



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.

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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 km² (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 m³ 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.

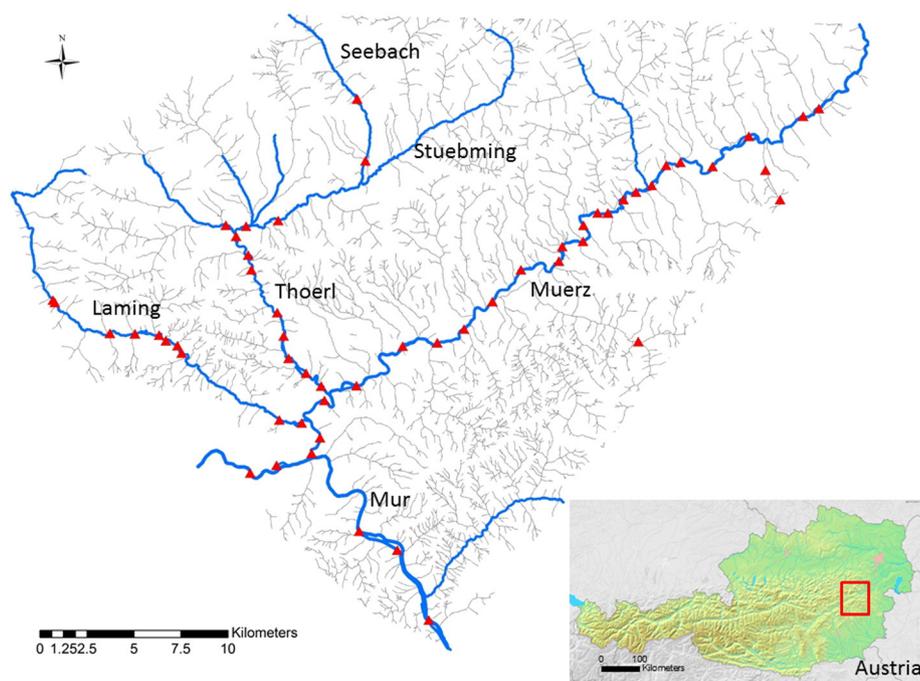


Fig. 1. Study area in the eastern Central Alps in Styria, Austria, defined by the minimum convex polygon for all otters showing the running and standing water bodies. Blue = watercourses ≥ 4 m, grey = streams < 4 m. Red triangles = reservoir dams ($n = 55$). (For interpretation of the references to colour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

2. Methods

2.1. Study area

The field study was conducted from May 2010 to March 2013 in the eastern Central Alps in Styria, Austria in the area of Bruck an der Mur (N47°24'36", E15°16'7"; Fig. 1). The area covers approximately 1760 km², with about 3090 km length of watercourses. All rivers and streams in the study area belong to the catchment basin of the river Mur, which has a mean annual discharge of 110 m³/s. The main valley in the study area is named after the river Muerz (mean annual discharge: 20 m³/s). The waters are mainly inhabited by brown trout (*Salmo trutta*) and European grayling (*Thymallus thymallus*). The area at lower altitude is dominated by iron industry, intensive agriculture and urban areas. In the secondary valleys, the landscape changes to agriculture and forests. The elevation of the valley floor ranges from 458 to 974 m, with the surrounding mountains up to 1850 m. The rivers Mur and Muerz and the larger streams are channelled in large parts and dammed for electrical power generation (dams heights up to 5–10 m; Fig. 1).

