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Site-specific and seasonal variation in habitat use of Eurasian otters (*Lutra lutra*) in western China: implications for conservation

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ABSTRACT

As a top predator, the Eurasian otter (*Lutra lutra*) is an indicator of healthy freshwater ecosystems and a flagship species for conservation. Once widespread in China, the species is now distributed mainly in the upper reaches of the great rivers of western China. However, a lack of knowledge on local otter populations continues to hinder their conservation in China. Here, we conducted a detailed study on habitat use of Eurasian otters in Yushu City and Tangjiahe National Nature Reserve in western China using transect surveys. At both study sites, otters preferred to defecate on large rocks close to or protruding from the river and about 50 cm above the waterline. In Yushu, no spraints were found along the 5 km river bank section in the downtown area, with otters preferring spraining sites with natural banks, riparian zones, and lower human population density. However, this pattern was not obvious at Tangjiahe, where river transformation and human disturbance are minor. Otter river use intensity was negatively correlated with elevation and human population density in Yushu in both seasons. In Tangjiahe, otter river use intensity was positively correlated with prey mass and flow rate and negatively correlated with human population in spring, but positively correlated with human population and negatively correlated with flow rate in autumn. These results reflect the flexible habitat use strategies of otters at different sites, underlining the necessity to study otters living in different regions and habitat types. We provide suggestions for river modification and call for more site-specific studies to promote otter conservation in China.

Keywords: *Lutra lutra*; Spraining site; Habitat selection; Conservation; Local scale

INTRODUCTION

Freshwater ecosystems cover only 0.8% of the Earth's surface (Gleick, 1996) but contain a disproportionately high biodiversity, including one third of the world's vertebrates (Dudgeon et al., 2006). They also provide essential resources and services for humans, including drinking water, food,

recreation, irrigation, and transportation (Brauman et al., 2007; Grizzetti et al., 2016; Zilio et al., 2021). Freshwater ecosystems are among the most endangered in the world (Sala et al., 2000) due to overexploitation, water pollution, flow modification, habitat degradation, and exotic species invasion (Dudgeon et al., 2006). Despite this, they have received less research attention and conservation action than other types of ecosystems, such as forests (Abell et al., 2017; Dudgeon et al., 2006).

Top predators play important roles in maintaining ecosystem balance by controlling the population structure of lower trophic level animals via cascade effects (Rodríguez-Lozano et al., 2015). As one of the top predators in freshwater ecosystems, Eurasian otters (*Lutra lutra*) are an indicator of healthy water systems and a flagship species for conservation (Duffy, 2002; Sergio et al., 2008). They are widely distributed in Asia, Europe, and Africa in various water bodies, including streams, rivers, lakes, and coastlines (Kruuk, 2006). These otters were once widespread in China (Zhang et al., 2018), however their populations declined dramatically in many regions between the 1950s and 1980s due to overexploitation and habitat destruction (Li & Chan, 2018). At present, they are primarily found in the upper reaches of the great rivers of western and northeastern China, although sporadic records are also reported in other areas (Li & Chan, 2018; Zhang et al., 2018). Human activities, such as water pollution, sand mining, river modification, and overfishing, are severe in most Chinese rivers (Chen et al., 2017, 2020, 2021; Zhang & Li, 2020), and continue to pose a threat to otters. In addition, although listed as a class II protected animal in China since 1989, otters have long been neglected by researchers and conservation practitioners in China, resulting in very few studies being conducted (Zhang et al., 2018). Our limited knowledge on local otter populations also continues to hinder their conservation in China.

Eurasian otters have been relatively well-studied in Europe at both the continental and local scales (Cianfrani et al., 2013; Krawczyk et al., 2016; Scorpio et al., 2016; Weinberger et al., 2016). However, species often face site-specific threats and information obtained from studies in one area may not fit another. Due to their vast distribution range and adaptability to different ecosystems/human disturbance levels, otter populations show site-specific habitat preference in response to food and shelter availability and human disturbance at smaller scales. For example, otters in south Korea and central Spain show opposite preferences for water depth (Almeida et al., 2012; Jo & Won, 2019). Similarly, otters in undisturbed areas of Scotland prefer to live in low-elevation areas (Green & Green, 1981), whereas in Spain they select against low-elevation regions to avoid human disturbance (Elliot, 1983). To conserve otter populations in China, local-scale studies are essential to reveal the specific threats and conservation opportunities among different otter populations.

Here, we conducted a detailed study on habitat use of Eurasian otters in Yushu (Qinghai Province) and Tangjiahe National Nature Reserve (Sichuan Province) in western China, where otters are reported at a relatively high rate (Zhang et al., 2018). We used number of sprainting sites as an indicator of otter activity and habitat preference (Bas et al., 1984; Jo & Won, 2019) and identified important environmental variables impacting sprainting sites and habitat use intensity at the local scale. Our study provides specific information on habitat requirements at the two sites and should help guide future conservation actions to better protect otter populations living in similar habitats in western China.

