



Human disturbance and habitat structure drive eurasian otter habitat selection in heavily anthropized river basins

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Abstract

Assessing habitat selection is essential to protecting threatened species but also to understand what factors influence species that, although globally not currently in decline, act as flagships of their ecosystems and remain highly vulnerable to human impacts, such as the Eurasian otter. This paper examines otter habitat selection at the river reach scale in two heavily anthropized river basins. Both river basins encompass a wide spectrum of human pressures and biogeographic units, which offers an excellent opportunity to assess otter responses to anthropogenic activities in different scenarios. Through two modelling approaches (structure-agnostic way and *a priori* hypothesized habitat factors) we demonstrate that otters currently inhabiting these human-dominated landscapes show a trade-off between a preference for highly productive areas and for well-structured and safe areas. We suggest that habitat simplification and human disturbance, which were of minor relevance to the dramatic decline of otter populations in the 20th century, are emerging as potential threats in the context of worldwide increasing land use intensification. Furthermore, we found that otter habitat requirements were remarkably more stringent for breeding site selection than for occurrence, particularly concerning variables related to human disturbance. The results of this work provide tools for integrating ecological criteria oriented to effective otter conservation into river management in human-dominated landscapes, as well as serving as methodological support for lowland river restorations. Our results suggest that long-term otter conservation in anthropized rivers will depend on ensuring the availability of habitat patches that maintain sufficient structural complexity away from intensely outdoor recreational activities.

Keywords Carnivore ecology · Freshwater environments · Habitat selection · Human recreation · *Lutra lutra* · Riverine habitats

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Introduction

Freshwater biodiversity is critically threatened worldwide and stresses on riverine ecosystems are increased by steadily rising human demands for water and land (Beechie et al. 2010; Strayer and Dudgeon 2010). The improvements in water quality achieved in recent years in western countries have not been sufficient for riverine ecosystems recovery (Geist 2011) and most of the investments in river habitat restoration over the last decades have failed (Bernhardt et al. 2005). Human impacts related to flow regime, river morphology, instream structure, nutrient pollution, invasive species, and longitudinal, lateral and vertical connectivity continue to compromise the ecological functioning in middle-lower river reaches throughout Europe (Meybeck 2003; Strayer 2010; Palmer et al. 2014). These impacts result in simple and artificialized river systems that have lost most of the physical, chemical, and biological processes capable of regenerating natural habitats (Sear 1994). It is not uncommon for river management to be oriented toward removing river processes and dynamics, when it is the recovery of these processes that should be the main objective of river restoration (Beechie and Bolton 1999). In consequence, 46% of all freshwater habitats are threatened according to the European Red List for terrestrial and freshwater habitats (Jansen et al. 2016) and 60% of the surface water bodies are in bad ecological status according to the biotic monitoring programme of the Water Framework Directive (EEA 2018), a percentage that would be higher if only the middle-lower river reaches were taken into account. Most of the biological indicators commonly used in biotic monitoring programmes obtain the highest values in oligotrophic upper river reaches (e.g., Simon 1999). This is because the downstream area is typically more altered by human activity than the upstream area (Grizzetti et al. 2017), but also because they are deeply different and require specific analyses and biotic indicators because e.g., they contain very differentiated ecological communities.

Although habitat loss has long been identified as the most important threat to biodiversity (Fahrig 2003), human activity steps up the processes leading to habitat degradation and fragmentation at an unprecedented rate and scale (Brooks et al. 2002). In light of accelerated habitat loss, understanding how limiting factors influence umbrella species distributions provides ecological information critical for habitat conservation and restoration (Morris 2003), as it enables the diagnosis of the biodiversity loss factors. Thus, the assessment of habitat selection, defined as hierarchical processes of scale-dependent behavioural responses which result in disproportionate use of habitat features relative to their availability (Rosenzweig 1981), is an essential part of theoretical and applied ecological research (Manly et al. 2002) vital for optimal biodiversity management and conservation (Morrison et al. 2012; Nicola and O’Riain 2017). This is especially relevant in heavily human-modified areas of threatened ecosystems, such as riverine environments, where species run into their tolerance limits (Treves and Bruskotter 2014) and emerging drivers to biodiversity loss are being identified (e.g., exotic species and human outdoor recreation).

The Eurasian otter (*Lutra lutra*, Annex II and IV of the EU Habitats Directive) is a flagship semi-aquatic mammalian top predator that inhabits a broad range of middle-lower river reaches in most of Europe and part of Asia, has large spatial requirements and is sensitive to a wide range of human impacts (Macdonald and Mason 1994; White et al. 1997; Kruuk 2006), making it a potential umbrella and target species (Bifulchi and Lodé 2005) in the increasingly widespread middle-lower river restoration projects (Bernhardt and Palmer 2011). After dramatic declines in the second half of the twentieth century, the otter

has recovered part of their European population mainly thanks to species protection and water quality improvement (Roos et al. 2015). Otter partial recovery in central and western European countries has prompted several studies that have emphasised novel aspects of its diet and distribution, highlighting its adaptability to new trophic resources and its presence in human-dominated landscapes (Barbosa et al. 2001). Otter distribution and abundance are influenced by both natural and anthropogenic factors. Some studies have proposed that the factors driving otter habitat use and breeding are mainly those related to the availability of food resources and, secondarily, shelter (Elmeros and Madsen 1999; Ruiz-Olmo et al. 2001). Some authors showed the relevance of stable, productive and complex riverine habitats (Yoxon 2000; Prenda et al. 2001; Ruiz-Olmo and Jiménez 2008) and of well-preserved riparian vegetation (Cianfrani et al. 2011; Carone et al. 2014) for otter conservation, suggesting a negative influence of human landscape modification (Clavero et al. 2010), exotic species proliferation (Dettori et al. 2022) and an avoidance of human infrastructures (Baltrūnaitė et al. 2009). In contrast, others highlighted their flexibility in habitat selection as their geographical range increases (Delibes et al. 2009) and some even suggested that their presence-absence are not a reliable indicator of habitat quality (Madsen and Prang 2001; Romanowski et al. 2013).

Although several studies have focused on Eurasian otter habitat requirements there is a lack of knowledge about what factors determine fine-scale otter habitat selection in a broad anthropogenic gradient, and its habitat constraints in anthropized areas remain widely unknown. Adequate assessment of otter habitat selection requires detailed fine-scale otter and habitat data and, at the same time, a broad spatial and temporal scale because otters have home ranges up to 40 km and can travel more than 20 km in a single day (Saavedra 2002). Drawing on this insight, studies based on insufficiently wide environmental gradients (both natural and anthropogenic) or that do not consider fine-scale habitat features may lead to erroneous, partial, or unsustainable conclusions about species-habitat relationships (Austin and Van Niel 2011). The return of the carnivores to some anthropized areas where they had been previously extirpated (Enserink and Vogel 2006) offers the possibility to understand how they interact with different anthropogenic gradients and which ones play the most important role in their distribution. In this light, our fine-scale study of Eurasian otter in the heavily anthropized Besòs and Tordera basins is a good opportunity to understand which factors drive the otter conservation in a context of a great diversity of human alterations, which are usual and/or emerging along their distribution range. This is especially relevant considering that habitat selection information on charismatic and umbrella species usually is the basis for effective habitat conservation and for developing proper management recommendations to obtain guidelines and targeted measures for habitat conservation and restoration (Yoccoz et al. 2001; Morrison et al. 2012).

This study aims to model Eurasian otter fine-scale habitat requirements in a broad natural and anthropogenic environmental gradient within a heavily anthropized context. We focused on understanding which human impacts and which habitat processes or features most influence otter habitat selection by analysing their effects on three types of otter data: occurrence, habitat use intensity and breeding. We hypothesised that some factors related to human-induced alterations that are still growing in scale and intensity in most European rivers, such as habitat structural simplification and human disturbance, could significantly influence habitat selection in heavily anthropized rivers. In relation to this, we expected to find a trade-off in otter's habitat selection whereby the avoidance of human impacts on river

habitats must be balanced with the preference for high-productivity habitats. Furthermore, we expected that otter breeding would be more vulnerable than presence to human impacts, such as riverbank modification and disturbance.