2.2. Radio telemetry

Otters were trapped with soft-catch traps (No. 3, Oneida Victor Inc., Cleveland, Ohio) coupled with GSM trap alarms (Ó Néill et al., 2007). Captures took place in spring and autumn between 2010 and 2012 (Table A1 supplementary material). Trapping actions lasted from five to seven nights. During a given trapping action, traps were set in four to six locations. On average, one otter was caught within 32 trap nights. Once caught, the otter was removed from the trap within 30 min of capture and put into a solid transport box. Intraperitoneal implantation of the transmitter (model 325/L, 42 g, 9.4 × 2.3 cm, life span ca. 15 months; model 400/L, 95 g, 9.7 × 3.3 cm, lifespan ca. 31 months, Telonics Inc., Mesa, Arizona) was carried out in a nearby vet-ambulance after the animal had been sexed and its age estimated. For recovery, otters were kept in a box at a quiet place. All otters were released within 24 h at the location of capture. Animals were then tracked in bouts between sunset and sunrise by a single person on foot and from car using a receiver (Sika, Biotrack Ltd., Dorset UK), a handheld 3-element Yagi-antenna and an omnidirectional antenna placed on the car roof. Tracking bouts ranged from 90 to 945 min (mean = 340 min) and covered at least one whole night per month per individual. Within bouts, the location of the focal animal was taken every 15 min. To increase independent locations, animals were additionally tracked 1–2 times every week at random times at night for two consecutive locations. Day resting sites were located at least twice per week. The observer used a GPS (extrex H, Garmin Ltd.) for his location and took the bearing to the animal with a handheld compass. For every observation, activity of the animal was deduced from the variation in signal strength 3–5 min before taking the bearing and by comparing location and strength of the signal to the previous and the following bearing. Activity was classified into three categories: (1) active, (2) passive and (3) unknown. The accuracy of the location of the animal was estimated by the observers using the distance to the animal, the spread of the signal and short-term cross-triangulations done by the observer. The accuracy was categorised as within (1) 10 m, (2) 20 m, (3) 50 m, (4) 100 m and (5) more than 100 m of the estimated location.

The location of the animal was then calculated in ArcView 3 (ESRI, 2002) using the bearing and the location of the observer. Animals were tracked until the sender failed, the animal disappeared or until the field study ended in March 2013 (Table A1). Trial runs to estimate tracking error were conducted at night during the study with the same materials. There, a transmitter was positioned at the bank side at various distances to the observers. Observers estimated the accuracy for each fix with the mentioned categories above. Tracking error and estimated accuracy were visually compared using boxplots. Tracking error

data was congruent for the different classes of accuracies. Locations with accuracy > 100 m and data from the first ten days after surgery were excluded for all analyses.

2.3. Habitat selection at population level

For the habitat selection at the population level the available area was constructed as a 100% minimum convex polygon (MCP) using ArcGIS 10 (ESRI, 2011). Habitat categories were designated as main river (watercourses ≥ 4 m width) and tributaries (watercourses < 4 m width) (Table 1a). Individuals were considered as the sample units. Habitat selection was assessed with an Habitat Selection-Index (HS-Index) based on the Jacobs-Index (Jacobs, 1974) with the formula

$$HS = (u - a) / (u + a - (2u \times a)) \times 100$$

where u is the proportion of the resource used and a the proportion of its availability. Values for HS range from 100 to –100 (maximum preference to avoidance). Habitat type was considered to be significantly selected when its mean value on the Jacobs-Index was different from 0 and the 95% credible intervals did not encompass 0. Analyses were done using a Bayesian approach with the package "arm" in R 3.2.2 (R Development Core Team, 2015).

2.4. Home range size and habitat selection at home range level

For home range estimations, active and passive locations were included in the analyses (with resting sites only once). Two home range estimators were used to calculate availability of habitats in R: 95% fixed kernel density contours by the package "adehabitat" (Calenge, 2006) and 95% local convex hulls by the package "t-locoh" (Lyons et al., 2013). The results of the different estimators were compared using a t-test. As otters foraged in or along water bodies, the actual home ranges used here are the waters within the calculated home range. Foraging habitat selection was assessed exclusively with active locations outside resting sites. The dataset for this analysis was further subset by using locations that were sampled at least 24 h apart to reduce spatial autocorrelation. A used-availability design was applied, where availability of habitat was estimated by a set of random locations that was 10 times larger than the number of used locations. The random locations were drawn using the standard toolbox in ArcGIS 10, setting the extent of the area to the home range given by the kernel density estimator. Habitat was classified into four categorical habitat types: (1) main riverbed (including main discharge, reservoirs and residual waters), (2) abstracted water (the power plant channel and the downstream water outlet), (3) tributaries and (4) standing water (Table 1b, also see Fig. A1). A logistic regression model with habitat type as covariate and animal as random effect was fitted, where the binary response indicated whether the habitat was available (0) or used (1).

