RESEARCH ARTICLE

Potential of restored gravel pits to provide suitable habitats for Eurasian otters in anthropogenic landscapes

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In anthropogenic landscapes, which are usually characterized by the existence of highly heterogeneous patchworks of habitats with different conservation status, restored gravel pits have the potential to play a conservation role for semiaquatic species such as Eurasian otters (*Lutra lutra*). Here, we report an otter habitat suitability analysis on a complex fluvial system in an anthropogenic landscape to understand the role of different artificial water bodies (i.e. irrigation channels and ditches) and natural water bodies (i.e. rivers) related to a restored gravel pit lagoon system as providers of suitable habitats for otters. We implemented seven sampling campaigns during 2016 and 2017 consisting of 19 transects across all existing types of water bodies. We integrated 34 environmental variables with otter habitat use, measured by three spraint marking intensity indicators. We found that otter use of water bodies was not related to the natural or artificial origin of the water. Three key factors influenced habitat suitability: riparian vegetation tree cover, forestland use (either natural or planted) within 100 m from the banks, and the level of human disturbance. Our results suggest that otters' tolerance of human activities might be lower in key areas of their territory compared to areas they pass through or explore. We argue that restored gravel pit lagoon systems can potentially play a role in providing suitable habitats for otters in anthropogenic landscapes.

Key words: environmental factors, habitat suitability, human disturbance, lagoon system, *Lutra lutra*, wildlife conservation

Implications for Practice

- Local actions related to the restoration and/or maintenance of tree cover (natural or planted) in riparian vegetation and within 100 m from watersides seem to favor use of habitats by otters.
- Local actions at the gravel pit lagoon systems, such as the reduction of bankside steepness, can improve suitability of restored habitats for otters.
- Human disturbance is a key limiting factor in otters' use of water bodies and therefore should be managed in restoration projects; it can be buffered by vegetation cover.
- Restorations of gravel pit lagoon systems should consider their connectivity with the surrounding fluvial system and the availability of suitable habitats in the landscape; small water infrastructure features can be used to improve connectivity.

Introduction

Anthropogenic landscapes are the result of land-use changes due to agriculture, urban development, and other human activities to harvest natural resources (mining, timber industry, water management, etc.). These activities cause degradation and fragmentation of natural landscapes, thereby affecting biodiversity and modifying ecosystem function and structure (Fahrig 1999; Czech et al. 2000). Consequently, populations of native wildlife

might be affected by the reduction of suitable habitats and threatened by varying degrees of human disturbances in most of the remaining habitats. Nevertheless, the highly heterogeneous patchwork of anthropogenic habitats can offer new opportunities for some species (McKinney 2002; Grimm et al. 2008). For example, it has been seen that some species prosper in novel environments created in urban and anthropogenic areas, which are characterized by predictable anthropogenic food for generalist mammals such as foxes (*Vulpes vulpes*; Wandeler et al. 2003) or raccoons (*Procyon lotor*; Gross et al. 2012). Furthermore, some generalist mammals which were pushed out of many areas

Author contributions: DM-C, MDJ, RdT conceived and designed the research; DM-C, L.C, MDJ, RdT performed field works and experiments; DM-C, RdT analyzed the data; all authors wrote and edited the manuscript.

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doi: 10.1111/rec.13129

Supporting information at:

<http://onlinelibrary.wiley.com/doi/10.1111/rec.13129/supinfo>

of Western Europe by human activity during the twentieth century are recovering and expanding their home ranges to occupy anthropogenic habitats, as the case of the Eurasian otter (*Lutra lutra*, L.; “otters” hereafter) (e.g. Marcelli & Fusillo 2009; Clavero et al. 2010).