Materials and methods

Study area

We evaluated otter habitat selection using occurrence, habitat use intensity and breeding data from the Tordera and Besòs river basins, which are situated inside and around the Barcelona metropolitan area (41°25′–41°52′N, 2°05′–2°51′E, Fig. 1). There are among the most anthropized river systems across Europe. Both rise in the Montseny mountains (maximum altitude: 1712 m) and run through alluvial plains with a highly altered and fragmented ecological matrix until reaching the Mediterranean Sea. The predominant uses in the alluvial plains are residential, industrial, and agricultural. The human population density ranges from 1.5 inhabitants/km² at the headwaters to 15,000 inhabitants/km² at the Besòs river mouth. Despite their small size (1038 km² and 898 km²), both basins have a great variety of river habitats due to a combination of a great diversity of biogeographical conditions and types of human alteration on a small scale. The mosaic of heavily disturbed and well-preserved reaches adds relevance to the ecological assessment because it allows working

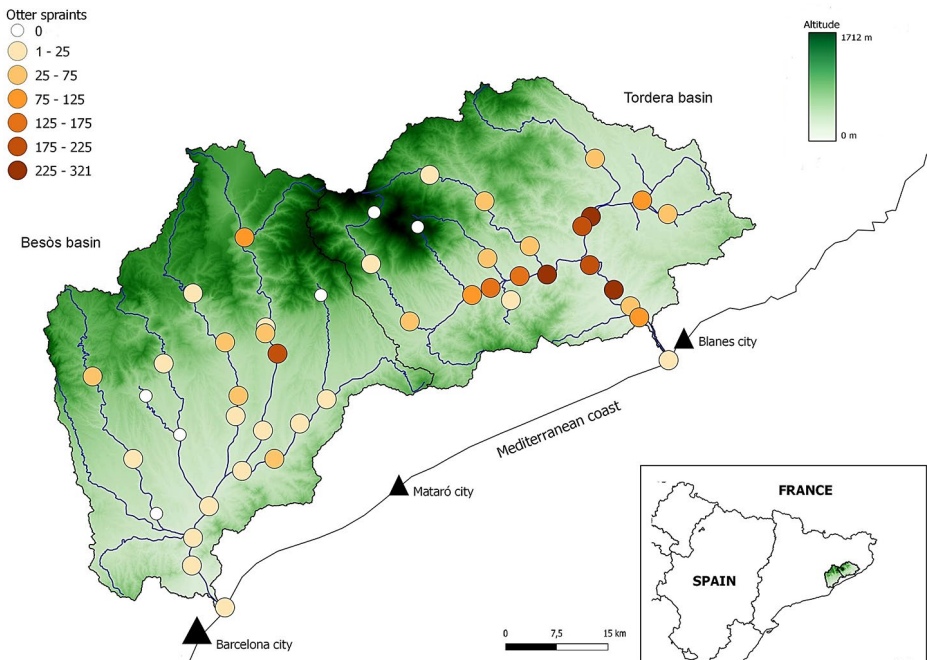


Fig. 1 Study area and location of the 47 transects where otter presence-absence and habitat use intensity otter surveys were carried out. The gradient from white to deep red represents the cumulative sum of spraints counted over the 8 sampling replicates conducted between 2019 and 2021. Symbol colour is mapped to spraints numbers at each transect during the study period

with very long environmental gradients. The human alterations include most of the impacts related to the current river habitat degradation, among others: loss of lateral and longitudinal connectivity, aquifer overexploitation, instream structure simplification, eutrophication, water pollution, recreational uses and presence of invasive species. The biogeographical conditions vary from the biological communities associated with oligotrophic and cold streams in the upper reaches to the biological communities associated with intermittent and anastomosing Mediterranean rivers in the lower reaches. The average flow is between 4 and 6 m³/s in the main courses of the two basins and varies spatially and seasonally, with severe droughts in summer and regular floods during spring and autumn. Average annual precipitations exceed 1000 mm in the upper reaches and goes down to around 600 mm near the coast.

The Eurasian otter became extinct from the study area during the second half of the 20th century, at the same time as it disappeared from many rivers in western Europe mostly due to industrial pollution and direct persecution (Roos et al. 2015). Dispersive otters have been detected in the study area regularly again since 2010, and the first instance of reproduction after local extinction was documented in 2018 (Tolrà and Ruiz-Olmo unpublished data). Thanks to a population monitoring program, we know that currently the two river basins together hold a population of about 25 otters, with an average of 3 family groups per year (2019–2021).

Data sampling

Otter data

Otter occurrence and otter habitat use intensity data were assessed by a seasonal survey of 47 transects (Fig. 1) following the methodology proposed by Macdonald and Mason 1994. Surveys consisted of searching for otter signs (spraints and footprints) along linear 600 m transects and counting all the otter spraints deposited in the sampled area. The location of transects was selected to incorporate all the representative riparian habitats of the study area, considering both the biogeographic gradient and the anthropogenic gradient. The transects were carried out between the winter of 2019 and the summer of 2021. Each transect was conducted 8 times, every season in 2019 and in winter and summer in 2020 and 2021. Therefore, in total we obtained a database with 376 surveys of otter presence and habitat use intensity in 47 different transects. Autumn and winter were classified as cold period and spring and summer were classified as warm period. To minimize biases due to otter spraint detectability and to obtain comparable data between transects, sampling was always carried out 10 days after the last day of significant rain (> 5 mm).

Although the number of spraints should be used with caution, considering dispersive movements and temporary use of trophic resources or river reaches, based on previous experience and as both older and more recent works have suggested (Jenkins and Burrows 1980; Jefferies 1986; Reuther et al. 2000; Rivera et al. 2019; Hong et al. 2020), otter recent spraints count per regular distance is an optimal indicator of otter habitat use intensity. This indicator is associated with parameters such as frequency, number, permanence, and interactions between individuals and is a commonly used monitoring approach to assess otter habitat use intensity proxies (Mason and Macdonald 1987; Romanowski et al. 2013; Sittenthaler et al. 2020).

Otter reproduction was assessed yearly (from 2019 to 2021) in Spring. It consisted of the survey of 68 transects (Figs. 2), 47 of which coincided with those surveyed to obtain the presence and habitat use otter data. In the transects where moderate-high otter habitat use intensity was detected (>20 spraints), and in adjacent areas one camera (Browning model) trap was placed. The camera traps recorded video and were maintained throughout the monitoring period to identify and analyse the movements of possible family groups. In all cases cameras were aimed in the direction of the most important latrines (accumulations of spraints) along the transect. The latrines are a primary olfactory and visual attractor for otters, so if family groups of otters are present, they are easily captured by the cameras. We defined two subcategories of otter reproduction according to the data obtained in each transect. When a family group with small cubs was regularly detected (at least 5 consecutive months) in one of the transects it was categorized as a “Breeding site”, whereas the transects where family groups were detected sporadically received the subcategory of “Family groups”. The subcategory “Family groups” includes both the transects with continuous (Breeding site) and irregular presence of family groups. Transects where no family groups were detected were classified as “No breeding” sites.