2.5. Foraging habitat selection within home range

The main riverbed was divided into three habitat functions (a) main discharge, (b) reservoir and (c) residual water (Fig. A1) and its ecomorphology was assessed (BUWAL, 1998). At the fine scale we included the following variables that have shown to be important for otter presence in other studies: water width, water depth, bank type, bank reinforcement type, riparian vegetation type and riparian vegetation width. We additionally included distance to roads (proxy for human disturbance), distance to hydropower plant (source of fragmentation), distance to fishponds (patch of abundant food) and the presence of wood and algae in the water as those are beneficial to fish (Hafs et al., 2014). This information was attributed to the shapefiles of water bodies obtained by the Austrian Department for Meteorology. All predictor covariates are listed in Table 1c. Continuous covariates were centred and scaled. The interaction between habitat function of the main riverbed

Table 1
Variables used for habitat selection analysis at three spatial scales.

Variables	Description	Measurement [unit]	
a) Population level			
River width	<4 m or ≥4 m	Categorical	
b) Home range level			
Habitat type	Main riverbed	Original riverbed	Categorical
	Abstracted water	Water diverted from the reservoir to the hydropower plant (power plant channel) and back to the main riverbed (downstream water outlet)	Categorical
	Standing water	Lakes, ponds and fishponds	Categorical
	Tributary	All small streams flowing in the main rivers	Categorical
c) Within home range level			
Function of the main riverbed	Main discharge	Unhindered flow of all discharge within the main riverbed	Categorical
	Reservoir	Slow moving water above the dam, sandy and deeper bottom	Categorical
	Residual water	Regulated flow below the dam until tail water from hydroelectric power station joins	Categorical
River width	Main riverbed width	Continuous [m]	
Depth	Variability of water depth within the river	Ordinal (1–3, with 1 = large, 3 = no variability)	
River bank modification	Alterations and bank reinforcement	Ordinal (1–5, with 1 = none, 5 = completely altered)	
Vegetation width	Width of natural or semi-natural vegetation measured from waterside	Continuous [m]	
Vegetation type	Type of vegetation from the river perspective	Ordinal ("natural" (forest, reed, herbaceous stretches with at least 1 tree/bush within 25m), "foreign" (herbaceous, meadow, grass), "artificial" (none))	
Algae	Estimated amount of algae in riverbed	Ordinal (from 1 = none to 3 = exceeding)	
Wood debris	Wood washed up at the bankside	Ordinal (from 1 = heaps to 3 = none/little)	
Distance to fishponds	Known fishponds within home ranges	Continuous [m]	
Distance to dams	Dams for hydropower plant	Continuous [m]	
Distance to roads	Paved roads	Continuous [m]	

and river width was added to the model, because the potential fragmentation of rivers could be more pronounced in small rivers than in larger ones. Moreover, random slopes for all covariate parameters to account for inter-individual differences were included in the model.

Fine-scale habitat selection was then assessed with a conditional use-availability design (Manly et al., 2002). To obtain a resource selection function (RSF) we applied a step-selection function approach (Fortin et al., 2005; Thurfjell et al., 2014), where observed steps (the linear segment between two consecutively observed points) are compared to a set of random steps with the same starting point. To generate the random points, we followed the protocol of Fortin et al. (2005), where random steps for a given starting point differ in length and direction, and the average distribution of step lengths and angles for a given animal is determined based on the distributions of all the other individuals. From those two distributions, random steps were drawn independently. This protocol allows the animal to move in every direction. Species that move along linear features are, however, restricted in their potential paths. In our study area, the otters moved mainly along rivers and streams with rare excursions to ponds near the riverbed. Therefore, we set up a linear network with the extension "Network Analyst" in ArcGIS 10 along all watercourses. As the distribution of the angles is inherently given by the linear system (i.e. only forward and backward movement is possible) only the distribution of the step lengths was used. Where watercourses enlarged to more than double their size (e.g. when entering a lake), we built a network grid over the area to represent the water area available and connected it with the main network (Fig. A2). Animal movement was modelled along this network. To obtain the distribution of step lengths, the distance between any two consecutive tracking locations with the interval of 15 min of all animals was calculated with the tool "New Route" in the Network Analyst. For each realised step by an animal, 10 random step lengths were drawn from the respective distribution of all other animals. For each of these step lengths, at least two locations were obtained with a potential forward and backward movement, plus additional locations with sideward movement when watercourses merged or connected to a lake. The exact locations for all potential endpoints with a fixed step length

