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Flexible habitat selection paves the way for a recovery of otter populations in the European Alps

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ABSTRACT

Carnivores are threatened worldwide through habitat loss and persecution. Habitat destruction is a major threat for the Eurasian otter. Its populations declined drastically in Europe but are now expanding again, including into the Alps. Here, flood prevention and hydropower have massively altered the riverine landscapes.

We evaluated the recovery potential of otters by testing the impact of major factors of habitat transformation and human disturbance on multiple spatial scales. In a hierarchical approach, we investigated spatial use and foraging habitat selection of nine otters in a long-term radiotracking study in the eastern Central Alps. We combined fine scale habitat selection analysis with individual movements by applying a step-selection function approach to the linear river system in a novel way.

At home range scale, otters preferred the main riverbeds to abstracted water and tributaries, whereas at fine scale, there was no significant preference for pristine sections within the watercourses. Otters selected for reservoirs in streams with a width smaller than 12 m and otherwise preferred foraging in residual waters and stretches with main discharge.

At this stage of recovery, otters show a surprising flexibility in their habitat selection. This is promising for the species' future expansion into former abandoned areas. However, given that the traditional fish stocking regime might contribute to this recovery by providing profitable hunting grounds after stocking events, there is an increased risk of human-wildlife conflicts. Our results demonstrate a high adaptability of a threatened carnivore to altered landscapes and show how this flexible behaviour opens opportunities for recovery.

1. Introduction

Environmental change due to human activities is one of the major threats to biodiversity (Vitousek et al., 1997). Carnivore species are considered to be especially sensitive to changes in land-use and to human disturbances due to their large spatial requirements, dietary specialisation and low reproduction rate (Ripple et al., 2014). With factors such as legal protection and habitat restoration some threatened species have recovered or are re-expanding again into historically occupied areas, e.g. Eurasian lynx (*Lynx lynx*) and wolf (*Canis lupus*) (Chapron et al., 2014). However, due to the massive anthropogenic impact worldwide, species have to adjust to habitat transformation and high levels of human disturbance. Changes in habitat structure often alter the availability of resources like food, which in turn requires behavioural plasticity in combination with altered habitat selection or acceptance of novel food resources (Contesse et al., 2004). Positive population trends of some carnivores like cougar (*Puma concolor*) or lynx have shown that those species are far more adaptable to using modified landscapes than previously anticipated (Bouyer et al., 2015; Knopff et al., 2014). It is therefore crucial to understand the adaptability of a species to altered landscapes and its selection of habitats within them to implement conservation measures.

One of the species returning to former areas of its distribution is the Eurasian otter (*Lutra lutra*) (e.g. Elmeros et al., 2006; Ferna, 1998; Kranz and Toman, 2000; Prigioni et al., 2007). The otter is a semi-aquatic carnivore with an almost exclusive specialisation in fish, (Krawczyk et al., 2016). The otter is therefore closely linked to the existence of aquatic habitat. In the last century, otter populations have declined in many parts of Europe, resulting in large-scale extinction (Foster-Turley et al., 1990). A major cause for the decline, besides excessive hunting and the nowadays heavily restricted PCBs, is attributed to habitat deterioration and loss due to river regulations, dam constructions and

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modifications to the riparian landscape (Kruuk, 1995). Today, the otter is classified as "Near Threatened" according to the IUCN red list (Roos et al., 2015). In recent years, the species is expanding its distribution again and individuals have even been reported to settle in heavily modified landscapes (e.g. Kranz and Toman, 2000; Kloskowski et al., 2013). This has challenged the notion of the otter being a flagship species of pristine and healthy environments (Bifolchi and Lode, 2005; Reid et al., 2013) and it has raised questions of what kind of habitats they select within anthropogenic altered landscapes. Although the Eurasian otter is the most thoroughly studied otter species (Kruuk, 2006), so far only a few studies have addressed the ecology of otters in modified landscapes (Bueno-Enciso et al., 2014; Kloskowski et al., 2013; Pedroso et al., 2014; Sales-Luís et al., 2007; Weber, 2011).

Since the late 1990s, a growing otter population is re-expanding into the eastern Central Alps (Kranz and Poledník, 2014; Kranz et al., 2013). Within less than two decades, the species has recolonised the Austrian state of Styria (Kranz and Poledník, 2012), with an estimation of 2.8 individuals/10 km^2 (Kranz et al., 2013). This is surprising as the valley bottoms in the Alpine arc belong to the most recent and rapidly transformed landscapes in Europe (Stöcklin et al., 2007). Here, a multitude of hydropower plants strictly regulate the flow regime of the rivers. Large parts of the watercourses have been altered by channelisation and most of the natural river banks have been converted to revetments (Comiti, 2012). In the last century, much of the riparian vegetation has been reduced, converted to agricultural lands or replaced by human settlements (Naiman et al., 1993). Despite increasing efforts to restore watercourses, riparian vegetation remains very restricted and under ongoing anthropogenic pressure (Comiti, 2012). These alterations of the riverine ecosystem have strong negative effects on the aquatic fauna such as the abundance of fish (Bain et al., 1988) and, as a consequence, on otter distribution (Kruuk, 1995).