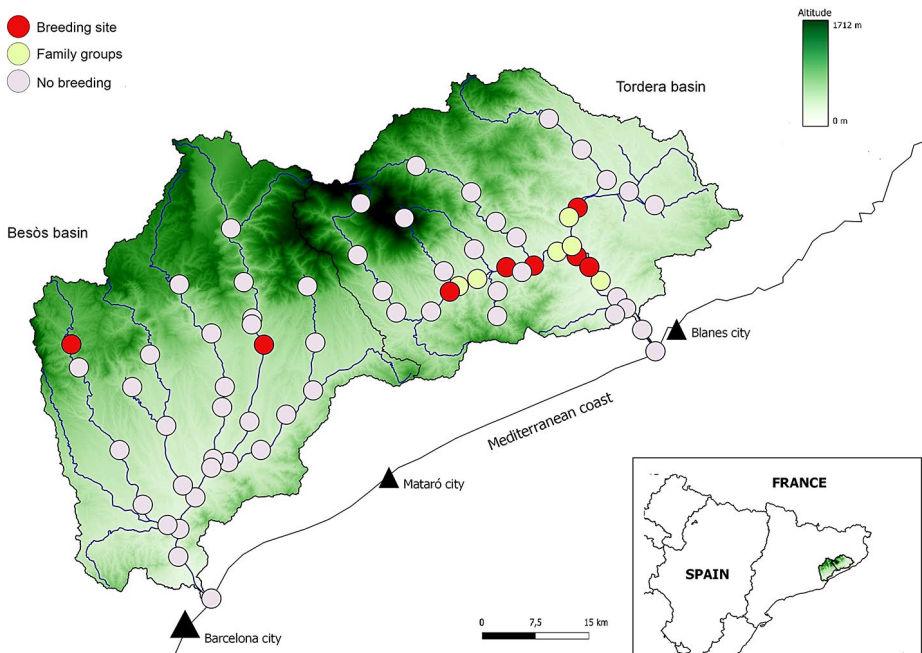


Fig. 2 Study area and location of the 68 transects where otter reproduction and habitat surveys were carried out between 2019 and 2021. Red circles indicate river reaches where constant presence of otter family groups was detected for at least 5 consecutive months and were considered otter breeding sites. Green circles indicate river reaches with irregular presence of otter family groups. Grey circles indicate river reaches without presence of otter family groups, considered non-breeding sites

Habitat measurements

A set of 22 environmental variables were collected in the same transects of 600 m where otter surveys ($n=68$) were carried out. To understand drivers of otter habitat selection we collected measurements a priori associated to three principal hypothesized latent factors at the transect scale, i.e., habitat structure, habitat productivity, human disturbance, with variables recorded as continuous values, percentages, or scores as appropriate (Table 1). Altitude, distance to the sea, distance to roads, distance to urban centres, and resident population within a 2 km perimeter were extracted from GIS layers (National Database and Digital Elevation Model 2×2 m) using ArcGIS v 10.6 Software (ESRI 2011). Field measurements of habitat variables were performed in 2020 during the spring, when environmental conditions are most representative of each river reach. Habitat variables recorded on site were water

Table 1 Variables recorded in the sampling transects and used to explain the Eurasian otter habitat selection, including their unit, code and range

Environmental variables (unit)	Code	Range
Altitude (m)	ALT	0 to 788 m
Distance to sea (km)	DSEA	0 to 58.79 km
Water temperature (°C)	TEMP	10.4 to 19.6 °C
Water conductivity (µS/cm)	COND	32 to 542 µS/cm
Average channel depth (cm)	DEPTH	10 to 85 cm
Average channel width (m)	WIDTH	2 to 40 m
Flow velocity (1–5)	VELOC	Predominate slow waters to predominate fast waters
Large woody debris (1–10)	DEBWOOD TRIBU	Absence of large woody debris within riverbed to >10 of large woody debris within riverbed
Tributaries and wetlands (1–10)	FORM ISLARM	Absence of tributary streams and wetlands within 1 km around the transect to >1 important tributary stream and a wetland within the transect
River form (1–10)	POOL	Linear riverbed form to >2 meandering curves and abundance of moderate curves
Islets and arms (1–10)	REFU	Absence of islets and arms to >10 medium-sized arms (length 8–35 m) and >5 large-sized arms (length >35 m)
Pools (1–10)		Absence of >1 m depth pools within the riverbed to >10 pools within the riverbed
Riverbank refuges (1–10)		Heavily altered riverbanks without refuges to riverbanks with an abundant refuge (shrubs, large woody debris, roots, rock systems, etc.)
Distance to urban centres (m)	DURB POPU	20 to 3620 m 0 to 200,000 inhabitants within 2 km perimeter
Human population (1–10)	ACCSHUM	Absence of roads, paths and riverbed accesses to roads or paths on both riverbanks with two regular riverbed accesses
Human accessibility (1–10)	DROAD	1 to 4270 m
Distance to roads (m)		
Tree cover (%)	VEGARB	0 to 100%
Helophytic cover (%)	VEGHELO	0 to 30%
Exotic vegetation (%)	VEGEXO	0 to 100%
Water permanence (1–10)	STAB	Minimum 15 days completely dry to permanent flow with a minimum depth of 60 cm
Aquatic vegetation (1–15)	VEGAQU	Absent surface and bottom aquatic vegetation to abundant surface and bottom aquatic vegetation

temperature (°C), water conductivity ($\mu\text{S}/\text{cm}$), channel depth (cm), channel width (m), flow velocity (score range: 1–5) large woody debris (score 1–10), tributaries and wetlands (score 1–10), river form (score 1–10), islands and arms (score 1–10), pools (score 1–10), riverbank refuges (score 1–10), human accessibility (score 1–10), tree cover (%), helophytic cover (%), exotic vegetation (%), aquatic vegetation (score 1–15) and water permanence (score 1–10). Water temperature and water conductivity were measured using a YSI® parametric probe as the average of two measurements along the 600 m sampled. Channel depth and channel width were estimated as the average of three measurements representative of the sampled transect.

Statistical analysis

Significant differences in habitat characteristics between otter-present and otter-absent river reaches and between breeding and non-breeding river reaches were tested using two-sample Wilcoxon tests in order to identify which habitat variables from the complete dataset were relevant for otter breeding and presence. Afterwards we tested for correlation in habitat variables using the Spearman coefficient to reduce redundancy in the dataset ($r \geq 0.65$), because the results of regression models may be affected by correlation among the covariates (Dormann et al. 2013).

To model otter habitat selection, we took two different but complementary approaches. The first approach aimed to model the relationships between otter and the main, *a priori* hypothesized habitat gradients or factors in anthropized rivers, i.e., productivity, habitat structure and human disturbance, using dimensionality reduction techniques to obtain appropriate latent scores for each of these three groups of variables, which were then used in a regression framework. The second approach aimed to analyse the relationships between otter and predictor variables in a structure-agnostic way, i.e., without imposing an *a priori* structure to the candidate variables. To do this, we entered all predictors into a variable selection procedure to obtain sets of the most parsimonious models using the information-theoretic approach (Burnham and Anderson 2002).

For the first modelling approach, principal component analysis (PCA) was used to reduce the dimensionality of the three groups of environmental variables to obtain appropriate scores for the latent habitat factors. Our interest was in the additive effect of the main human disturbance and habitat structure variables expected to have an impact on otter habitat selection. Thus, PCA was performed separately on the three data matrices: human disturbance (3 variables), habitat structure (5 variables), and biogeographical (11 variables). The broken stick model, which was used to identify the optimal number of principal components of each PCA (Jackson 1993), suggested that one component was appropriate in all three cases. The three habitat factors thus obtained were used for otter habitat selection modelling. Relationships between otter data and habitat factors were analysed using mixed-effects generalized linear models (GLMM; McCullagh and Nelder 1989) with transect and year random effects as needed to control for pseudoreplication. Two-way interactions were included in the models when found statistically significant in likelihood ratio tests. Models were fitted to the negative binomial distribution (after overdispersion was detected) to evaluate the relationship of the habitat factors to otter habitat use intensity (i.e. spraint counts). The variable «Period» (cold vs. warm) was included in all GLMM models for occurrence and habitat use intensity. GLMMs with binomial error distribution and logit link were used to estimate

the strength of the associations between habitat factors and otter occurrence and between habitat factors and otter family groups. Due to the small number of otter breeding sites, this subcategory was not included in the habitat factor analyses.