Otters have a wide distribution, with a range that covers parts of Europe, Asia, and Africa (Roos et al. 2015). They adapt well to a wide variety of aquatic habitats, such as highland and lowland lakes, rivers, streams, marshes, swamp forests, or even coastal areas (Mason & Macdonald 1986). Therefore, otters constitute a case of a species that can potentially adapt to habitats with different degrees of human disturbance. Nonetheless, during the last third of the twentieth century, otters suffered a sharp population drop and their distribution shrank (Roos et al. 2015). Today, otters are classified as “Near Threatened” with overall decreasing trends in their populations, according to the 2019 World Conservation Union red list of threatened species. However, in the last decades in Western Europe, and in particular in the Iberian Peninsula, the recovery of otter populations and the range expansion of their distribution have been well documented (Conroy & Chanin 2000; Clavero et al. 2010). The reduction of water pollution and the increase of prey availability have been pointed out as potential drivers for the recovery of this species (e.g. Roos et al. 2001; Almeida et al. 2012a). In Spain, invasive crayfish species (*Procambarus clarkii* and *Pacifastacus leniusculus*) have been shown to be a key component of otter diets in anthropogenic landscapes and suboptimal habitats, fostering the recovery of otter population in these areas (Barrientos et al. 2014; Bueno-Enciso et al. 2014). Indeed, human alteration of freshwater habitats sometimes provides said habitats with similar ecological characteristics to central stretches of rivers (i.e. calm water and high density of prey). References in the scientific literature reveal that otters’ use of anthropogenic habitats, such as dams and smaller reservoirs (e.g. Ruiz-Olmo et al. 2005a; Pedrosa et al. 2007), ponds (e.g. Ruiz-Olmo & Jiménez 2009), river-canal systems (Kloskowski et al. 2013), rivers in urban settings (e.g. Sleeman & Moore 2005), and irrigation channels (e.g. Ruiz-Olmo et al. 2005b), is not uncommon.

To carry out effective recovery plans, it is important to identify suitable areas along the expansion range where the target species can establish and disperse, so that these areas can be targeted for conservation and restoration actions (Klar et al. 2008; Guisan et al. 2013). The management of endangered species often relies on habitat suitability modeling to design strategies for species conservation (Hirzel et al. 2011). In the Mediterranean region, otter habitat suitability analyses have mainly focused on well-conserved and natural areas (Robitaille & Laurence 2002; Prigioni et al. 2007; Clavero et al. 2010).

A paradigmatic example of human-related habitats that species could recolonize is the case of restored areas previously degraded by human activity, as restored gravel pits. Gravel pits are usually located in river valleys where the water table is high and where aggregate extraction often leads to the emergence of water bodies. These artificial areas offer a great opportunity for nature conservation, since restoration and reclamation of areas affected by mining activities is compulsory in many European countries (i.e. Directive 2010/75/EU). There are many examples

in the literature where the application of ecological restoration, as well as appropriate management and landscape planning, can minimize the negative effects of human-dominated landscapes on biodiversity (e.g. Hobbs & Harris 2001) or even completely restore the community structure of the managed habitat (e.g. Noël et al. 2011; Emmrich et al. 2014). Different types of restoration can have different consequences on the biodiversity enhancement. For example, Šebelíková et al. (2019) studied restored coal mines in Central Europe and found that plant species richness was higher on spontaneously revegetated sites than in sites restored following forestry reclamation methods. Moreover, the restoration of gravel pits and open mining sites have been usually reported to progressively increase local biodiversity, for example for birds (Šálek 2012), amphibians (Vojar et al. 2016), and bats (Kerbirou et al. 2018). There are even occasions where natural spontaneous succession may facilitate gravel pit restoration (e.g. Rehounkova & Prach 2007).

In this article, we aimed to understand the potential role of restored gravel pits in providing suitable habitat for otters in anthropogenic landscapes. In particular, we studied the environmental features of the area used by otters across a variety of water body types present within the study area, which included a lagoon system within a partly restored gravel pit, an irrigation channel, small ditches, and the Duero River. In addition to the environmental features, we gave special attention to the natural or artificial origin of the water bodies analyzed. Given the otter common use of anthropogenic habitats discussed above, we expected to find that otter use of water bodies would not depend on the water body type but on its environmental features such as riparian vegetation cover, pools’ presence, shelter availability, and human disturbances (e.g. López-Martín et al. 1998; Clavero et al. 2010; Teresa et al. 2014). Specifically, we aimed to answer the following questions: (1) Which environmental factors influence otter habitat use in anthropogenic landscapes? (2) Can restored gravel pits provide suitable habitats for otters compared to other types of water bodies in anthropogenic landscapes?

Methods

Study Area

This study was carried out in an area located in northwestern Spain, approximately 10 km away from the city of Valladolid. The area consists of a complex fluvial system in an anthropogenic landscape which includes a restored lagoon system in its center within an active gravel pit with standard features. The lagoon system consisted of 10 lagoons of different sizes, which were the results of the restoration of the old pit-face that took place between 1998 and 2010. Restoration actions occurred as the pit-face progressed. Today, the closest lagoon is 1.2 km away from the active pit-face, and the furthest is 2 km away. Restoration actions consisted of the stabilization of lagoon slopes by flattening the shores and planting trees around them. Poplars (*Populus* sp.) and to a lesser extent pines (*Pinus pinaster*) were used. Waterside riparian vegetation cover was left to restore naturally. As a result, the tree structure around the lagoons is very heterogeneous both spatially and demographically, ranging from almost absent to tree buffer

areas of more than 100 m wide. Since the restored lagoon system is part of an active gravel pit, public access is forbidden during nonbusiness hours, when only the gravel pit land owners and a few occasional fishermen access it.