MATERIALS AND METHODS

Study sites

In 2019, two field teams conducted simultaneous otter surveys in Yushu and Tangjiahe (Figure 1) in two different seasons (15 April–20 May and 8 November–16 December). Before the formal surveys, team members conducted preliminary otter surveys together in 2018 at both study sites to ensure similar survey experience and skills. Yushu is located on the Tibetan Plateau, with an elevation ranging from 3 530–3 860 m a.s.l. (Han et al., 2021). The Batang and Zhaqu rivers (widths of 43±2 m and 25±1 m, respectively) run through the downtown area of the city. Both rivers are tributaries of the Tongtian River in the upper reaches of the Yangtze River. Average annual temperature is ~2.9 ℃ and average annual precipitation is ~487 mm (Sun et al., 2019). Vegetation along the rivers is mainly alpine meadow (Lu et al., 2016). Large sections of both rivers in and around the city have been modified, with instream boulders cleared and river banks reinforced. Areas with concentrated human populations are also impacted by increased water pollution, traffic noise, artificial illumination, domestic animal use (e.g., dogs and yaks), and recreational activities by and on the rivers. Over 90% of Yushu residents are Tibetan. Fortunately, due to their religious beliefs, local people seldom harm wildlife directly, such as via fishing and hunting.

Tangjiahe is located in Qingxi Town, Guangyuan City, Sichuan Province. The Qingzhu River (width of 15±1 m) runs through the reserve and is a tributary of the Pailung River in the Yangtze River watershed. Our survey site also covered a small section of the river outside the reserve, with an elevational range of 800–1900 m a.s.l. Average annual temperature is ~12℃ and average annual precipitation is ~1 100 mm (Hu, 2005). The main vegetation along the river is mixed evergreen and deciduous broadleaf forest. Unlike Yushu, Tangjiahe is a well-protected reserve with few residents living within its boundaries. Rivers here are natural with little modification. However, the river section outside the reserve is subject to human disturbances similar to those in Yushu, as well as fishing and potentially poaching.

Field survey and data collection

We divided the rivers into 1 km sections and surveyed each section by walking a transect (1 km long×10 m wide) along one side of the river to search for otter sprainting sites (Figure 1). These river sections were treated as sample units. Surveys were conducted by 2–3 person teams. Once a sprainting site was found, we recorded the coordinates using a hand-held GPS (Garmin GPSMAP 629SC, USA) and number of spraints. We also noted features of the sprainting site (regardless of whether it was on the bank or in the river), including substrate type and size, shelter (or not), shelter type,
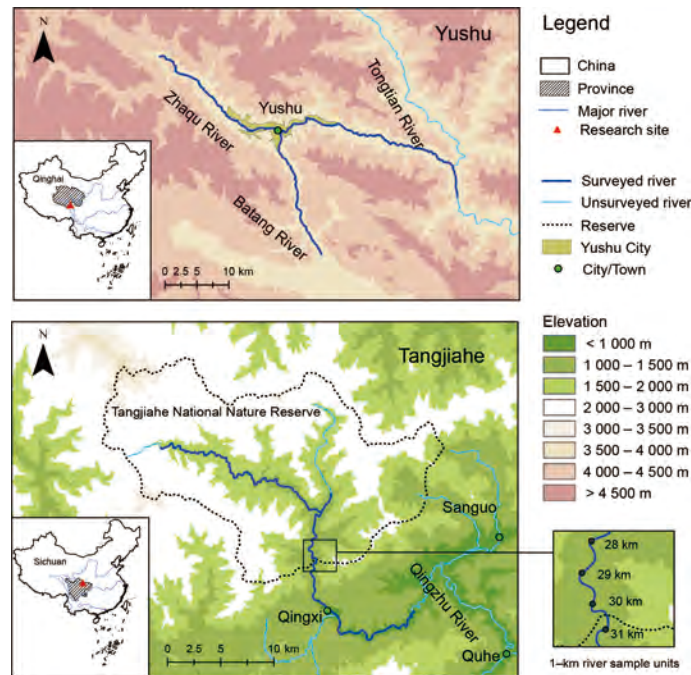
Figure 1 Location of rivers in Yushu (Qinghai Province) and Tangjiahe National Nature Reserve (Sichuan Province) where otter surveys were conducted Inset map in lower right corner illustrates division of surveyed rivers into 1 km sample units.

distance to water (with a negative figure indicating that the site was on rocks protruding out of the river, and a positive figure indicating that the site was on land), and height from water. We also recorded other river characteristics such as flow rate, water depth, and bank type (see Table 1 for details), which were measured from the bank. Considering the accuracy of the GPS units (usually 3–10 m at our study sites), we only recorded locations of sprainting sites that were ≥10 m apart. Spraints at sites within 10 m of recorded sites were assigned

to the nearest recorded site.