Human presence has been shown to have adverse effects on otters (Juhász et al., 2013; Prenda et al., 2001) but has been questioned as a general cause for disturbance (see Kruuk, 2006). Females can exhibit a higher sensitivity to humans as shown in other mammals, because females choose more remote and pristine habitat for reproduction (Ramesh et al., 2015). In the Alps, main roads are often close to the watercourses in the valley ground. Additionally, humans visit riparian landscapes for their spare activities, thus probably influencing spacing behaviour of otters.

The objective of this work was to assess the habitat preferences of otters at different scales in a region with a mosaic of modified and natural stretches of watercourses, abstracted waters for hydropower use and standing waters such as ponds. We were especially interested in understanding if modifications of watercourses and human disturbance affect foraging habitat selection of otters. In natural watercourses, fish biomass per m^3 decreases with increasing river width (Schager and Peter, 2001), and is lower in regulated stretches than where the water flow is natural (Fette et al., 2007). Therefore, we expected otters to prefer the most natural stretches at any given scale because fish biomass modulates presence of otters.

We analysed habitat selection at three scales: population, home range and within home range (Johnson, 1980). At the population scale, we expected a sex-specific difference in the location of home ranges, with territories of females in less disturbed areas. At the home range scale, we predicted that otters mainly forage in the main riverbed or in standing water such as fishponds where fish densities are high. At the fine scale, we expected otters to forage in the most natural parts of rivers while avoiding regulated stretches.

Most models for habitat selection assume that the animals move freely within the landscape. However, many species are restricted in their movements to quasi-linear features, like hedges or rivers. For those species, the analyses that rely on methods based on two-dimensions may not capture their real habitat selection in relation to the perceived habitat availability and the results may be biased. Fortin et al. (2005) introduced the step-selection function method (SSF), where habitat selection analysis is combined with the species-specific animal movement pattern. To identify fine-scale foraging habitat selection, we developed a novel approach to apply a SSF to the linear system of watercourses.

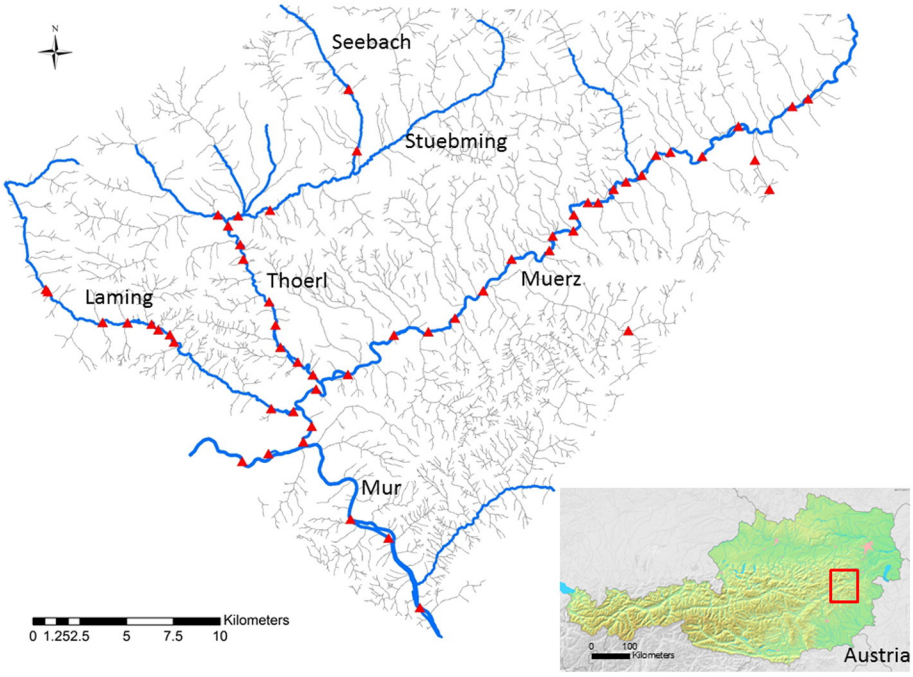

Fig. 1. Study area in the eastern Central Alps in Styria, Austria, defined by the minimum convex polygon for all otters showing the running and standing water bodies. Blue = watercourses ≥ 4 m, grey = streams < 4 m. Red triangles = reservoir dams (n = 55). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)