The restored lagoon system belongs to a complex fluvial system that comprises the Duero River in its middle course (40 m of approximate average width, a.a.w.), a large irrigation channel (built in 1886; 6 m a.a.w.), and a ditch (0.5–1 m a.a.w.) that connects the irrigation channel with the river, crossing the west end of the gravel pit (Fig. 1). The Duero River flows parallel to the irrigation channel 1 km away from the south edge of the gravel pit. The irrigation channel flows through the north edge of the gravel pit

and has a sidewalk, which is often used by walkers, bikers, and fishermen. The channel sides are fully covered with natural vegetation and are relatively well conserved as one moves away from the urban areas.

According to CORINE Land Cover (CLC 2012), agriculture and urban (i.e. cities, towns, and industrial area) occupied 45 and 15% of the surface in our study area, respectively (Fig. 1D). Around one third of the area (35%) is forested, mainly by pine trees (*P. pinaster*) in plantations dedicated to crude resin extraction. To a lesser extent, we also found riparian forests (mostly *Salix* sp. and *Populus* sp.), poplar plantations (*Populus* sp.), and oak dehesa forests (*Quercus ilex*) at different levels of preservation.

Figure 1. Study area. (A) Location of Valladolid Province in Spain; (B) location of the study area within Valladolid Province; (C) fluvial system of the study area and location of the gravel pit lagoon system; (D) land use adapted from CLC (2012) categories. Numbers in brackets indicate the percentage of each use in the whole area.

Figure 2. Location of the 19 sampling transects in the study area. The box on the top left zooms in the gravel pit lagoon system transects. Transects 1–6 are located in the Duero River, 7–12 in the irrigation channel, 13–18 in the gravel pit, and transect 19 in a ditch.

Sampling Design

Transects. We performed 19 transects (600 m long) following a standard method for otter surveys (Reuther et al. 2000), in all water body types present in the area, including artificial lagoons, the Duero River, irrigation channels, and ditches (Fig. 2). Transects were arranged as follows: six transects in six different lagoons in the gravel pit lagoon system, six in the Duero River, six in the irrigation channel, and one in the ditch. To consider the otter dispersion home range for Mediterranean ecosystems (20–40 linear km), we placed the sampling transects within 15 km around the gravel pit (Ruiz-Olmo et al. 1995; Saavedra 2002). Therefore, the study size area consisted of 30 linear km in both the Duero River and the irrigation channel, and the approximately 2 km² of the restored gravel pit lagoon system.

Sampling Campaigns. We carried out seven sampling campaigns in two consecutive years: during April to July of 2016 and May to July of 2017. In each campaign, two experienced observers (i.e. DM-C and RdT) walked every transect, one behind the other, searching for spraints (i.e. otter feces). Spraint location was registered with a handheld global positioning system. All spraints found were removed to avoid double counting in following campaigns.

Otter Habitat Use

We used spraint marking intensity to infer habitat use intensity by otters as suggested by several authors (e.g. Guter et al. 2008; Ben-David 2013). Otter spraints are usually deposited in prominent and/or visible locations and can be either left isolated or in the same site, forming latrines. Latrines have been highlighted as indicators of important sites for otters in terms of habitat use, resource availability (Kruuk 2006; Sulkava 2006; Guter et al. 2008), and social interactions (Rostain et al. 2004; Kalz et al. 2006; Barocas et al. 2016). To test if

environmental features affected the density of latrines and isolated spraints differently, we defined the following three spraint marking intensity indicators:

- (1) *Spraint marking site intensity*: the number of spraint marking sites per 600 m. Marking sites were considered independent if ≥ 1 m apart (Fusillo et al. 2007).
- (2) *Latrines marking intensity*: number of latrines per 600 linear m. We considered sites with ≥ 3 spraints as latrines.
- (3) *Isolated spraint marking site intensity*: number of marking sites with one or two spraints per 600 m.

Habitat Characterization

We evaluated the effect of 11 groups of environmental variables consisting of 34 attributes (Table S1), which were selected based on previous otter habitat suitability studies (e.g. Robitaille & Laurence 2002; Ruiz-Olmo et al. 2005b; Prigioni et al. 2007). Specifically, the variable groups referred to bankside type, bankside structure, channel material, width, number of pools and tributaries, riparian vegetation cover within 5 m from the banks, aquatic vegetation cover, land use within 100 m from the banks, human disturbances, and distance to roads. We also recorded the type of water body (natural vs. artificial).