were calculated with the tool "Service Area" in Network Analyst. From this pool of potential steps with the same step length one was randomly chosen to be included in the data. This resulted in 10 control steps with each of differing length, representing what was available to the animal when moving (Fig. A3). As this is a matched case-control design, it was analysed with a conditional logistic regression model (Hosmer and Lemeshow, 2004).

To obtain population-level parameter estimates, a two-stage modelling approach (Fieberg et al., 2010) was used by employing automated routines that were provided by the "Ts.estim()" function from the R-package "TwoStepClogit" (Craiu et al., 2011). Deviance residuals for each stratum (i.e., each set of one used with 10 available points) from the regression were then checked for autocorrelation, following the protocol in Appendix C in Forester et al. (2009).

Using the parameter estimates (β_1, \dots, β_n) from the conditional logistic model, a RSF that estimates the preference of a habitat depending on the predictor covariates $x = x_1, \dots, x_n$, can be obtained by

$$RSF(x) = w(x) = \exp(\beta_1 x_1 + \dots + \beta_n x_n).$$

For any values of the covariates x , $w(x)$ represents the RSF score that approximates the respective proportion between the used and the available frequencies (Johnson et al., 2008). Values of $w(x) > 1$ thus indicate that habitats were over-proportionally selected by the animal with respect to their availability, while $w(x) < 1$ represents habitats that were avoided.

To assess the interaction between habitat category and river width, we used the fitted model to calculate RSF scores changing with river width for each of the three habitat functions (main discharge, reservoir, residual water) separately, plugging the mean of the remaining covariates into the model. Pointwise 95% confidence intervals of the RSF were obtained by using the estimated variance-covariance matrix $V(\beta)$ of the β -estimates and employing the approach described in Fox (2003,

Section 2). The $V(\beta)$ matrix was estimated via a two-stage bootstrap using 200 iterations in total (Efron and Tibshirani, 1986).

3. Results

Between May 2010 and March 2012, 10 otters (three males and seven females) were captured and equipped with implanted transmitters. Nine of them could be tracked for more than six months and were included in the analyses (mean duration in days = 658, min = 252, max = 1032). Combined, the individuals were tracked 13,525 times (mean = 1502, min = 617, max = 2953), with every individual tracked on average 54 times per month (SD \pm 12, Table A1).

3.1. Habitat selection at population scale

The MCP for all individuals combined covered an area of 929 km², consisting of the habitats main rivers (196 km, 500 ha water surface) and tributaries (1483 km, 313 ha; Fig. 1). When only water area was considered as available to the animals, all individuals used main rivers most of the time (97.5% of all locations) and only occasionally tributaries (345 locations, 2.5%) during their active periods. They showed no sex-specific difference but overall strong evidence for habitat selection of main rivers (HS-Index = 99.99, 95% CI = 99.97–99.99).