For the second modelling approach, multimodel inference based on the Bayesian information criterion (BIC) was used to identify which habitat variables best explained otter habitat selection. The BIC selects more parsimonious models compared to Akaike's information criterion (AIC) and helps reduce the number of variables for interpretation purposes (Johnson and Omland 2004; Grueber et al. 2011). We developed a set of candidate models for otter occurrence and for otter habitat use intensity using the uncorrelated habitat variables ($r \leq 0.65$). We ranked candidate models using BIC weights. Models with the highest weight were better supported and explained more variance. Only candidate models with ≤ 2 BIC value compared to the best model were considered (Burnham and Anderson 2004). GLMM with negative binomial distribution was used to assess the association between covariates and otter habitat use intensity data, whereas GLMM with binomial error distribution and logit link function was used to assess the associations between covariates and otter occurrence. As above, all models included the variable «Period» (warm vs. cold) and transect random effects on the intercept. Model selection was done by exhaustive search among all model with up to five predictors (including Period) and no interactions. Due to the limited number of otter reproduction cases, the associations between covariates and both breeding sites and family groups occurrence were evaluated using univariate logistic models. For each type of breeding data, we represented and tested the significance of the predictor variables by means of a chi-squared test and assessed the goodness of fit of the models with McFadden's pseudo- R^2 . McFadden's pseudo- R^2 values from 0.2 to 0.4 indicate good model fit (Hensher and Stopher 1979). Spatial autocorrelation of model residuals was assessed by visual inspection of residuals on spatial plots, and with Moran's I, permutation tests, and Moran scatterplots using package *spdep*. We did this on separate GLM models per period and year, and generally found no convincing evidence of spatial autocorrelation to warrant more complex models.

All statistical analyses were performed in R version 4.3 (R Development Core Team, 2010) using the packages *lme4* (Bates et al. 2015) and *vegan* (Oksanen et al. 2019).

Results

Otters were detected in 220 of the 378 surveys conducted over the study period. The average spraints number per transect was 7.45 and the maximum spraints number per transect was 67. Between 2019 and 2021, 11 otter family groups were identified in the study area. These family groups as a whole regularly occupied 8 river reaches (breeding sites) and, including those visited irregularly, in total occupied 14 river reaches (Fig. 1). We found significant differences in the Wilcoxon test between habitat variables of breeding and non-breeding sites and between habitat variables of presence and absence sites (Table 2). The results showed differences between breeding and presence-only sites. Otters generally occurred in middle and lower river reaches, with greater water width and water depth, lower flow velocity, and high aquatic vegetation and helophyte cover. They also showed a clear preference for river reaches with high values for variables related to both riverbank and instream structure. Human population and distance to urban centres were not significant for otter presence,

Table 2 Comparison and statistical differences of habitat variables on otter breeding and non-breeding sites and otter presence and absence sites. Values represents means and standard errors. P-values are the result from two-sample Wilcoxon test between otter breeding and non-breeding sites and otter presence and absence sites

	Otter reproduction		Otter occurrence		Wilcoxon test (p)	
	Breeding	No breeding	Presence	Absence	Breeding	Presence
Distance to sea (km)	24.56±2.93	25.85±1.66	25.16±0.71	27.51±1.17	ns	ns
Altitude (m)	119.25±43.12	156.75±23.23	118.47±6.32	238.41±21.41	ns	p<0.001
Channel depth (cm)	42.06±7.57	28.42±2.33	34.32±1.36	31.68±1.70	p<0.01	p<0.001
Channel width (m)	10.06±2.43	7.65±0.97	8.83±0.46	7.85±0.76	ns	p<0.001
Human accessibility (index)	3.25±0.45	5.28±0.29	4.78±0.13	5.87±0.16	p<0.05	p<0.001
Distance to urban centres (m)	1563.75±227.234	935.02±129.30	861.31±49.75	959.68±91.50	p<0.05	ns
Human population (index)	1.25±0.23	2.73±0.18	2.57±0.08	2.68±0.13	p<0.01	ns
Distance to roads (m)	192.62±99.35	190.53±76.07	121.59±16.11	125.54±23.65	ns	ns
Tributaries and wetlands (index)	6.50±0.96	4±0.36	5.36±0.21	3.15±0.20	p<0.05	p<0.001
Large woody debris (index)	8.38±0.50	4.53±0.24	5.57±0.14	3.84±0.14	p<0.001	p<0.001
River form (index)	6.63±0.62	3.47±0.26	4.59±0.16	2.49±0.09	p<0.001	p<0.001
Islands and arms (index)	6.88±0.76	3.77±0.28	4.74±0.16	2.95±0.13	p<0.01	p<0.001
Pools (index)	9.13±0.12	6.32±0.21	7.02±0.11	6.61±0.14	p<0.001	p<0.05
Riverbank refuges (index)	5.88±0.12	3.12±0.16	3.79±0.10	3.06±0.09	p<0.001	p<0.001
Water permanence (index)	7.75±0.41	5.46±0.36	6.24±0.18	5.97±0.22	p<0.05	ns
Tree cover (%)	6.50±0.33	5.50±0.43	5.30±0.18	5.75±0.28	ns	ns
Helophyte cover (%)	5.87±0.61	4.38±0.30	5.14±0.15	4.44±0.19	ns	p<0.01
Exotic vegetation (%)	4.50±0.50	6.10±0.29	5.71±0.13	5.64±0.21	p<0.05	ns
Water temperature (°C)	16.59±0.44	16.13±0.31	16.36±0.13	15.76±0.24	ns	ns
Water conductivity (µS/cm)	525.50±96.64	557.23±44.48	577.99±21.21	597.55±29.50	ns	ns
Flow velocity (index)	2.37±0.32	2.95±0.14	2.62±0.06	3.23±0.09	ns	p<0.001
Aquatic vegetation (index)	10.88±0.77	8.37±0.42	9.43±0.19	8.44±0.30	p<0.05	p<0.05

whereas human accessibility was significantly lower in river reaches with presence of otters. In contrast, for otter breeding, all three variables related to human disturbance showed a significant negative effect. Tree cover, distance to roads, distance to sea, and variables related to the physicochemical water characteristics were not determinants for both otter breeding and presence. Water permanence values did not change significantly between presence and absence sites whereas showed higher values at breeding sites than at non-breeding sites.

Relationships between otter and key habitat factors

Key habitat factors that were extracted from each data matrix were human disturbance (explained 68.33% of the matrix variance), habitat structure (explained 55.43% of the matrix variance), and habitat productivity (explained 39.78% of the matrix variance). High values of the human disturbance factor corresponded to river reaches with high human accessibility close to urban centres in areas with high human population densities. High habitat structure values corresponded to river reaches with a heterogeneous river form and abundance of large woody debris, pools, riverbank refuges, and islands and arms. High values of habitat productivity corresponded to slow flow velocity river reaches with high water temperature and conductivity and with abundant aquatic vegetation. Loadings are shown in Table 3.

Multiple regression models revealed the importance of these three habitat factors (Fig. 3; Table 4). Both otter occurrence and habitat use intensity increased in environments with high habitat productivity, low human disturbance, and high habitat structural complexity (p-value: <0.01 in all cases), with particularly strong responses at low disturbance and high productivity, as shown by the negative interaction of these two factors in both models. Both otter habitat use intensity and occurrence were significantly (p-value:<0.001) higher in the cold period (autumn and winter). The probability of family groups responded to the same habitat characteristics, with a particularly significant association to the habitat structural complexity (p-value:< 0.01, $z=2.79$). These results indicated that, in addition to the productivity natural gradient, otter habitat use was mostly limited by human disturbance and structural simplification.