The value of both riparian vegetation cover and human disturbances was calculated as the average of the visual estimate carried out by two experienced observers (i.e. RdT and LC) every 200 m of the transect once per year. For the riparian vegetation cover variable, observers estimated the percentage of herbaceous, bush, tree, and bare soil cover within 5 m from the banks. Land-use variables represented the land-use cover (i.e. percentage of agriculture area, forests, highways and roads, industrial, meadows, urban, urban green areas, and water bodies) within 100 m from the banks. Land uses and distance to roads were calculated using Geographical Information Systems (ArcGIS 10.2.2) based on the CLC 2012 database. Human disturbance was defined as a

numerical discrete variable with four potential values: (0) none or very rare, (1) occasional, (2) usual, and (3) common disturbance. Table S1 includes a detailed description of the levels of human disturbance variables.

In addition to the environmental variables described above, we defined the following numerical discrete variables to account for potential sources of sampling errors when modeling spraint marking intensity (Table S2):

- *Detection difficulty*, which considers the difficulty of detecting otter spraints, due to the riparian vegetation cover and the structure of the bank, which account for observer errors.
- *Accessibility difficulty*, which considers the difficulty that otters encounter when accessing the banks of water bodies, accounting for animal errors (i.e. absence of or low spraint marking not due to habitat quality, but to bank access difficulty).

We used a difficulty scale that ranged from 0 (no difficulty at all in finding spraints or accessing the bank) to 3 (high difficulty). Similar to riparian vegetation cover, both variables were visually estimated once per year by the same two observers for each 200 m of transect. The final value is the average of all those estimates.

Data Analysis

Habitat Suitability Modeling. We performed a habitat suitability analysis to determine the effect of the environmental features of the surveyed transects on the intensity of use by otters, measured by their spraint marking intensity. The analysis specifically accounted for the type of water body (i.e. natural vs. artificial) to understand the role that restored gravel pit lagoon systems could play on providing otter habitats in anthropogenic landscapes. We used zero inflated (ZI) models, which are very common in animal ecology studies when the number of zeros in the dependent variable is higher than what could be expected (Wenger & Freeman 2008; Zuur et al. 2009). Not accounting for that excessive number of zeros could result in unreliable coefficient estimates and over-dispersion. The distribution of our data fulfilled this condition: we found false zeros at a rate of 24% (i.e. transects where no spraints were found in a given sampling campaign but were found in the other), which is above the expected proportion of zeros in a Poisson distribution simulated from our data (3.6%).

ZI models have two parts: a logit model that predicts excess zeros, and a Poisson (or Negative Binomial) count model. In this way, ZI models allow differentiation between true and false zeros. In our case, true zeros were those that are due to habitat characteristics (such as otters not sprainting in a given transect because of the poor habitat quality). False zeros could be due to observer errors (such as the observer missing some spraints) and/or animal errors (wherein the habitat is suitable, but the otter is not present).

We tested both zero-inflated Poisson (ZIP) GLM and a zero-inflated Negative Binomial (ZINB) GLM models. Both approaches use a binomial GLM to model the likelihood of

getting false zeros and then a Poisson distribution (ZIP model) or a negative binomial distribution (ZINB model) to model the likelihood of getting the rest of the values (including true zeros). The *glmmTMB* package of R software was used for the analyses. The log-likelihood, Akaike information criterion (AIC), and Bayesian information criterion (BIC) were used to select the model that best fit the data. In addition, models were validated by plotting the residuals and ensuring that there were no residual patterns.

We tested the effect of all environmental variables characterizing the habitat in ZI models (Table S1). We found high correlation among *Land use* variables and also among *Riparian vegetation cover* variables (Tables S3 & S4). Therefore, to avoid collinearity problems in the models both *Land use* and *Riparian vegetation cover* were included in the models as gradients which were determined using two separated principal component analyses (PCA). PCA were conducted using the *FactoMineR* package in R software. According to the PCA results (Table S5), the gradients that best describe the riparian vegetation cover within 5 m from the water's edge were: (1) the *Tree-Baresoil gradient* (principal component 1; 58.5% of variance explained, coordinates on PC of tree coverage [16.0], bush coverage [5.1], herbaceous coverage [9.1], bare soil coverage [−16.0]), and (2) the *Tree-Herbaceous gradient* (principal component 2, 26.9%, coordinates on PC of Tree coverage [10.9], bush coverage [3.0], herbaceous coverage [−11.4], bare soil coverage [5.4]). The gradients that best describe the land-use coverage within 100 m from watersides were: (1) the *Forest-Agriculture gradient* (principal component 1, 57.1%, coordinates on PC of agriculture area [−22.2], forest area [24.4], urban area [−3.3]), and (2) the *Urban gradient* (principal component 2, 39.2%, coordinates on PC of agriculture area [−14.2], forest area [−10.7], urban area [21.3]).