3.2. Habitat selection at home range scale

Individual home ranges entered the analysis as available area. They were calculated using 10,562 locations (mean \pm SD per animal = 1173 \pm 550, Fig. A4). The 95% fixed kernels converged at a relative high bandwidth ($h = 700$) due to the linearity of the freshwater system. Home range size varied between the two estimators with mean river lengths of 85.1 km (\pm 27.5 SD) in kernels and 32.2 km (\pm 11.8 SD) in local convex hulls. While the length of the main riverbed with the abstracted water and standing water were consistent between the two estimators at approximately 20 km (T-statistic = -0.1335 , $p = 0.89$), the main difference of river length between the estimators was due to the inclusion of tributaries by the kernel estimator: kernels = 65.0 km, LocoH = 11.6 km (T-statistic = 5.8, $p < 0.001$, Fig. A5). Home range size in males was approximately a third larger compared to the females (kernel: F = 16.1 \pm 3.4 km, M = 28.3 \pm 2.9 km; LocoH: F = 18.3 \pm 6.1 km, M = 25.2 \pm 4.1 km). Females had distinct boundaries between them but overlapped with home ranges of the males. Contrary to the expectation that females would select for the most pristine and remote habitat, they also had home ranges in large rivers ($N = 2$). Both estimators yielded similar results for habitat selection (mean number of independent locations used per animal = 109 \pm 39). Logistic regression with standing water as reference category showed a positive selection of the main riverbed (estimate = 1.68 \pm 0.30) and a negative selection of tributaries (estimate = -0.89 ± 0.34 , both $p < 0.0001$) while the use of abstracted water was indifferent (estimate = 0.45 \pm 0.42, Fig. A6). For small scale habitat selection, we focused on the main riverbed as this was positively selected and holds a high diversity in functions.

3.3. Foraging habitat selection within home range

In the two-step conditional logistic regression analyses, all variables that were available to all individuals were included (see Table 1c). The autocorrelation values of the residuals were mostly found to be within 95% confidence bands around zero, indicating no interference by autocorrelation. Foraging habitat selection in the main riverbed appears to be influenced by distance to roads (a proxy for disturbance) and by the river width in dependence on the function of the main riverbed (Table 2, Fig. 2). Animals preferred foraging at a greater distance to roads. In streams up to a width of 12 m, reservoirs were highly preferred over main discharge and residual waters. Once the river enlarged, reservoirs were avoided ($w(x) < 1$), while the preference for stretches with

Table 2

Two-step conditional logit over all nine animals. Significant factors are in bold.

Covariates	Beta	SD	p-Value (Wald)
Distance to road	0.063	0.031	0.020
Function of riverbed: width (Main discharge as reference category)			
Residual water: width	3.115	1.621	0.027
Reservoir: width	-2.036	1.126	0.035
Distance to dam	-0.103	0.077	0.090
River width	0.599	0.45	0.092
Algae	0.057	0.058	0.162
Distance to fishpond	-0.098	0.101	0.166
Type riparian vegetation	-0.035	0.041	0.194
Width riparian vegetation	-0.038	0.073	0.303
Function of riverbed (Main discharge as reference category)			
Reservoir	0.207	0.515	0.344
Residual water	0.288	1.285	0.411
Wood debris	0.027	0.086	0.377
Riverbank modifications	-0.002	0.038	0.474
Variability in depth	-0.002	0.054	0.483
Material bank side	0.000	0.033	0.500

main discharge and residual waters increased ($w(x) > 1$). The confidence intervals for main discharge are well above unity for rivers more than 12 m, indicating a clear selection of main discharge, given that the watercourse is broad enough.

4. Discussion

Our results show that otters cope surprising well within the human-modified landscape of the Alpine valleys. At three different scales (population, home range and within home range) otters preferred the main riverbed to remote tributaries and standing water. This highlights the importance of the main riverbed as key habitat for otters. However, contrary to our predictions, the studied otters did not show a preference for pristine sections within the main riverbed at the fine scale. Instead, they exploited heavily modified stretches and seemed well adapted to the