We systematically set four control sites 200 m apart in each 1 km river section and recorded environmental variables corresponding to those recorded at sprainting sites, except for variables that were not applicable (e.g., size of rock where spraints were found). We set a fishing trap (size: 32 cm×24 cm×5 m, mesh: 4 mm, entrance: 15 cm) with bread as bait at every control site to evaluate abundance of otter prey in each section. To avoid catching otters accidentally, we set traps in

Table 1 Environmental variables applied for habitat use analysis of Eurasian otters in current study

Variable group	Variable (unit)	Description	Data source	Analysis
River characteristics	Water depth (cm)	Depth of water 1 m from river bank	Transect survey	Sprainting site selection & river use intensity
	Flow rate (m/s)	Flow rate of water 1 m from river bank (measured by a Global Water FP111 current meter)	Transect survey	Sprainting site selection & river use intensity
	Elevation (m)	Vertical distance above sea level	https://www.91weitu.com	Sprainting site selection & river use intensity
	Riparian zone	Transitional zone between water and river bank, which may flood during rainy season but is dry at other times, usually without vegetation: 1 - with riparian zone; 0 - without riparian zone	Transect survey	Sprainting site selection & river use intensity
	Bank type	1 - artificial bank, 0 - natural bank.	Transect survey	Sprainting site selection & river use intensity
	Bank×riparian zone	1 - artificial bank without riparian zone; 0 - other situations	Transect survey	Sprainting site selection
Human disturbance	Population density (indiv./ha)	Human population density	https://www.worldpop.org/	River use intensity
Prey abundance	Prey mass (g)	Mass of all prey caught in fishing trap	Transect survey	River use intensity
	Fish number	Number of fish caught in fishing trap	Transect survey	River use intensity
	Fish mass (g)	Mass of fish caught in fishing trap	Transect survey	River use intensity

the daytime when otters are relatively inactive (Han et al., 2021). Traps were set before 0900 h and retrieved after 1 500 h to ensure they were in the river for at least 6 h. No otter was caught during the study. We recorded number of species, number of individuals per species, and total mass of each trap (for all species and for fish only). Once measured and recorded, all prey were released at the same location where they were caught.

In total, the surveys covered 68 km and 64 km of rivers in Yushu in the two seasons, respectively, in both urban and suburban areas. In Tangjiahe, the surveys covered 30 km of river in spring (inside the reserve) and 50 km of river in autumn (inside and outside the reserve). However, we were unable to survey prey abundance in some sections (e.g., we avoided setting traps in the densely populated downtown area of Yushu). Finally, we surveyed prey abundance in 30 km and 29 km of rivers in Yushu in the two seasons, respectively, and surveyed 30 km of rivers (all inside the reserve) in both seasons in Tangjiahe.

Statistical analyses

Sprainting site selection: We summarized the basic characteristics of the otter sprainting sites, e.g., type of substrate defecated on. We then compared six variables in the sprainting and control sites, which are reported as key factors affecting otter sprainting site selection (Almeida et al., 2012; Depue & Ben-David, 2010), using the non-parametric Wilcoxon rank-sum test for continuous variables and *Chi*-square test for binominal variables. The variables included bank type ("1" as natural bank, "0" as artificial bank), riparian zone ("1" with riparian zone, "0" without riparian zone), an interactive variable between the two (artificial bank without riparian zone defined as "1", and other situations defined as "0"), elevation, flow rate, and water depth (Table 1). Elevation data (8.05 m resolution) were obtained from 91 Weitu (v18.7.7, https://www.91weitu.com). For each sprainting site, we extracted in ArcMap (v10.6.1) values of elevation of the cell in which the site was located. Although vegetation is an important variable in determining sprainting sites according to previous studies (Bas et al., 1984; Macdonald & Mason, 1982), we did not include vegetation in our analysis as it was relatively homogeneous along the rivers at both study sites, i.e., alpine meadow in Yushu and dense forest in Tangjiahe. We also removed the variable "riparian zone" in Tangjiahe for the same reason. Furthermore, the percentage of artificial bank without a riparian zone was quite low in Tangjiahe (<5%), thus this variable was removed from analysis at this site.

River use intensity: We calculated the number of sprainting sites per 1 km river section as an index of habitat use intensity. With this index as the dependent variable, we conducted negative binomial regression models to identify environmental variables that significantly influence otter habitat use. Nine variables were considered in our analyses based on reported habitat preferences of otters (Table 1). For example, otters prefer shallower rivers as deeper water may make fishing more difficult (Almeida et al., 2012), and higher human disturbance reduces otter habitat use intensity (Cortés et al., 1998). Variable values at each river section were

calculated as averages of data collected at the four control sites within the section. Human population data (100 m resolution) were obtained from WorldPop (https://www.worldpop.org/). We calculated the mean values of elevation and human population density for each 1 km river section in ArcMap (v10.6.1). For binary variables, we calculated the proportions of "1".

Before running the models, we conducted Spearman correlation tests between continuous variables and removed those with collinearity problems (i.e., Spearman rho>0.75, Supplementary Tables S1, S2). Elevation in Tangjiahe was removed because it was highly collinear with human population density (Spearman rho=0.853, *P*<0.001). In Yushu, however, elevation and population showed a bell-shaped relationship (Population=2.52×Elevation−3.41×10^{-4}×Elevation^2 −4 660, F=12.67, R^2=0.259, *P*<0.001). Population was positively correlated with elevation at <3 700 m (near center of Yushu), but negatively correlated with elevation at >3 700 m. Therefore, both elevation and human population density were retained in the following modeling procedures.

Various combinations of the remaining variables were used to develop 8–14 *a priori* models hypothesized to explain otter river use intensity (Supplementary Tables S3–S6). We used Akaike's Information Criterion corrected for small sample sizes (AICc) as the index of model fit. The model with the smallest AICc value was considered the best supported model, and models with ΔAIC≤2 were considered as having equivalent support. We calculated Akaike weight (ω_i) for each candidate model and found no single model superior to others (i.e., ω_i≥ 0.9) (Supplementary Tables S3–S6). We then applied a model-averaging approach to derive coefficients of variables from the set of top models that had a cumulative ω_i over 0.9. Variables with a standard error (*SE*) greater than the coefficient were removed from the final model. We calculated relative importance for each variable in the final model based on the ω_i values of the top models.

