigra, Austrian oak, Quercus cerris, and common beech, Fagus sylvatica. Fallow deer, Dama dama, roe deer, Capreolus capreolus, and wild boar are common in all the sampled areas, while red deer was present only in the SB. No reliable estimates of ungulate density are available.

Several taxa of anurans and urodeles are present in the area, most of them characterised by negative population trends. The common toad, *Bufo bufo*, is assessed as vulnerable, with reported decrease of over 30% in the last 10 years in Italy. The Italian crested newt, *Triturus carnifex*, and the smooth newth, *Lissotriton vulgaris*, lost around 25% of their living sites in the last 10 years and they are assessed as near threatened. The statuses of the Alpine newt, *Ichthyosaura alpestris*, the agile frog, *Rana dalmatina*, the edible frog, *Pelophylax esculentus*, and the pool frog, *Pelophylax lessonae* were assessed as least con-

cern, but their populations are declining or status unknown. Italian populations of the European common frog, *Rana temporaria*, the Italian stream frog, *Rana italica*, and the Italian tree frog, *Hyla intermedia* are estimated to be stable and are assessed as least of concern. All the amphibian species sampled need standing or slow-moving waters for breeding and larval development, except for *Rana italica*, which generally favours fast flowing streams for reproduction (Lanza et al. 2009).

Sampling and data analysis

A total of 28 pools were sampled (Table 1), including 18 pools created or largely modified by wild ungulate with recent signs of their use ("ungulate pools"; signs included hoof-prints inside or around the pool, modified pool bed areas due to wading and wallowing, and lack of vegetation) and 10 pools without recent signs of ungulate use, which have been created or maintained by people or originated due to natural topography ("non-ungulate pools"). Most (7) of the non-ungulate pools were fenced, which prevented access of ungulates to the pools. Either entire area was fenced (AC) or individual pools (other areas). The pools were of various sizes (from 40 cm to approximately 50 m in diameter). Based on size and water quality we grouped the pools in three categories: large ponds (>3 m diameter), small ponds (≤3 m in diameter, predominately clear water) and mud-holes (≤3 m in diameter, muddy water) (Table 2). We decided to include mud-holes in this study, as they are highly influenced by wild boar wallowing and we regarded them as the areas with highest ungulate disturbance. Fieldwork was conducted in 2014. Each pool was sampled twice, once per day during daytime hours in spring and summer, from May to August. Since various amphibian sampling methods can be combined to provide the best population estimates in specific circumstances, we combined dip-nets and visual encounters, which are also two of the most common amphibian sampling techniques (Gunzburger 2007). Fishing net with a diameter of 40 cm with a handle of 117 cm was used for sampling turbid pools. In case a pool was small enough, the whole area of the pool was sampled. If a pool was too large for us to reach all parts from the shore with the net, only part (approximately 60%) of the pool was sampled. In this case, we estimated the percentage of habitat types in the pool and adjusted the proportion of net catches accordingly. Captured amphibians were collected in a small box filled with water, to prevent the resampling of the same animal. For pools with very clear water, no net was used and the amphibian count was made visually. Due to difficulties of reliably distinguishing green frog species (Pelophilax sp.) in the field, we did not differentiate between individual species in our samplings for this genus.

We considered only the species that occurred throughout the entire study area. For this reason, we removed *Rana temporaria* and *Hyla intermedia* from further analysis. R software (version 3.2.0) was used for the analysis. We ran Wilcoxon rank sum test to compare the number of species in respect to the pool type. Frequencies in occurrences of amphibian species between the pool types were compared using Fisher's exact test.

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Table 1. Number of ungulate and non-ungulate pools sampled in each study area.

	WWF Nature Reserve of Ghirardi	Regional Park of Suviana and Brasimone lakes	Natural Reserve of Contrafforte Pliocenico	Amphibian Centre
Ungulate pools	9	1	7	1
Non-ungulate pools	5	1	0	4

Table 2. Number of amphibian species (mean ± SD) per ungulate and non-ungulate pools in respect to the pool size. The number of pools sampled from each type is presented in parentheses.

	Large pools	Small pools	Mud-holes
Ungulate pools	1.4 ± 0.8 (7)	1.0 ± 1.2 (7)	0.0 (4)
Non-ungulate pools	1.2 ± 1.1 (8)	2.0 ± 1.4 (2)	N/A

Results

Overall the average number of amphibian species found in the non-ungulate pools (mean \pm SD: 1.4 \pm 1.1; n = 10) was higher compared to ungulate pools (0.9 \pm 1.0; n = 18;) but not statistically different (Wilcoxon rank sum test: W = 70, p = 0.32). In the large pools the number of species was larger in the ungulate pools (ungulate pools: 1.4 \pm 0.8; n = 7; non-ungulate pools: 1.2 \pm 1.1; n = 8), while in the small pools more species were found in the non-ungulate pools: (ungulate pools: 1.0 \pm 1.2; n = 7; non-ungulate pools: 2.0 \pm 1.4; n = 2), but also not statistically different (large pools: W = 30, p = 0.81; small pools: W = 3.5, p = 0.36). No amphibians were found in the ungulate mud-holes (n = 4).