Relationships between otter and habitat variables

Five models were found with substantial support ($\Delta\text{BIC} \leq 2$ compared to the best model) for predicting otter habitat use intensity (Table 5). Models combined structure, productivity, and human disturbance variables. Specifically, these models included two habitat structure variables, two habitat productivity variables, and one human disturbance variable. All four models also included period (cold or warm season), showing its importance for otter space use. The best fitting mixed effects generalized linear models showed that the otter habitat use intensity increased significantly (p-value: <0.05) with increasing river form, large woody debris, and tributaries and wetlands, and decreased with increasing water velocity and human accessibility (Fig. 4). In the case of otter occurrence, only two models stood out, with a BIC well below 2 units of other models. They included one habitat structure variable, two habitat productivity variables and, unlike the otter habitat use intensity models, did not include any human disturbance variables. The period of the year was also a decisive variable in otter distribution. The best fitting mixed effects generalized linear models showed that the

Table 3 Factor loadings for each habitat variable and first principal component accumulated variation for each data matrix

Parameter	Human disturbance	Habitat structure	Habitat productivity
	Factor1 (68.33%)	Factor1 (55.45%)	Factor1 (39.78%)
DURB	-0.861		
POPU	0.928		
ACCSHUM	0.669		
DEBWOOD		0.766	
FORM		0.856	
ISLARM		0.729	
POOL		0.521	
REFU		0.805	
ALT			-0.665
TEMP			0.879
VELOC			-0.784
VEGARB			-0.755
VEGHEL			0.635
VEGEXO			0.335
VEGAQU			0.846
STAB			0.041
TRIBU			0.368
DROAD			-0.213
CONDU			0.747

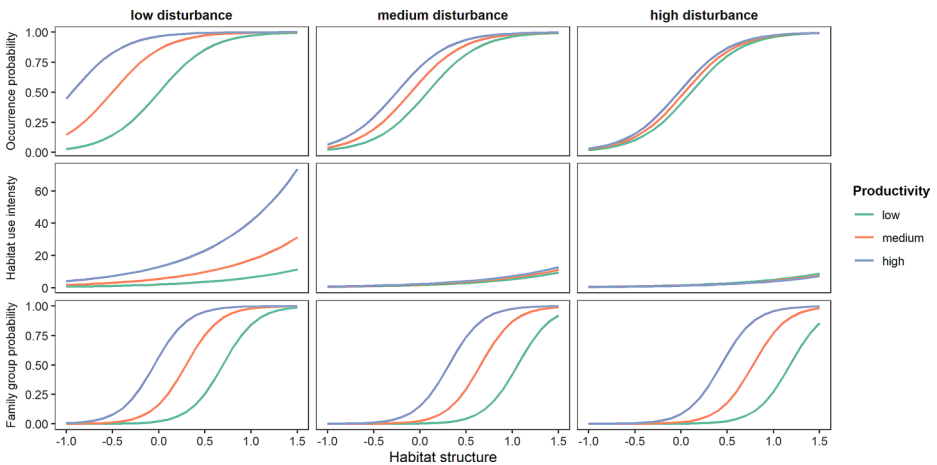


Fig. 3 Model predictions of occurrence probability, habitat use intensity, and family groups occurrence of otter in the warm period in relation to key habitat factors. Habitat structure factor is on the x-axis, with prediction for human disturbance (columns) and habitat productivity (colour) at their first, second (median) and third quartiles

Table 4 Results of mixed effects generalized linear models for predicting otter occurrence and habitat use intensity, and of generalized linear models for family groups in the study area. Period (cold or warm) was included as a fixed factor in the habitat use intensity and occurrence data. Transect ID was included as a random factor in the habitat use intensity and occurrence data. Binomial error distribution was used to model occurrence and family groups data and negative binomial distribution was used to model habitat use intensity data

	Coefficient	Std. error	z value	p value
<i>OTTER OCCURRENCE</i>				
Intercept	0.581	0.430	1.349	0.177
Human disturbance	-2.195	1.128	-1.947	0.052
Habitat structure	3.572	0.992	3.599	<0.001
Habitat productivity	2.057	0.692	2.974	<0.01
Period: Cold period	2.525	0.394	6.412	<0.001
Disturbance-Productivity interaction	-4.385	1.449	-3.026	<0.01
<i>OTTER HABITAT USE INTENSITY</i>				
Intercept	0.909	0.219	4.149	<0.001
Human disturbance	-1.553	0.554	-2.804	<0.01
Habitat structure	1.158	0.421	2.748	<0.01
Habitat productivity	0.890	0.340	2.615	<0.01
Period: Cold period	1.019	0.133	7.647	<0.001
Disturbance-Productivity interaction	-3.142	0.790	-3.975	<0.001
<i>OTTER FAMILY GROUPS</i>				
Intercept	-3.479	1.070	-3.252	<0.01
Human disturbance	-3.479	1.552	-2.242	<0.05
Habitat structure	5.626	2.017	2.789	<0.01
Habitat productivity	4.229	2.061	2.052	<0.05

Table 5 Model-selection statistic by BIC criterion for the otter habitat use intensity and otter occurrence. Only candidate models with $BIC \leq 2$ compared to the best model are shown

Δ	Model predictors	BIC	Weight
<i>OTTER OCCURRENCE</i>			
	Period+FORM+VELOC	315.621	0.42
	Period+FORM+VELOC+TRIBU	317.302	0.18
<i>OTTER HABITAT USE INTENSITY</i>			
	Period+FORM+VELOC	1827.68	0.24
	Period+TRIBU+FORM+VELOC	1828.23	0.18
	Period+ACC-SHUM+TRIBU+FORM+VELOC	1828.69	0.14
	Period+ACCSHUM+FORM+VELOC	1828.80	0.14
	Period+DEBWOOD+FORM+VELOC	1829.63	0.09

otter occurrence probability increased along with increasing river form, and tributaries and wetlands and decreased with increasing water flow velocity.

Otter breeding key habitat variables

Four habitat structure variables were the best-supported predictors ($p < 0.05$ & McFadden’s pseudo- $R^2 > 0.2$) of the otter breeding probability, both for breeding sites and for presence of family groups (Fig. 5). These were riverbank refuges, large woody debris, and river form. In this light, otter breeding habitats were characterized by structurally well-preserved

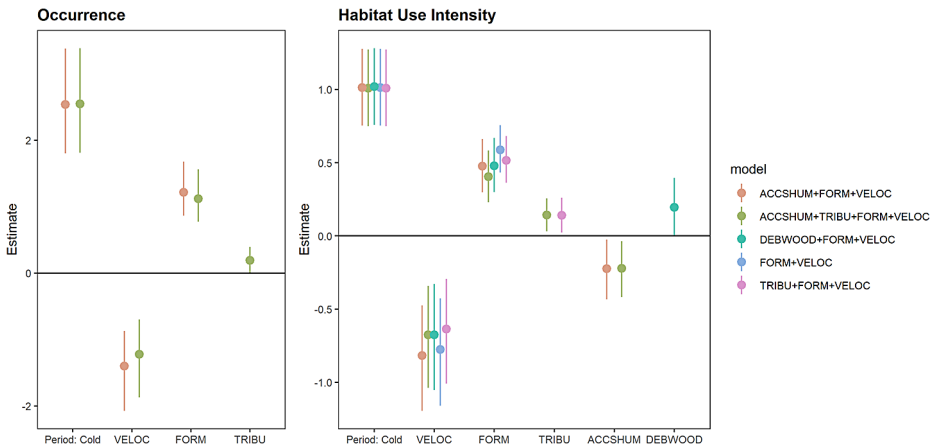


Fig. 4 Models with substantial support ($\Delta BIC \leq 2$ compared to the best model) for predicting otter occurrence and otter habitat use intensity. The estimates of the predictors of the best models are shown (left: occurrence, right: habitat use intensity). Each colour corresponds to a different model. Period was included in all models

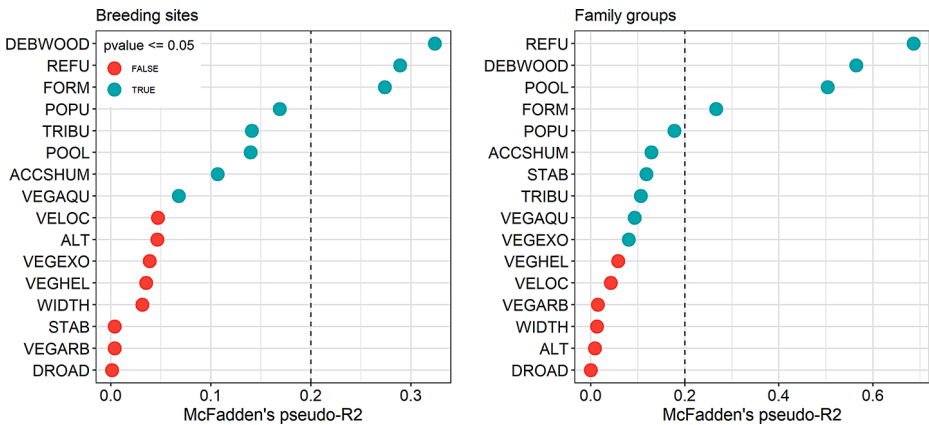


Fig. 5 Univariate logistic models between breeding sites and predictors (left) and family groups and predictors (right). Red circles represent non-significant variables ($p > 0.05$) and blue circles represent variables with significant associations ($p < 0.05$). X-axis represents McFadden's pseudo- R^2 values. The vertical dashed line crosses the x axis at $R^2 = 0.2$

river reaches with a high amount of large woody debris within the riverbed, abundance of pools, presence of riverbank refuges (also including amounts of large woody debris), and a complex river form close to those configured by river natural dynamics (meandering). Pool abundance had a more prominent role on the presence of family groups, as judged by its R^2 .