Additionally, considering the uneven spatial distribution of sampling transects (Fig. 2), we evaluated the potential existence of autocorrelation. We calculated Moran's Index, using the *Ape* package of R software, for the three intensity indicators in each sampling campaign. No autocorrelation was found in any case; therefore spatial variables were not included in the models.

To specifically explore if there were differences in spraint marking intensity among water body type (i.e. lagoon, river, irrigation channel, and ditch) and water body origin (i.e. natural or artificial) we tested the effect of seldom variables as fixed effects categorical variables in the models. We included the variable *sampling campaign* as a random effect in the model, to remove the spraint marking intensity variability associated to seasonal and annual effects (e.g. seasonal otter behavior, weather, water level, prey availability, and more). Finally, we also tested the potential effect of lagoon restoration date, and the age of the channel by including an *age* variable in the models.

Results

We found 438 spraint sites (188 latrines and 250 sites with one or two spraints) across the seven sampling campaigns. There was a remarkable variability in all spraint marking intensity indicators between and within transects across sampling campaigns

Figure 3. Average (gray points) and SD (bars) otter spraint marking locations intensity across water body types (blue bars; “artificial” water bodies correspond with lagoon, channel, and ditch transects, and “natural” water bodies correspond with river transects), transects (green), and sampling campaigns (red).

(Fig. 3; Table S6). Both the highest (*Spraint marking site intensity* $\bar{X} \pm \text{SD}$ across sampling campaigns: 13.7 ± 3.8 ; *Latrines marking intensity*: 7.9 ± 3.5 ; *Isolated spraint marking site intensity*: 6.0 ± 2.9) and the lowest values for the three indicators were found in lagoon transects (*Spraint marking site intensity* $\bar{X} \pm \text{SD}$ across sampling campaigns: 0 ± 0 ; *Latrines marking intensity*: 0 ± 0 ; *Latrines marking intensity*: 0 ± 0).

Habitat Suitability

According to the log-likelihood, AIC, and BIC the best otter habitat suitability models were the ZINB models. The models showed that the same habitat variables had a significant effect on the three marking intensity indicators (Table 1) and that neither of the spraint marking intensity indicators were related to the type of water bodies (natural vs. artificial) (Fig. 3). High riparian vegetation tree coverage and forest land use within 100 m from banks had a positive effect on spraint marking intensities. *Tree-Herbaceous riparian vegetation cover gradient* had a positive effect on all marking intensity indicators: 0.061 ± 0.012 for *Spraint marking sites intensity*, 0.038 ± 0.018 for *Latrines marking sites intensity*, and 0.064 ± 0.015 for *Isolated spraint marking site intensity*. Similarly, the *Forest-Agriculture gradient* had positive effect on “Spraint marking sites intensity” (0.041 ± 0.010), on “Latrines marking sites intensity” (0.047 ± 0.014), and on “Isolated spraint marking

site intensity” (0.031 ± 0.013). Conversely, *Urban land use* had a negative effect on all marking intensities (-0.049 ± 0.012 [*Spraint marking sites intensity*], -0.063 ± 0.019 [*Latrines marking sites intensity*], -0.041 ± 0.014 [*Isolated spraint marking site intensity*]). Finally, *Human disturbance* had a negative effect on *Intensity of marking sites* (-0.356 ± 0.167) and *Intensity of latrines sites* (-0.716 ± 0.259) but no effect was found on *isolated spraints intensity*. In addition, *Human disturbance* had interaction effects on land use and riparian cover vegetation gradients, reducing the positive effect of both *Tree-Herbaceous riparian vegetation cover gradient* and the *Forest-Agriculture land use and Urban gradients*. This interaction effect was found for the three spraint marking intensity indicators. On the top of the above-mentioned habitat variables effect we observed that *Spraint marking sites intensity* and *Isolated spraint marking site intensity* tended to decrease slightly among sampling campaigns as the year progressed (Fig. 3). Finally, *bankside height* had a negative effect on all spraint marking intensities. The rest of the environmental variables tested (incl. restoration dates) had no significant effect on the ZINB models. Specifically, we found no association between marking intensity indicators and water body type (i.e. ditch, irrigation channel, gravel pit lagoons, and river) or water body origin (i.e. natural or artificial).