We summarized prey survey results at both sites. Prey consisted of fish, frogs, toads, crabs, and water shrews. For each 1 km river section, prey variables (including prey mass per trap, fish mass per trap, and fish number per trap) were calculated as the average of the four traps within the section. We then compared prey variables and vacant rate of fishing traps between the two seasons using Wilcoxon rank-sum and *Chi*-square tests. Because prey abundance was only surveyed in a portion of the river sections, we ran a series of separate models with one more variable ("prey mass") with a smaller sample size. Fish mass and fish number were removed because they were highly collinear with prey mass (Supplementary Table S2). Due to the high vacant rates of fishing traps in autumn at both sites, we only performed models with prey variables in spring at both sites. Following the same procedures above, we found that prey mass had no significant influence on otter river use intensity in Yushu (Supplementary Table S7). Thus, we retained model sets without prey variables to fully utilize the data collected on other environmental variables in Yushu.

All statistical analyses were conducted in R (v4.0.4) with the packages "MASS" (Venables & Ripley, 2002) and "MuMIn" (Bartoń, 2020).

RESULTS

We recorded 450 and 821 sprainting sites in Yushu and Tangjiahe, respectively. In Yushu, six river sections, five of which were located in the downtown area, had no spraints in either season (Figure 2). The average number of sprainting sites per 1 km river section was 2.9±0.3 in spring and 4.0±0.5 in autumn. There were fewer sprainting sites in urban areas than in suburban areas in both seasons (spring: 2.4±0.7 vs. 3.1±0.4, W=631, P=0.049; autumn: 2.8±0.7 vs. 4.6±0.6, W=604, P=0.022). In Tangjiahe, only one river section located upstream had no sprainting sites in either season. The average number of sprainting sites per 1 km river section was 4.7±0.7 in spring and 13.6±1.8 in autumn. In autumn, the number of sprainting sites inside and outside the reserve did not differ significantly (13.3±2.2 vs. 14.0±3.1, W=313.5, P=0.398).

The otters defecated on various substrates, including rocks, soil, sand, grassland, and concrete floor. However, 60.3% and 99.3% of sprainting sites were found on rocks in Yushu and Tangjiahe, respectively. The average distance from a sprainting site to the riverside was 0.6±0.2 m (n=260) in Yushu and −1.6±0.2 m (n=405) in Tangjiahe. The average size of rocks defecated on was 1.02±0.09 m² in Yushu (n=244) and 3.35±0.43 m² in Tangjiahe (n=388), while the average height of rocks from the water was 55.8±1.8 cm (n=292) in Yushu and 50.4±1.4 cm in Tangjiahe (n=405).

In Yushu, 10.7% (n=48) of sprainting sites were under a shelter (in contrast to open space), whereas 9.4% (n=78) of sprainting sites were under a shelter in Tangjiahe. Otters used both natural and artificial shelters. Natural shelters included boulders, tree roots, and soil caves. Artificial shelters included bridges, river bank cavities, and concrete pipes. The percentage of natural shelters was 57.4% in Yushu and 97.4% in Tangjiahe.

Sprainting site selection

The average elevation of sprainting sites was lower than the control sites in both Yushu and Tangjiahe (Figure 3). Despite elevation, otters in Yushu defecated more at locations with natural banks and riparian zones, and less at locations that have artificial banks without riparian zones (Figure 3). However, no differences were found in the flow rate or water depth. In Tangjiahe, however, no environmental variables, other than elevation, differed between the sprainting and control sites (Figure 3).

River use intensity

We captured more prey in spring than in autumn at both sites (Table 2; Figure 4). The vacant rates of fishing traps were also much higher in autumn than in spring at both sites.

In Yushu, otters were more likely to use river sections at lower elevations and with lower human population densities in both seasons (Table 3). No other variable, including bank type, riparian zone, water depth, and flow rate, was correlated with river use intensity by otters in either season.

In Tangjiahe, we found river use intensity was positively correlated with flow rate and prey mass, but negatively correlated with human population density in spring (Table 4). In autumn, otters were more likely to use river sections with higher human population density and lower flow rate. Other variables were not correlated with river use intensity in either season.