In addition to these four key breeding variables, there were other significant ($p \leq 0.05$) but less well-supported ($McFadden's\ pseudo-R^2 < 0.2$) variables. Both human accessibility and the resident human population significantly affected otter breeding, which even when selecting productive river reaches with abundant aquatic vegetation, moved away from the more human-populated and accessible river reaches. The availability of wetlands and rel-

evant tributaries was also linked to both breeding sites and otter family groups occurrence, while water permanence and exotic vegetation were slightly associated with family groups, with these selecting river reaches with sufficient habitat stability and avoiding areas with a higher predominance of exotic vegetation (Fig. 6).

Discussion

Our results suggest a strong anthropogenic influence on European otter habitat selection in human-dominated landscapes. According to our hypothesis, we found a clear trade-off in otter habitat selection. Otters preferentially selected high biological productivity habitats, generally found in higher-order river reaches and low-elevation areas (Matthews 1998), but concurrently avoided fine-scale human disturbance and habitat structural simplification, which also occurred more intensely in middle and lower river reaches. As a result, otters generally established in lowland adequate habitat patches within an unsuitable habitat matrix. Although otters were present in lower reaches, all breeding sites and core areas were conglomerated in middle reaches. This preference for the middle over lower reaches is

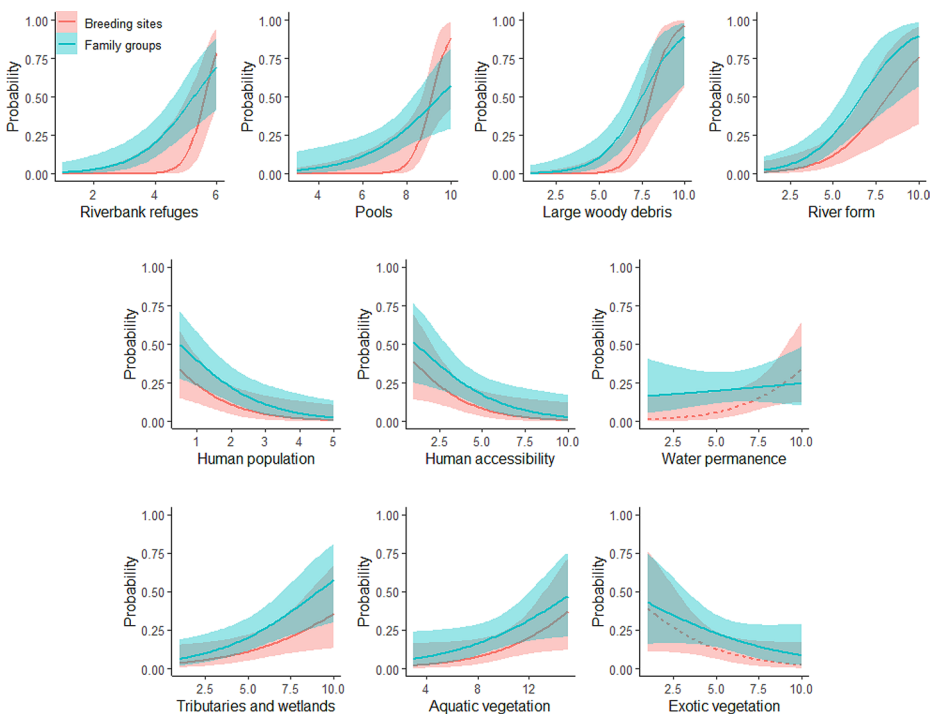


Fig. 6 Effects of riverbank refuges, pools, large woody debris, river form, human population, human accessibility, water permanence, tributaries and wetlands, aquatic vegetation and exotic vegetation from generalized linear models on otter breeding sites (red) and otter family groups (blue). Shown are predicted values (line) and 95% confidence limits. The top panel row shows the most supported associations ($p < 0.05$ & McFadden's pseudo- $R^2 > 0.2$). Non-significant variables for both breeding sites and otter family groups are not displayed. Non-significant associations are shown with a dashed line. For more details, see Fig. 4

consistent with findings in other anthropized areas (Calzada et al. 2022; Clavero et al. 2010; Marcelli and Fusillo 2009) but does not correspond to what would be expected in natural or less-altered river basins, where otters breed near river mouths (Saavedra 2002). Thus, although the mitigation of the prevailing restrictions on otter presence over the last century (i.e., organochlorinated pollutants and direct persecution, Kruuk 1995) has allowed otters to recolonise some regions in Europe (Marcelli et al. 2012; Ros et al. 2015), our results point out that in human-dominated riverscapes otters are still heavily constrained, both geographically and population-wise, by human-induced factors.

To our knowledge, this is the most comprehensive analysis of the otter habitat selection in human-dominated landscapes, contributing to fill a knowledge gap on the impact of current human-induced habitat alterations on otter distribution. While some studies have explored which landscape and coarse resolution variables may constrain otter distribution in human-dominated areas (Clavero et al. 2010; Marcelli and Fusillo 2009), our work has aimed to understand the drivers of the otter habitat selection at the river reach scale (Austin and Van Niel 2011) by emphasising fine-scale features underlying river landscapes and human pressures. Our results suggest that some factors identified as determinants for otters in studies based on coarser habitat data may have masked fine-scale factors more directly involved in otter habitat selection.

On the other hand, most previous studies used only otter presence-absence data (e.g., Barbosa et al. 2001; Madsen and Prang 2001; Prenda et al. 2001; Romanowski et al. 2013), which have substantial limitations and can bias habitat selection models of wide-ranging species (Gese 2001), especially when annual and season replication is insufficient. Owing to their opportunistic foraging behaviour (Clavero et al. 2003), otters may use feeding grounds that would not sustain a sedentary population and occasionally visit sites relatively far from their core areas. Given their large daily and seasonal spatial requirements, otters must cross non-suitable habitats around or between high-quality habitat patches (Sulkava et al. 2007). Thus, due to the combination of high mobility and intense marking activity, with dozens of spraints daily deposited at conspicuous sites (Carss et al. 1998; Reuther et al. 2000), otters are usually detected in river reaches that are close to source areas regardless of their habitat characteristics. In this light, presence-absence data may overestimate otter populations resulting in errors or biased conclusions on their habitat preferences. In addition, our results suggest that during the cold period otters extend their home range, probably due to a combination of reduced food accessibility and greater energy requirements to balance their metabolism and heat loss (McNab 1989). We found an effect of season on otter habitat use intensity and occurrence, with a significantly broader distribution in autumn and winter (72.34% presence surveys) than in spring and summer (44.84% presence surveys). Seasonal variations in otter distribution could significantly affect the accuracy and comparability of the presence-absence data depending on the time of year it is obtained. To avoid biases, our study is based on a four-year series of seasonal (cold and warm periods) surveys, including both occurrence and a proxy of habitat use intensity data. In addition, we incorporated reproduction assessment.