Regarding the modeling of false zeros, the binomial GLM component of ZINB model showed that the *Tree-Herbaceous riparian vegetation cover gradient* had a positive effect on the

Table 1. Results of the zero inflated negative binomial other habitat suitability models. Only significant parameters are shown. No effect of water body type (natural vs. artificial) was found. NS, not significant.

Parameters	Spraint Marking Sites Intensity (no. of spraint marking locations per 600 m)			Latrines Marking Sites Intensity (no. of latrines per 600 m)			Isolated Spraint Marking Site Intensity (no. of marking sites with one or two spraints per 600 m)		
	Estimate $\pm$ SE	Z value	p value	Estimate $\pm$ SE	Z value	p value	Estimate $\pm$ SE	Z value	p value
Count model coefficients (negative binomial with logit link)									
(Intercept)	2.420 $\pm$ 0.330	7.331	<0.001***	2.060 $\pm$ 0.517	3.989	<0.001***	1.683 $\pm$ 0.413	4.074	<0.001***
Habitat variables									
Tree-herbaceous gradient	0.061 $\pm$ 0.012	5.161	<0.001***	0.038 $\pm$ 0.018	2.107	0.035*	0.064 $\pm$ 0.015	4.445	<0.001***
Forest-agriculture gradient	0.041 $\pm$ 0.010	4.073	<0.001***	0.047 $\pm$ 0.014	3.328	<0.001**	0.031 $\pm$ 0.013	2.411	0.016*
Urban gradient	-0.049 $\pm$ 0.012	-4.231	<0.001***	-0.063 $\pm$ 0.019	-3.259	<0.001***	-0.041 $\pm$ 0.014	-3.001	0.003**
Disturbance	-0.356 $\pm$ 0.167	-2.132	0.033*	-0.716 $\pm$ 0.259	-2.767	0.006**	-	-	NS
Tree-herbaceous gradient * disturbance	-0.031 $\pm$ 0.007	-4.753	<0.001***	-0.022 $\pm$ 0.01	-2.298	0.022*	-0.031 $\pm$ 0.008	-3.794	<0.001***
Forest-agriculture gradient * disturbance	-0.022 $\pm$ 0.006	-3.495	<0.001***	-0.024 $\pm$ 0.009	-2.766	0.006**	-0.017 $\pm$ 0.008	-2.229	0.026*
Urban gradient * disturbance	-0.022 $\pm$ 0.005	-4.379	<0.001***	-0.025 $\pm$ 0.008	-3.031	0.002**	-0.021 $\pm$ 0.006	-3.479	<0.001***
Bankside height	-0.510 $\pm$ 0.100	-5.073	<0.001***	-0.420 $\pm$ 0.168	-2.491	0.013*	-0.448 $\pm$ 0.121	-3.703	<0.001***
Random effects									
Sampling campaign	0.02446	0.1564	SD	Variance		SD	Variance		SD
Zero inflated model coefficients (binomial with logit link)				<0.0001		<0.0001	0.003826		0.06186
(Intercept)	-	-	NS	-	-	-	-	-	NS
Detection difficulty	-1.284 $\pm$ 0.463	-2.774	<0.01**	-1.718 $\pm$ 0.680	-2.527	0.012 *	-1.031 $\pm$ 0.442	-2.334	0.196*
Tree-herbaceous gradient	0.049 $\pm$ 0.018	2.706	0.0046**	0.054 $\pm$ 0.021	2.585	0.009 **	0.044 $\pm$ 0.017	2.503	0.012*
Log-likelihood	-269.0			-185.4			-224.4		
AIC	565.9			398.7			476.8		
BIC	606.3			439.1			517.2		
df	19			19			19		

probability of obtaining false zeros, meaning that the higher the herbaceous coverage compared to tree coverage on the banks is, the higher the probability of obtaining false zeros (Table 1). Likewise, the higher the *Detection difficulty* is, the higher the probability of obtaining false zeros.

Discussion

In this study, we wanted to analyze the environmental factors influencing otter habitat use in anthropogenic landscapes and explore the role of restored gravel pits in providing suitable habitats for otters. As expected, in the anthropogenic landscape under study, otters used all existing types of water bodies and did not show a clear preference for any of them, demonstrating high flexibility in their use of habitat, which is in accordance with previous results (e.g. Lowry et al. 2013; Weinberger et al. 2016). Although the use of territory was unaffected by the type of water bodies, it was related with three key environmental attributes: (1) the gradient of tree coverage of banks, (2) the land use within 100 m from the banks, and (3) the level of human disturbances. These results confirm the importance of riparian tree vegetation buffer for otter habitat suitability, as previously stressed by other authors (e.g. López-Martín et al. 1998; Remonti et al. 2011; Teresa et al. 2014). In the relatively homogeneous anthropogenic landscape we have studied, where agricultural cropland covers one third of the land use, tree coverage and forested buffer areas might be providing the protection, tranquility, and shelter that other habitat heterogeneity features (such as small islands, pools, river junctions, boulders and rocky areas, or flood material) otherwise provide in natural areas (e.g. Clavero et al. 2010; Ruiz-Olmo 2014) and which did not exist in the landscape under study.