DISCUSSION

We conducted a detailed study on habitat use of Eurasian otters in China. At both study sites, otter spraints were found in all river sections, except for the downtown area of Yushu. As reported in other areas (e.g., Jo & Won, 2019), otters in our study showed flexible habitat use strategies at different sites
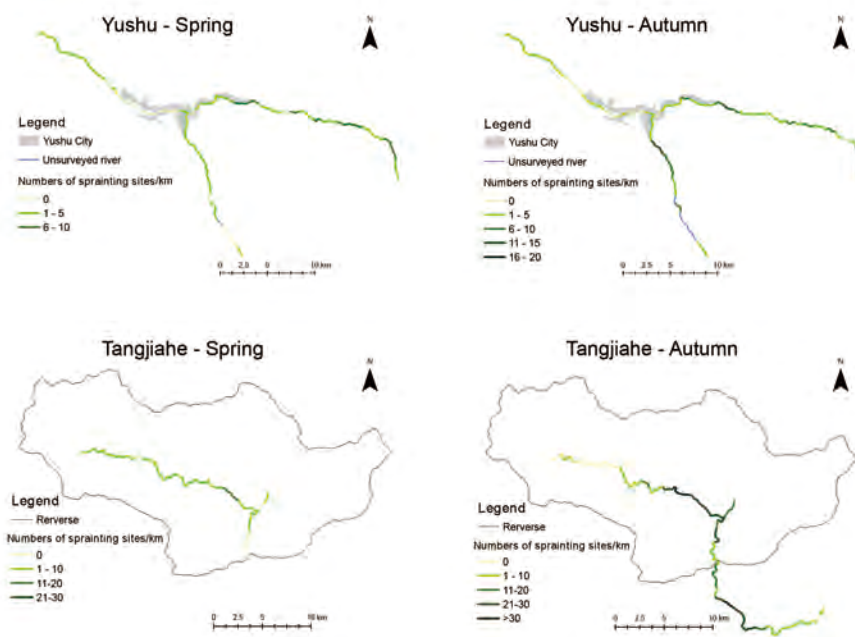

Figure 2 Distribution of sprainting sites in Yushu and Tangjiahe in two seasons
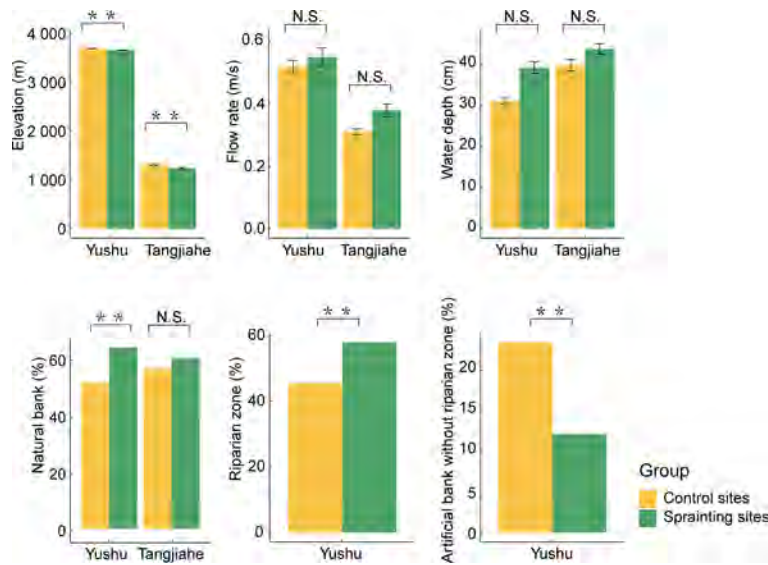
Figure 3 Comparisons of environmental variables between sprainting and control sites (mean±*SE*)

**: Comparison significant at 0.01 level. N.S.: No significant difference.

Table 2 Fish species captured by traps in Yushu and Tangjiahe

Site	Family	Subfamily	Species	Abundance spring	Abundance autumn
Yushu	Cyprinidae	Cyprininae	*Carassius auratus*[*]	2	0
		Schizothoracinae	*Schizopygopsis* spp.	1 737	934
			Ptychobarbus kaznakovi	180	7
		Noemacheilinae	*Triplophysa* spp.	103	30
			Lefua sp.	1	0
Tangjiahe	Cyprinidae	Gobioninae	*Belligobio nummifer*	172	30
		Leuciscinae	*Phoxinus* spp.	1 022	64
		Schizothoracinae	*Schizothorax* spp.	116	139
	Cobitidae	Noemacheilinae	*Homatula* spp.	16	0
	Sisoridae		*Euchiloglanis davidi*	0	1

[*]: *Carassius auratus* is an exotic species, which was released by local people due to religious beliefs.
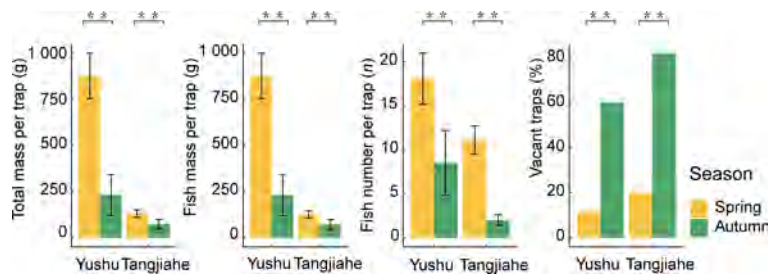

Figure 4 Comparisons of prey survey results between seasons (mean±*SE*)

**: Comparison significant at 0.01 level.

and in different seasons.