Habitat structure drives otter habitat selection

The strong influence of habitat structure on otters revealed by our analyses probably is related to the fact that a high habitat structural complexity offers more diverse foraging and

resting opportunities and is associated with higher biodiversity than homogeneous environments (MacArthur 1970). Otters mainly use the interface between aquatic and terrestrial habitats (Kruuk 1995). Therefore, they require that both riparian and riverbed areas have appropriate structural characteristics within their home range. Within the riparian area, riverbank refuges played a major role in otter distribution and habitat use intensity and, together with large woody debris and river form, were also the most relevant habitat features for the selection of breeding sites in our study area. Thus, consistent with other studies that emphasise the relevance of riparian quality habitat for otters (Elmeros et al. 2006; Kruuk 2006; Weinberger et al. 2019), our results suggest that otters require a sufficient extent of well-structured riparian habitats, providing secure resting sites, protection from high floods, natal den substrates and complementary trophic opportunities. Regarding the riverbed area, otters preferred river morphologies closer to those generated by natural physical dynamics, avoiding channel incision and human-induced simplification. River hydrogeomorphic processes and river-floodplain connectivity are linked with the river form and instream structure (Frisell et al. 1986; Newson and Large 2006), which in turn are connected with diversity and abundance of ecological niches and freshwater biodiversity (e.g., Harvey and Clifford 2008) and therefore with greater accessibility to trophic resources for otters. Although hydro-geomorphologic integrity has widely recognised effects on biodiversity and functioning of river ecosystems (e.g., Eloisegi et al. 2010) surprisingly little research has previously suggested associations between riverbed structural complexity and otter habitat selection at the reach scale level (but see Ruiz-Olmo and Jiménez 2008; Scorpio et al. 2016). The strong association between otters and well-structured habitats in our study area might be enhanced by the intensive channel straightening and structure simplification that occurs in large proportions of the lower-middle river reaches in the Besòs and Tordera basins, suggesting that otters tend to concentrate their activity in local, well-structured habitats patches within a less-suitable, structurally simplified habitat matrices.

As integral elements of instream structure, stream pools and large woody debris contributed to explaining all aspects of otter habitat selection and were particularly relevant for breeding site selection. Large woody debris is a recognised key component of river aquatic habitats since it promotes stepped-channel profiles, pool habitats, energy flow dissipation and organic matter accumulation, and overall provides high levels of physical diversity (Bilby and Likens 1980; Brooks et al. 2004; Roni et al. 2015), and are associated to increases in river fish, amphibian and invertebrate populations (Thevenet and Stutzner 1999; Dolloff and Warren 2003; Kail et al. 2007; Schneider and Winemiller 2008; Thompson et al. 2017; Dalbeck et al. 2020), which are the main prey for otters (Mason and Macdonald 1986; Krawczyk et al. 2016). The link between otters and large woody debris could be particularly relevant in low and medium-flow river reaches, where this feature has an even greater role in shaping habitat structure and local ecosystem functioning (Dominguez and Cederholm 2000; Anlanger et al. 2022).

For its part, the major role of pools in our study area is consistent with Delibes et al. 2000 and Ruiz-Olmo et al. 2007, who suggested an association between otters and pools in Mediterranean ecosystems during the dry season. Stream pools are a relevant feature for freshwater biodiversity as their availability increases the heterogeneity of depth, flow velocity, and riverine habitats, especially in fast-flowing areas, which contribute to increased biological productivity and prey populations (e.g., Matthews 1998; Pollock et al. 2003; Cunningham et al. 2007; Smith and Mather 2013). Moreover, especially in intermittent

streams, stream pools increase the abundance and resilience of aquatic and semi-aquatic fauna in low-water level scenarios (Magoulick and Kobza 2003; Davey and Kelly 2007; Beesley and Prince 2010) and increase habitat stability during the dry season (Magalhães et al. 2002), which was identified as critical for otter breeding in Mediterranean rivers by Ruiz-Olmo and Jimenez 2008. Therefore, the relevance of pools for otters could be particularly prominent in low-flow or intermittent rivers, which are progressively spreading in Europe due to drought intensification and aquifers overexploitation for irrigated agriculture (Dudgeon et al. 2006; Rupérez-Moreno et al. 2016; Marx et al. 2018).

River habitat features can vary considerably on a fine-scale (Gostner et al. 2013), shaping a river reach-scale mosaic of simple and more complex habitat structure. Our analyses suggest that, if sufficient longitudinal connectivity is maintained, otter home ranges in human-dominated riverscapes might consist of well-structured habitat patches interspersed among poorer-quality habitats. In this light, even though our results show that the highest occurrence and, above all, the highest activity and breeding probability were concentrated in well-structured habitats, otters occurred regularly in suboptimal habitats. This may partially explain the incongruences with studies that found otters in apparent low-quality areas, such as feeding grounds in heavily simplified river reaches, and even the exploitation of human-made niche opportunities found for Weinberger et al. 2016 in the Alps, or the use of poorly structured habitats by inexperienced and low-fitness individuals suggested by Ruiz-Olmo and Jimenez 2008. On the other hand, considering that the success of source populations in well-preserved habitat patches may trigger an expansion into sink populations in poorer habitats (Baltrūnaitė et al. 2009; Delibes et al. 2009; Clavero et al. 2010; Romanowski et al. 2013) it must take into account that the time of recolonisation and the source-sink population dynamics can be relevant factors in the spatial habitat exploitation by the species (Pulliam 1988). In this regard, although otter recolonisation in our study area started more than 15 years ago and the population numbers, abundance and distribution have stabilised (Tolrà and Ruiz-Olmo unpublished data), if the most structured habitat patches allow good individual recruitment, it is possible that in the future some of the less-fit individuals may be displaced, and even attempt to breed, in more poorly structured habitats. Future work is needed to disentangle interactions between otter habitat selection, population size and recolonisation time.

Human disturbance constrains otter habitat selection

We found a general pattern in which otters selected areas furthest from human settlements and with lower human population density within high-order river reaches. Our results are consistent with some studies (e.g., Baltrūnaitė et al. 2009; Romanowski et al. 2013; Weinberger et al. 2019) that suggested otter sensitivity to human disturbance in addition to the factors related to environmental gradients, but contrast with other studies that found no significant relationships (e.g., Madsen and Prang 2001). Inconsistencies between studies are most likely due to poor representativeness of low anthropized areas and the application of different scales or proxies to assess human disturbance, which may bias results because each type of disturbance may have unique effects (Suraci et al. 2021). Focusing only on one proxy of human disturbance may lead to erroneous conclusions (Nickel et al. 2020). For example, distance to roads or houses was used as the only proxy for human disturbance in some studies (Durbin 1998; Weinberger et al. 2016; Juhász et al. 2013), whereas

otters were not affected by distance to roads on our study, but were influenced by other human disturbance-related variables. Thus, although roads are currently the principal cause of human-induced mortality for otters (Grogan et al. 2001; Hauer et al. 2002), our results suggest that fine-scale otter habitat selection is not affected by infrastructures that do not lead to increased habitat frequentation or modification. However, we found that noticeably affected by human accessibility, which was the most relevant human disturbance-related variable for otters in our study.

Avoidance of high human-accessible river reaches suggests that otters, like other apex carnivores (Ordiz et al. 2021), are noticeably affected by outdoor recreational activities in human-dominated landscapes. Although high availability of adequate resting and breeding structures may increase otter tolerance of human disturbance (Macdonald and Mason 1994), our analyses suggest that high levels of human accessibility might prevent otter reproduction and establishment regardless of habitat quality because of their risk perception. This is consistent with Weinberger et al. 2019, who demonstrated that the availability of non-disturbed resting sites is a fundamental requirement for otters. The importance of human accessibility to otters may have been overlooked until recently because otters shape their space use by balancing the costs and benefits of the available habitats (Travis and Dytham 1999) and may use different river reaches with different characteristics for feeding grounds and resting (Sulkava 2007) so that otters exploit large areas and can regularly visit high human accessibility reaches where trophic resources are abundant, but have stronger selection against this risk at breeding and resting sites. This is analogous to other carnivores such as wolves, lynxes, and bears, which also avoid human areas especially during daytime (Ordiz et al. 2017; Ripari et al. 2022; Salvatori et al. 2023), and consistent with the fact that human disturbance can promote spatiotemporally varying habitat selection (Richter et al. 2020), in which the nocturnal activity resulting from temporal segregation would allow for spatial coexistence to some extent (Gaynor et al. 2018). In that sense, at the population level, otters might be unaffected by the existence of localised high human-accessible river reaches (e.g., near villages or fishing places) that they would avoid for resting and breeding, and instead be strongly affected by large-scale human accessibility (e.g., extensive riverwalks).