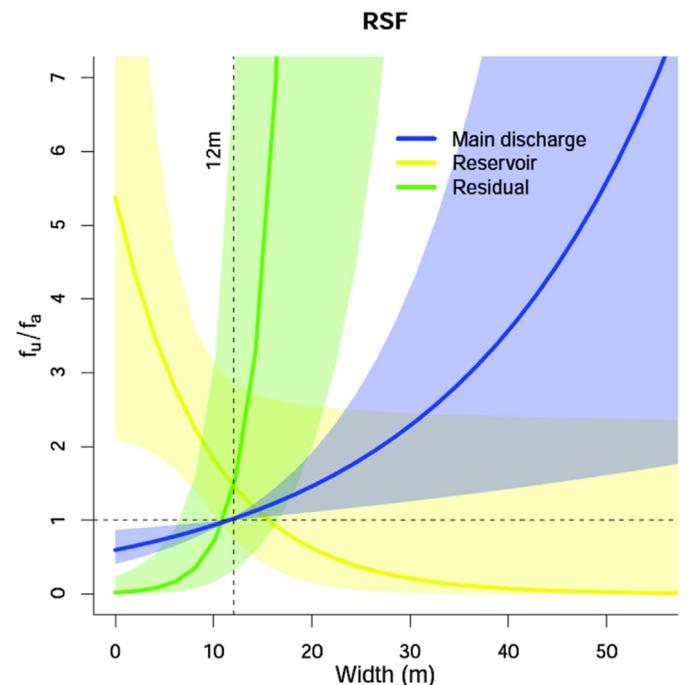


Fig. 2. Resource selection function (RSF) changing with width conditionally on each of the three habitat functions of the main riverbed (main discharge, reservoir and residual). The proportion f_u/f_a relates used and available frequencies. Shaded areas encompass all pointwise 95% confidence intervals.

altered landscape. This study provides evidence on foraging habitat selection of otters, supporting the results of the studies on prey selection by otters in human dominated landscapes (Kloskowski et al., 2013; Pedroso et al., 2014). These results show a flexible habitat selection of a threatened mammal and give a promising perspective for the recovery potential in the Alps by the expanding otter population. Our findings are also encouraging for many other areas with indications of recovering otter populations.

4.1. Effect of fish distribution on foraging habitat selection

The importance of the main riverbeds in foraging habitat selection of otters can most likely be attributed to fish abundance (Clavero et al., 2003). All of the radiotracked otters placed their home ranges along main riverbeds with a width of more than four metres but avoided the extensive network of tributaries. Otters have been shown to prefer hunting in small streams (e.g. Durbin, 1996) which is well explained as fish biomass is negatively correlated to river width (Schager and Peter, 2001). However, the negative selection of smaller streams and tributaries of otters in the Alps mirrors the state of these smaller waters: A substantial part of the tributaries are continuous or seasonal torrents, which are heavily modified for flood hazards (Merwald, 1986). The alterations disconnect those streams from the main rivers and reduce thus fish abundance.

Conversely, the change of the natural discharge of a river or stream to reservoirs and residual waters should have a negative impact on the habitat selection of otters as fish abundance is expected to be higher in natural stretches of rivers (Fette et al., 2007). River bank modifications, vegetation type and width, presence of algae and wood debris are used to identify good fish habitats (BUWAL, 1998) and were therefore used here as indicators for suitable otter habitat. Contrary to our expectations, otters living in a mosaic of altered and natural stretches of watercourses select for the modified parts.

We believe that a key reason for the preference for reservoirs is due to the unintentional food supply provided by humans. In the study area, fishing associations and private persons rent stretches of running fish waters (varying from <1 km to 10 km), where they stock fish (usually salmonid species) at any time of the year. At the release site, the increase of the fish biomass can be short-lived: stocked fish often disperse quickly downstream due to antagonistic behaviour of the resident conspecifics, low foraging efficiency, reduced stamina and a general habitat preference for open water (Weber and Fausch, 2003; Weiss and Schmutz, 1999). The strong current in streams (width < 12 m) may favour the downstream movement of hatchery-reared fish to the next reservoir. Often large shoals of fish could be observed few days after stocking events occurred upstream in the study area (I. Weinberger, pers. observation). The regime of fish stocking can thus temporarily change a prey-depleted reservoir into a rich foraging ground. Such aggregations of fish were not observed in the reservoirs of the wide rivers, possibly because stocked fish adapts more easily to the lower current of these rivers or because otters prefer to hunt in shallow waters at 0–3 m depth (Nolet et al., 1993). This would explain the negative habitat selection of reservoirs in large rivers (width > 12 m).