Effects of environmental variables on otter habitat use

In Yushu, both elevation and human population had a negative impact on otter sprainting site selection and river use intensity. These results suggest that otters in Yushu tend to use river sections at lower elevation with lower human population. Elevation is usually negatively correlated with human population density, therefore higher human disturbance at lower elevation usually drives otters to higher elevations, or to intermediate elevations to balance foraging efficiency as prey abundance is also negatively correlated with elevation (Elliot, 1983; Green & Green, 1981; Hutchings & White, 2000; Prenda & Granado-Lorencio, 1996). However, we found a bell-shaped relationship between elevation and human population in Yushu because the downtown area is located at the mid-elevation of these rivers. Below the downtown elevation, otters preferred river sections with lower human disturbance at lower elevations. This relationship may

exceed the negative impact of human populations on otters above the downtown elevation, resulting in an overall negative relationship between elevation and otters habitat utilization. We found that prey mass did not affect river use intensity of otters in Yushu. Local Tibetan people living in and around Yushu seldom eat fish or go fishing in the rivers. Thus, fish were abundant in Yushu compared with Tangjiahe (Figure 4) and may not be a limiting resource for otters.

In Tangjiahe, otter habitat use was negatively correlated with human population in spring, but positively correlated with human population in autumn. Considering the high collinearity between human population and elevation in Tangjiahe (Supplementary Tables S1, S2), these results indicated that otters preferred river sections at higher elevations in spring but lower elevations in autumn. Prey variables did not show a significant relationship with elevation in spring (Supplementary Tables S1, S2). Previous studies have reported that prey species in Tangjiahe, such as the dominant *Schizothorax* spp. and *Phoxinus lagowskii* species, move upstream to spawn in spring (Ding, 1994; Zhang & Zeng, 2015). Therefore, prey abundance is relatively high in upstream sections in spring, resulting in no significant relationship between prey abundance and elevation in our study. To avoid high human populations at lower elevations (Cortés et al., 1998; Prenda & Granado-Lorencio, 1996), otters used higher elevations more often in spring. In contrast, fish are reported to move downstream in autumn (Ding, 1994), resulting in higher prey abundance at lower elevation. Although we lack autumn prey data, this seasonal pattern of prey distribution is highly reasonable. Thus, to track and hunt fish in autumn, otters tolerated human disturbance and used river sections at lower elevations more often. Similar patterns have also been reported in the Iberian Peninsula (Clavero et al., 2010). Our results again suggest that otters are flexible in elevation selection, showing a tradeoff between food availability and the

water pollution/human disturbance associated with lower elevations (Elliot, 1983; Green & Green, 1981; Jo et al., 2017; Prenda & Granado-Lorencio, 1996), although at a much smaller scale. Similarly, otters showed the opposite preference for flow rate in Tangjiahe in the two seasons, probably due to the significant relationship between flow rate and elevation (Supplementary Tables S1, S2).

Our prey abundance survey method was not effective in autumn, probably due to the lower activity of fish at low temperature. Furthermore, we only surveyed prey during the day to prevent otters being trapped at night, which limited survey duration and efficiency. A more efficient survey technique, e.g., electrofishing (Grant & Harrington, 2015; Reid et al., 2013), would need to be applied in future studies to better assess the importance of prey abundance.

Effects of urbanization on otter habitat use

Urbanization had an obvious negative impact on the otters, with no sprainting sites found in the 5 km river section in downtown Yushu. Urbanization usually means a noisier, more crowded, less vegetated, and more polluted environment, as well as potential exposure to humans and domestic animals, which would affect otter habitat use (Clavero et al., 2010; Dettori et al., 2021; Fabrizio et al., 2019).

Shelters are important for otters to rest and breed (Melquist & Hornocker, 1983; O'Sullivan, 1993; Pardini & Trajano, 1999; Santos & dos Reis, 2012). Our results indicated that otters tolerated human disturbance by adapting to artificial shelters, e.g., bridges, river bank cavities, and concrete pipes in Yushu. In addition, a pilot study in Yushu reported that otters regularly visit artificial dens in the downtown area, indicating that shelter may be a limiting resource (Han, unpublished data). Thus, we recommend retaining natural shelters or providing artificial shelters in urban rivers for otters to facilitate their daily activity and dispersal.

Table 3 Model-averaged coefficients (±*SE*) for environmental variables associated with number of otter sprainting sites per 1 km river section in Yushu

Variable	Spring (68 km)			Variable	Autumn (64 km)		
	Coefficient	*SE*	Relative importance		Coefficient	*SE*	Relative importance
(Intercept)	19.342	3.850		(intercept)	17.593	4.156	
Elevation	−0.005	0.001	1.00	Elevation	−0.004	0.001	1.00
Population	−0.026	0.016	0.57	Population	−0.023	0.016	0.51
Water depth[*]	0.003	0.009	0.25	Water depth[*]	0.006	0.012	0.26

[*]: Variables were removed from final model due to a larger *SE* than coefficient.

Table 4 Model-averaged coefficients (±*SE*) for environmental variables associated with number of otter sprainting sites per 1 km river section in Tangjiahe

Variable	Spring (30 km)			Variable	Autumn (50 km)		
	Coefficient	*SE*	Relative importance		Coefficient	*SE*	Relative importance
(Intercept)-	1.503	0.613		(Intercept)	2.498	0.418	
Population	−4.062	1.455	0.95	Population	0.467	0.246	0.78
Prey mass	0.002	0.001	0.35	Flow rate	−0.745	0.643	0.44
Flow rate	2.921	2.579	0.19	Water depth[*]	0.002	0.018	0.14
Water depth[*]	−0.005	0.019	0.06	Natural bank[*]	−0.344	0.459	0.06

[*]: Variables were removed from final model due to a larger *SE* than coefficient.