Human disturbance was a critical factor in habitat suitability for otters. This was not only due to its direct negative effect but also to its negative interaction with waterside tree coverage and forested buffer areas. Nevertheless, low levels of human disturbances, such as occasional disturbances caused by fishermen, farmers, or even sporadic truck traffic at enough distance, as was the case of the gravel pit lagoon system, did not seem to have a severe negative impact on otter habitat suitability as Weinberger et al. (2016) also showed. Note that in the study area, only one out of the 19 surveyed transects had no or very rare human disturbances. We found that human disturbances had a higher negative effect on *Latrines marking site intensity* than on *Isolated spraint marking site intensity*, which had no significant direct effect but a negative interaction with riparian vegetation cover and land use gradient variables. This finding, which should be confirmed in further studies, suggests that otters' tolerance of human activities might be lower in key areas of their territory compared to areas they simply pass through or explore, and therefore would support our approach of using several spraint marking intensity indicators differentiating latrines and isolated spraints to study otter habitat suitability. In a similar vein, Weinberger et al. (2016) showed that, in an anthropogenic landscape in Austria, otters chose those areas for foraging where human disturbance was the lowest within their home ranges. This differs from the popular belief that otters can deal with high levels

of human disturbances based on increasing sightings of otters in highly anthropogenic areas, which could actually just be areas where the otters cross or explore. If one of the aims for the restoration of gravel pit lagoon systems is that they become substitute habitat for otters, the establishment of a set of measures to maintain human disturbances at a minimum range is of utmost importance. We found that the negative effect of human disturbances on otter habitats could be buffered by managing the riparian vegetation cover and creating forested buffer areas around the water banks.

As discussed above, otters' use of water bodies did not seem to be related to its natural or artificial origin or the type of water body. Actually, some of the restored gravel pit lagoons are between the habitats used with the highest intensity, showing that these could become suitable semiaquatic habitats for otters in anthropogenic landscapes if they fulfill some of the animals' environmental needs. Similar results have been reported for different types of taxa (e.g. Šálek 2012; Vojar et al. 2016; Kerbiriou et al. 2018). In this context, restored gravel pits could be functioning as substitute habitats analogous to natural lagoons by providing nursery, refuge and foraging for semiaquatic species in those anthropogenic landscapes where natural semiaquatic habitats have been lost. At the landscape level, restored gravel pit lagoon systems should be well connected to surrounding fluvial system to generate a network of patches of high-quality habitat, which are critical for the maintenance of healthy otter populations due to the high mobility of the species (Mason & Macdonald 1986; Saavedra 2002; Ruiz-Olmo et al. 2005b); otherwise, habitat restoration at local scales has the risk of generating trap habitats (Battin 2004). In this regard, the distinction between areas with high and low potential for otter use in anthropogenic landscapes is essential because they would require different actions and habitat quality status targets. In our case, the gravel pit was well connected to the surrounding fluvial system due to the proximity of the lagoon system to both the irrigation channel and the Duero River. The ditch was heavily used by otters and was very likely to connect the gravel pit with the river.

We used spraint marking intensity as an indicator of otter habitat use intensity. Some authors are skeptical about this method arguing that it relies on the uncertain relationship between spraint numbers and otter habitat use or density (e.g. Kruuk & Conroy 1987; Kruuk 1995; Calzada et al. 2010). However, other authors have found high correlation between spraint marking intensity and otter habitat use using camera-trapping (e.g. Guter et al. 2008; Rivera et al. 2019). Furthermore, molecular genetic research has found a positive correlation between the relative otter spraint density and the number of otter genotypes in the area (Lanszki et al. 2008). In fact several studies have found a positive correlation between the percentage of spraints and prey content within the spraints next to sites with high prey presence (Remonti et al. 2011; Almeida et al. 2012b), stressing the idea that the owner of a territory concentrates its scent on those key resource areas or habitats. In this sense, we were confident in the reliability of spraint marking intensity as indicative of the use of habitat by otters. On the other hand, we believe that the methodology we used to infer habitat use intensity could generate some sort of controversy since we