Lissotriton vulgaris, Triturus carnifex, and the green frogs were present in higher percentages in the non-ungulate pools and the common frog, Bufo bufo, was found only in these types of pools (Fig. 1). The Rana dalmatina was present in higher percentages in ungulate pools and the Rana italica was found only in this pool type. The Ichthyosaura

alpestris was found in a similar percentage of both types of pools. However, the differences in species occurrences between the pools were not statistically significant (Fisher's exact test; p > 0.15).

Discussion

The robustness of this preliminary study is limited by relatively small sample sizes, but the data presented indicate that ungulate activity did not have a major negative influence on the amphibian presence in our study areas, as we could confirm the persistence of several amphibian species in pools used by the ungulates. However, in the smallest water bodies intensively used by the ungulates (mud-holes), we did not find any amphibian. Overall we noted somewhat lower (although not statistically different) amphibian species richness in the pools regularly used by ungulates and some of the species appear to have difficulties adapting to regular disturbance caused by the wallowing and other activities of ungulates. On the other hand, we confirmed the presence of several amphibian species in pools created and/or maintained by the wild ungulates. This demonstrates trade-offs connected with the presence of wild ungulate populations for amphibian communities and highlights the importance of ungulates as ecosystem engineers, which can create new aquatic habitats for amphibians and maintain them by wallowing or trampling. The role of ungulates as

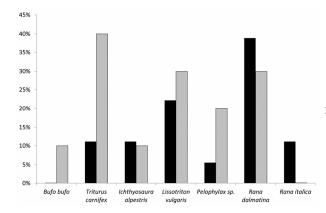


Figure 1. Percentages of pools of each type with detected presence for individual amphibian species; pools were separated among those modified and recently used by wild ungulates (black; n=18) and pools that were fenced or without evidence of recent ungulate use (grey; n=10)

ecosystem engineers might be especially important in areas where availability of surface water is naturally low, for example in karstic areas, where the surface water is rare and ponds maintained by humans are disappearing (Stanković et al. 2015). Therefore, we suggest that wild boar and other ungulate presence should not be a priori regarded as negative for amphibian conservation, but critically evaluated based on local conditions. To our knowledge, this is the first study reporting potential effects of ungulates on amphibian communities in Europe.

It is a common belief that pool bathing by wild ungulates, especially by the wild boar, represents a great threat to amphibians (Taylor & Hellgren 1997, Sebasti & Carpaneto 2004). This was also the reason for fencing of several pools in our study areas. Our data suggest that indeed some species might be negatively affected by ungulates and that in the frequent disturbance by ungulates in the smallest water bodies may prevent colonization by amphibians (e.g. mud-holes). On the other hand, we have repeatedly found amphibians in several pools regularly used by wild boars and noted that wallowing and prodding by wild boar can increase habitat heterogeneity by reshaping the pools.

It appears that size of the water body might be a crucial factor, as we observed decreased species richness in smaller ponds used by ungulates, but not in large ponds, where opposite pattern was observed. In large ponds, we noted that modifications usually concentrated in one area of the pool edge, while the rest was relatively undisturbed. It was already reported that such localized ungulate activity can create important feeding sites and refuges from dehydration (Beck et al. 2010, Cabrera-Guzmán et al. 2013), which might explain higher species richness in large ponds when used by ungulates. Also, temporary water ponds tend to desiccate faster if they are overgrown with vegetation and vegetation removal caused by ungulate engineering action can help to extend hydroperiod in temporary ponds (Curado et al. 2011, Hartel et al. 2014). It also should be noted that the effects are likely species-specific. For some species, it appears that disturbance reduces the possibility of their persistence (e.g. Triturus carnifex and Pelophylax sp.), while other amphibians appeared to be tolerant to disturbance or even preferred pools used by the ungulates (e.g. R. italica and R. dalmatina). Future studies will be needed to determine whether this observed preference might be connected to reduce competition with species less tolerant to disturbance. A side effect of wallowing can also be reduced vegetation, which has a species-specific effect. For example, some species like Lissotriton vulgaris are positively influenced by vegetation presence while others prefer open space (e.g. Bufo bufo) or banks with less vegetation (e.g. Triturus carnifex; Ildos and Ancona 1994, Denoël et al. 2013). Moreover, Rana dalmatina favour ponds with vegetation at early-medium successional stages and late vegetation succession stage are reported to be inhospitable for Pelophylax lessonae (Emanueli 2006, Hartel et al. 2009). We recommend further studies that would assess effects of ungulate activity on abundance of amphibians, not only species presence, and to quantify the number of aquatic habitats created by the ungulates in respect to the general habitat availability. This would enable evaluation of the overall tradeoffs of ungulate ecosystem engineering for amphibians on the population level. Effects exerted by ungulates on amphibian communities likely depend on the level of disturbance caused by the wallowing and trampling, which can be related to additional parameters, such as ungulate species, population structure and density, as well as the climate, and water resource availability. Additional research is needed to establish how these factors modulate the engineering of aquatic ecosystems by wild ungulates and its effects on communities therein. In addition to ungulates' effects on water habitats it would be also interesting to study their influence on amphibians due to modification of terrestrial habitats important for amphibians (e.g. trampling, and rooting of the leaf lit-

Several large mammals perform important roles as ecosystem engineers and greatly influence habitats in which they live (Naiman 1988, Wright and Jones 2004). Understanding their impact on other species has important management and conservation implications. Prudent managers should use this knowledge to incorporate ungulate management in their conservation programs targeting endangered wildlife that depend on habitats created or modified by these ecosystem engineers.

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