In Yushu, otters preferred to defecate at locations with natural river banks and riparian zones and tended to avoid artificial banks without riparian zones. Artificial banks without riparian zones are characterized by steep and high banks without a transitional zone, which may prevent otters from coming ashore. With the removal of river rocks and transformation of rivers in Yushu, otters have limited spots for resting, scent-marking, and communication. As a result, no spraining sites were detected in either season in the five 1 km river sections located in the downtown area of Yushu. In Tangjiahe, however, no differences in bank type between the spraining and control sites were observed, which was likely due to the abundance of river rocks and riparian zones along the rivers. The contrary findings between Yushu and Tangjiahe highlight the importance of providing landing spots along modified river banks during urbanization. We strongly recommend retaining rocks in and by rivers in regions where similar transformation projects are to be launched.

Otter conservation outside of protected areas

Protected areas are effective at conserving threatened species (Bruner et al., 2001; Taylor et al., 2011). However, most Chinese reserves are located at high elevations (You et al., 2018), thus only protecting upstream sections of rivers, such as in Tangjiahe. Currently, most remaining otter populations live outside of reserves (Zhang et al., 2018), e.g., rivers around Yushu. In addition, many wetlands or coastal mangrove/mudflat reserves may possess suitable habitat but do not currently contain otter populations. Relying on reserves to protect otters would be insufficient due to the limited coverage of otter populations in such areas. As seen in this study, even without hunting pressure in Yushu, human activities still had a negative influence on otters. Otters may face site-specific threats and thus need site-specific science-based management and conservation plans. In addition, local ecological knowledge in western China contributes to threatened species conservation outside of reserves (Zhang et al., 2021). Therefore, studies on the ecological knowledge, attitude, and perception of locals toward otters and otter conservation are needed to help solve potential human-otter conflicts outside of reserves.

CONCLUSIONS

Our study indicated that in western China, Eurasian otters survive in different habitat types under varied levels of human disturbance. Although otters avoided some river sections in downtown Yushu, they showed the potential to live in human-dominated landscapes, such as river sections outside the downtown area. We recommend retaining natural shelters or providing artificial shelters and landing spots to facilitate the daily activity and potential dispersal of otters when river bank transformation is needed for other reasons. Further studies are also required to clarify site-specific ecological requirements and threats to otters, as well as to understand local resident attitudes and perceptions toward otter conservation.

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

REFERENCES

Abell R, Lehner B, Thieme M, Linke S. 2017. Looking beyond the fenceline: assessing protection gaps for the world's rivers. *Conservation Letters*, **10**(4): 384−394.

Almeida D, Barrientos R, Merino-Aguirre R, Angeler DG. 2012. The role of prey abundance and flow regulation in the marking behaviour of Eurasian otters in a Mediterranean catchment. *Animal Behaviour*, **84**(6): 1475−1482.

Bartoń K. 2020. MuMIn: multi-model inference. R package version 1.15. 6.https://CRAN.R-project.org/package=MuMIn.

Bas N, Jenkins D, Rothery P. 1984. Ecology of otters in Northern Scotland: V. The distribution of otter (*Lutra lutra*) faeces in relation to bankside vegetation on the River Dee in summer 1981. *Journal of Applied Ecology*, **21**(2): 507−513.

Brauman KA, Daily GC, Duarte TK, Mooney HA. 2007. The nature and value of ecosystem services: an overview highlighting hydrologic services. *Annual Review of Environment and Resources*, **32**: 67−98.

Bruner AG, Gullison RE, Rice RE, da Fonseca GAB. 2001. Effectiveness of parks in protecting tropical biodiversity. *Science*, **291**(5501): 125−128.

Chen YP, Zhao Y, Zhao MM, Wu JH, Wang KB. 2021. Potential health risk assessment of HFRs, PCBs, and OCPs in the Yellow River basin. *Environmental Pollution*, **275**: 116648.

Chen YS, Qu X, Xiong FY, Lu Y, Wang LZ, Hughes RM. 2020. Challenges to saving China's freshwater biodiversity: fishery exploitation and landscape pressures. *Ambio*, **49**(4): 926−938.

Chen YS, Zhang SH, Huang DS, Li BL, Liu JG, Liu WJ, et al. 2017. The development of China's Yangtze River Economic Belt: how to make it in a green way?. *Science Bulletin*, **62**(9): 648−651.

Cianfrani C, Maiorano L, Loy A, Kranz A, Lehmann A, Maggini R, et al. 2013. There and back again? Combining habitat suitability modelling and connectivity analyses to assess a potential return of the otter to Switzerland. *Animal Conservation*, **16**(5): 584−594.

Clavero M, Hermoso V, Brotons L, Delibes M. 2010. Natural, human and spatial constraints to expanding populations of otters in the Iberian Peninsula. *Journal of Biogeography*, **37**(12): 2345−2357.

Cortés Y, Fernández-Salvador R, García FJ, Virgós E, Llorente M. 1998. Changes in otter *Lutra lutra* distribution in Central Spain in the 1964–1995 period. *Biological Conservation*, **86**(2): 179−183.

Depue JE, Ben-David M. 2010. River otter latrine site selection in arid habitats of western colorado, USA. *Journal of Wildlife Management*, **74**(8): 1763−1767.