Otter breeding in human-dominated riverscapes

As mentioned above, due to the species high seasonal and daily mobility (Sulkava et al. 2007), otter data occurrence does not discriminate between river reaches used recurrently by floating individuals or constant transit between different habitat patches, and the otter core areas. Therefore, especially if we consider habitat requirements are more stringent for breeding than for non-breeding individuals, the conservation measures aimed at enhancing otter occurrence need not be useful for promoting otter breeding. Females with cubs have high energetic demands (Elmeros and Madsen 1999), requiring high accessibility to trophic resources (Ruiz-Olmo et al. 2001), and are very vulnerable to disturbance and predation (Durbin et al. 1996), thus being more food-limited and refuge-dependent than other individuals. Our findings show how breeding habitat selection by otters is strongly influenced by human pressures in human-dominated landscapes, resulting in a trade-off between preference for highly productive areas, situated in the lower and middle river reaches, and avoidance of structural habitat simplification and human-made disturbance. Thus, despite otters can inhabit heavily anthropized areas at coarse scales and have relative habitat plasticity

for foraging (Mason and Macdonald. 1986; Kruuk 1995 and Durbin et al. 1996), have strict fine-scale habitat requirements for cubbing and den establishment area selection.

Although Weinberger et al. 2019 indicated that otter resting site selection is strongly associated with high riparian vegetation cover, our analyses revealed that otters might be more flexible in their requirements for vegetation cover, which could have masked the association with high structural complexity in previous studies. In our study females with cubs were associated with river reaches with riverbanks harbouring numerous refuges, riverbeds with abundant large wood debris and pools and with channel morphologies closer to those generated by natural physical dynamics. The fact that habitat stability and abundance of stream pools appeared to be more relevant for river reaches with family groups presence than in family core areas could indicate that females tend to carry their cubs outside natal den river reaches in areas with lentic habitats and permanent water availability, where trophic resources are more accessible and abundant throughout the year. This is consistent with studies carried out in less anthropized areas (e.g., Ruiz-Olmo et al. 2005), suggesting a general pattern.

Otters avoided river reaches close to urban centres and densely populated areas for reproductive activities but displayed no explicit aversion when dispersing or foraging. Therefore, we suggest that otter-perceived interaction risk with humans shapes their breeding habitat selection in human-dominated landscapes. The preference for low human disturbance river reaches for reproduction is consistent with the results of Beja 1996. Otters were more deterred by distance to urban centres than by roads, adapting their fine-scale spatial behaviour to their perception of the landscape of fear, showing an evident avoidance of human-accessible areas, but being indifferent to infrastructures that do not involve impacts on habitat or increased human frequentation. According to the predation risk allocation hypothesis (Lima and Bednekoff 1999), roads could act as a predictable risk that, once built, has no added impacts within the habitat, whereas human accessibility poses a recurrent unpredictable risk within the breeding habitat. Suggesting that otters could breed relatively close to human infrastructures if sufficiently secure and well-structured habitat patches are available, so that localised human accesses to habitat (e.g., fishing points) might impact otter breeding habitat selection less than extensive riverwalks, which generate large-scale disturbances. Human disturbance effects on otter reproduction might be intensified by the increasing presence of domestic dogs, numerous in our study area, which impact has been widely demonstrated for several species (e.g., Banks et al. 2007; Hughes et al. 2013) but requires further studies to properly assess its effect on otters. In this light, we encourage future studies to further investigate breeding habitat selection on a small-scale involving other anthropized river landscapes and larger numbers of breeding females.

Implications for conservation and management

Our findings indicate that increasing habitat structural simplification and outdoor recreational activities, although not the main factors of otter decline in the past century (Clavero et al. 2010; Roos et al. 2015) and still secondary role in some low anthropized areas (Delibes et al. 2009), may be emerging as threats for otters in lowland riverscapes situated in heavily anthropized areas. However, efforts to preserve European river habitats have so far focused above all on water quality and concentrated on oligotrophic and headwater environments (Schindler et al. 2016) leaving floodplains and their riparian habitats largely unprotected

(e.g., McCluney et al. 2014; Globevnik et al. 2020). Thus, for otter recovery and prevalence, it is necessary to provide instruments that enable and encourage governmental institutions to establish novel conservation measures to protect and restore the lowland river processes and biodiversity. We believe that our study can contribute to this by guiding river management focused on the conservation of otters in human-dominated scenarios, as well as to prevent future declines in currently less anthropized riverscapes.

The preference of otters for well-structure river reaches underlines the importance of preserving riverbanks, instream structure and natural geomorphological dynamics. This requires avoiding the river straightening and bank stabilisation that are detrimental to the multiple benefits provided by lateral connectivity, which induces the creation of riverbank refuges and promotes complex riverbed forms through processes of erosion, sedimentation and meandering (e.g., Paillex et al. 2009). Furthermore, river management should rule out the removal of instream structures (e.g., large woody debris) from the riverbed and riverbanks, which is still promoted by some European river management agencies, as these elements have direct benefits for otter foraging, by constituting habitats with abundant and accessible prey (Anlanger et al. 2022), and as refuges, by providing resting and breeding sites. Drawing on this insight, habitat creation or restoration to enhance sinuosity and floodplain reconnection, reintroduce instream structures, or recover wetlands well-connected to the river systems will have relevant positive effects on otter populations, even though more superficial actions such as the construction of artificial refuges or the planting of riparian vegetation will have vague repercussions since which do not address the root causes of habitat degradation. Moreover, due to the role of wetlands as refuges and their importance for breeding (Juhásk et al. 2013), their maintenance and restoration could also be decisive for the otters in these contexts. On the other hand, our results suggest that the promotion of new riverwalks and recreational activities sites, a now usual practice in European anthropized rivers due to their attractiveness for human leisure activities (Winter et al. 2019), could lead to a drastic reduction of suitable otter resting and breeding areas through increased human frequentation and loss of refuge structures in the riverbank. Considering these, the construction of extensive riverwalks should be limited in anthropized areas, where without regulation some local authorities may extend them along the entire middle and lower river reaches.

In human-dominated landscapes, comprehensive river restoration is often not feasible due to the existence of human activities and infrastructures that disrupt ecological processes (e.g., Monk et al. 2019) and the societal demands to recreationally enjoy the natural areas (e.g., Michel et al. 2021). Our findings showed that in heavily anthropized areas otter persist may not be compatible with human activities uniformly distributed in the riverscape. Nevertheless, we demonstrate that otters can persist if they have access to habitat patches that meet their specific requirements. In this light, to make river conservation and human activities compatible in heavily anthropized basins, we suggest that a feasible formula could be to promote segregation and mosaic of river section roles. The functional mosaic could combine areas with concentrated human disturbance with river reaches with management measures to restrict outdoor recreation, such as complete closure to the public or road closures in specific time windows (Whittington et al. 2019), together with management schemes that promote habitat structural complexity and natural river morphodynamics. These protected river reaches, which could be called otter micro-reserves due to the flagship character of the species (Kruuk 2006), would comprehensively benefit the riverine biodiversity because

otter is subject to common threats with many riverine biodiversity representatives to low-land river reaches, being considered an umbrella species (Bifolchi and Lodé 2005).

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Author contributions Arnau Tolrà: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing – Original Draft, Visualization, Project administration, Funding acquisition Jordi Ruiz-Olmo: Methodology, Resources, Writing - Review & Editing, Funding acquisition Joan Riera: Software, Formal analysis, Visualization, Data curation, Writing - Review & Editing.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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