removed the spraints during surveys. However, despite the fact that spraint behavior can function as a means of communication among otters, it is mainly associated with feeding and other forms of resource utilization (e.g. Ruiz-Olmo & Gosálbez 1997; Remonti et al. 2011). Therefore, we believed that spraint sites would have been restored between surveys, which was confirmed by the fact that there were no differences in marking intensities among surveys, neither for the first season (Friedman test; $\chi^2 = 0.871$, $df = 3$, $p = 0.832$) nor the second one (Friedman test; $\chi^2 = 4.792$, $df = 2$, $p = 0.091$). Finally, we acknowledge that the differential existence of prominent locations across transects might potentially influence spraint marking intensity. We did not account for this due to the difficulty of determining what a “prominent” location for otters is. Furthermore, in our case study, spraints were found in very varied places, most times not particularly prominent, such as short grass, on the middle of a path, or on rolling stone flat ground. Despite the mentioned potential biases, the coherence between the findings of our study with previous studies explained above seems to support the use of spraint marking intensities as indicators of habitat use intensity. However, our results should be taken with caution, and the extrapolation of the outcomes of our study has limitations related to the limited sample size and particular landscape features. Nevertheless, we found no reason to believe that the otter habitat preferences presented above would not apply to similar anthropogenic landscapes in the Mediterranean context.

The sampling protocols (repeated sampling) and statistical models used allowed us to account for both variability of otter sprainting behavior across sampling campaigns and potential false negatives in marking intensities. In our case, although we observed a slight decrease of marking intensities among sampling campaigns as year progressed which might be related to a known seasonal trend of otter spraint behaviour (e.g. Fusillo et al. 2007; Remonti et al. 2011), it was not statistically significant according to Friedman tests (see above). Still, this variability was accounted for in our models by including sampling campaign as a random term. This term includes the effect of different potential sources of variability, such as the seasonal and across year variability of weather, water level, or prey availability, which were not accounted for independently. However, as discussed above we did not find any strong seasonal effect on marking intensity indicators, and accordingly, it does not seem that the different component of the seasonal variability have had strong seasonal variation themselves. Note that prey availability has been shown to be an important factor for otter habitat use (e.g. Ruiz-Olmo et al. 2005b; Remonti et al. 2011); therefore, it would be interesting for future studies to develop otter diet surveys in restored gravel pit lagoon systems.

Finally, we used ZIP models, which rely on repeated sampling to determine the presence of false negatives, following Balestrieri et al. (2011) and Zuur et al. (2009). False negatives are more likely to happen in areas with low marking intensity (Ruiz-Olmo et al. 2001). Not accounting for those areas (which are likely to be quite numerous in anthropogenic landscapes) in the determination of habitat characteristics in habitat suitability analyses would bias the outcomes of the analysis toward the areas with high otter presence.

To summarize, we found that otter use of water bodies was not related to its natural or artificial origin but to its environmental features, and consequently that well-restored gravel pit lagoon systems have the potential to provide suitable habitat for otters in anthropogenic landscapes, as was the case in our study area. Tree riparian vegetation cover and forested buffer areas had a positive effect on habitat suitability, both directly and indirectly by reducing the negative effect of human disturbances, which was found to be a critical factor in habitat suitability for otters. Due to the case study nature of our research and the limitations discussed above, our findings should be complemented with future otter studies in gravel pit lagoon systems.

Acknowledgments

This study was funded by Hanson Hispania S.A., for the Quarry Life Award in 2016, the Fundación Tormes-EB, the Universidad Complutense de Madrid (project FEI16/10), and REMEDINAL3-CM (project S2013/MAE-271). C.R. was supported by XXII Propio de Investigación of the University of Córdoba and “Programa Operativo de fondos FEDER Andalucía.” We thank C. Remacha, J. P. Tris, and Dr P. Arana for the use of their laboratory and facilities in the Universidad Complutense de Madrid, M. R. Fernandez, for his advice in the statistical analysis, and A. J. Valdes and K. V. Mamani for their fieldwork and laboratory assistance.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Environmental variables considered for the Eurasian otter habitat suitability analysis.

Table S2. Description of variables considered for the Eurasian otter habitat suitability analysis to account for false zeros.

Table S3. Spearman correlation matrix of riparian vegetation cover variables.

Table S4. Spearman correlation matrix of land-use variables.

Table S5. Principal component analysis of land-use and riparian vegetation cover variables; coordinates on principal components.

Table S6. Otter marking intensity across sampling campaigns in the studied transects.

Guest Coordinating Editor: António Mira

Received: 10 December, 2018; First decision: 25 February, 2019; Revised: 30 January, 2020; Accepted: 30 January, 2020;