The selection for the residual waters is inverted to the selection of dam reservoir. Residual water is avoided when the river width is < 12 m but becomes strongly selected when wider. This is likely due to the amount of water discharge after the dam. In streams, the effect of water loss in the main riverbed is more pronounced than in rivers. Residual waters of large rivers may carry enough water in the meantime to sustain several fish species and therefore harbour more prey than streams.

Surprisingly, standing waters were negatively selected. Particularly fishponds harbour a higher fish biomass per area than the main river. Otters are known to be very attracted to fishponds (Kranz, 2000), a common source of human-wildlife conflicts. There were at least 120 managed fishponds in the study area, with many of them not effectively

protected against otter intrusion. It was unexpected to see that none was regularly visited by the studied otters. This indicates that food availability and accessibility within the watercourses is high enough for otters to sustain themselves. However, if prey density is decreasing, otters may rely more on unprotected fishponds. Thus, this endangered carnivore exhibits a behavioural plasticity in habitat use not uncommon in other carnivore species (Contesse et al., 2004; Moss et al., 2015).

4.2. Effect of human disturbance on otter habitat selection

Otters used the complete range from pristine streams to heavily modified large rivers. Contrary to the hypothesis that females choose more remote areas than males, the radio-tracked females were found in watercourses of all widths, with varying degrees of modification and human disturbance. However, the three females successfully rearing young had their territories in medium-sized streams (4–10 m width). Reproductive success may indeed be higher in less disturbed habitat, either due to a higher food availability, lower human disturbance or an avoidance of predation by conspecific males (Balme et al., 2013).

Human disturbance, expressed by distance to paved roads, played a more significant role than in other tracking studies (e.g. Durbin, 1998; Green et al., 1984). For foraging, otters chose the areas, where human disturbance was the lowest within their home ranges.

This is in accordance with other studies on carnivores, where human disturbance has been shown to shape behavioural patterns, e.g. red fox, cougar or lynx (Bouyer et al., 2015; Díaz-Ruiz et al., 2015; Smith et al., 2015).

Although the inference from a few radiotracked individuals needs to be treated cautiously, we are confident that the observed impact of human disturbance might be even more pronounced in situations with higher human pressure.

5. Conclusions and management implications

This study demonstrates that the endangered otter is among the carnivore species that appear to adapt to modified habitat and persist in human-dominated landscapes. This species copes well within semi-natural watercourses interspersed by a multitude of barriers and infrastructure for risk management and energy production. We showed that individual otters actually prefer to forage in highly modified habitats such as reservoirs and residual waters while they keep distance to human disturbance. This flexible foraging habitat selection may be the corner stone of otter expansion, particularly to areas with low disturbance by humans. Our results are highly promising for the recovery of the otter in the modern landscape of the Alps and Western Europe.

However, habitat requirements for foraging animals are strongly associated with the availability and accessibility to their main prey. Humans often alter prey abundance by husbandry and thus influence resource use by carnivores. The current regime of fish stocking seems beneficial to otter presence but, at the same time, reinforces the risk of human-wildlife conflicts. Our results suggest that as long as abundant prey is available, otters are highly tolerant of even strong modifications to their aquatic habitat. We suspect that fish stocking could be a crucial prerequisite for part of the observed preferences and may even act as a fragile driver for the currently observed geographic re-expansion of the species. However, otter densities in streams appear unaffected by stocking regime (Sittenthaler et al. 2015). Alternatively, the availability of resting sites may be another limiting factor for otter distribution in a human-dominated landscape as shown in other mustelid species (Manning et al., 2013) and needs to be explored. Contemporary efforts to restore rivers and streams may improve habitat quality and foster, in the medium term, otter recovery. Our result demonstrate that it is crucial to understand how the interplay of hydropower infrastructure and fish stocking regime influences the natural resources of predators and prey in order to manage and mitigate human-wildlife conflicts.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2016.04.017>.

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