Dettori EE, Balestrieri A, Zapata-Perez VM, Bruno D, Rubio-Saura N,

Robledano-Aymerich F. 2021. Distribution and diet of recovering Eurasian otter (*Lutra lutra*) along the natural-to-urban habitat gradient (river Segura, SE Spain). *Urban Ecosystems*, **24**(6): 1221−1230.

Ding RH. 1994. The Fishes of Sichuan, China. Chengdu: Sichuan Publishing House of Science and Technology. (in Chinese)

Dudgeon D, Arthington AH, Gessner MO, Kawabata ZI, Knowler DJ, Lévêque C, et al. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews*, **81**(2): 163−182.

Duffy JE. 2002. Biodiversity and ecosystem function: the consumer connection. *Oikos*, **99**(2): 201−219.

Elliot KM. 1983. The otter (*Lutra lutra* L.) in Spain. *Mammal Review*, **13**(1): 25−34.

Fabrizio M, Di Febbraro M, Loy A. 2019. Where will it cross next? Optimal management of road collision risk for otters in Italy. *Journal of Environmental Management*, **251**: 109609.

Gleick PH. 1996. Water resources. *In*: Schneider SH. Encyclopedia of Climate and Weather. New York: Oxford University Press.

Grant KR, Harrington LA. 2015. Fish selection by riverine Eurasian otters in lowland England. *Mammal Research*, **60**(3): 217−231.

Green J, Green R. 1981. The otter (*Lutra lutra* L.) in western France. *Mammal Review*, **11**(4): 181−187.

Grizzetti B, Lanzanova D, Liquete C, Reynaud A, Cardoso AC. 2016. Assessing water ecosystem services for water resource management. *Environmental Science & Policy*, **61**: 194−203.

Han XS, Dong ZY, Zhao G, Zhao X, Shi XY, Lü Z, et al. 2021. Using surveillance cameras to analyze the activity pattern of the Eurasian otters (*Lutra lutra*) and the efficiency of camera trap monitoring. *Biodiversity Science*, **29**(6): 770−779. (in Chinese)

Hu J. 2005. A Comprehensive Scientific Investigation Report of Tangjiahe Nature Reserve in Sichuan Province. Chengdu: Sichuan Science & Technology Press. (in Chinese)

Hutchings MR, White PCL. 2000. Mustelid scent-marking in managed ecosystems: implications for population management. *Mammal Review*, **30**(3–4): 157–169.

Jo YS, Won C. 2019. The sprainting behavior and habitat preference of the Eurasian Otter *Lutra lutra* along a montane stream in South Korea. *Mammal Study*, **45**(1): 3−11.

Jo YS, Won CM, Fritts SR, Wallace MC, Baccus JT. 2017. Distribution and habitat models of the Eurasian otter, *Lutra lutra*, in South Korea. *Journal of Mammalogy*, **98**(4): 1105−1117.

Krawczyk AJ, Bogdziewicz M, Majkowska K, Glazaczow A. 2016. Diet composition of the Eurasian otter *Lutra lutra* in different freshwater habitats of temperate Europe: a review and meta-analysis. *Mammal Review*, **46**(2): 106−113.

Kruuk H. 2006. Otters: Ecology, Behaviour and Conservation. Oxford: Oxford University Press.

Li F, Chan BPL. 2018. Past and present: the status and distribution of otters (Carnivora: Lutrinae) in China. *Oryx*, **52**(4): 619−626.

Lu L, Ren ZP, Yue YJ, Yu XT, Lu S, Li GC, et al. 2016. Niche modeling predictions of the potential distribution of *Marmota himalayana*, the host animal of plague in Yushu County of Qinghai. *BMC Public Health*, **16**: 183.

Macdonald SM, Mason CF. 1982. Otters in greece. *Oryx*, **16**(3): 240−244.

Melquist WE, Hornocker MG. 1983. Ecology of river otters in west central idaho. *Wildlife Monographs*, (83): 1−60.

O'Sullivan WM. 1993. The nature and distribution of otter resting sites on part of the river blackwater catchment, southern Ireland. *Biology and Environment:Proceedings of the Royal Irish Academy*, **93B**(3): 159−162.

Pardini R, Trajano E. 1999. Use of shelters by the neotropical river otter (*Lontra longicaudis*) in an atlantic forest stream, southeastern Brazil. *Journal of Mammalogy*, **80**(2): 600−610.

Prenda J, Granado-Lorencio C. 1996. The relative influence of riparian habitat structure and fish availability on otter *Lutra lutra* L. sprainting activity in a small Mediterranean catchment. *Biological Conservation*, **76**(1): 9−15.

Reid N, Thompson D, Hayden B, Marnell F, Montgomery WI. 2013. Review and quantitative meta-analysis of diet suggests the Eurasian otter (*Lutra lutra*) is likely to be a poor bioindicator. *Ecological Indicators*, **26**: 5−13.

Rodríguez-Lozano P, Verkaik I, Rieradevall M, Prat N. 2015. Small but powerful: top predator local extinction affects ecosystem structure and function in an intermittent stream. *PLoS One*, **10**(2): e0117630.

Sala OE, Chapin III FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, et al. 2000. Global biodiversity scenarios for the year 2100. *Science*, **287**(5459): 1770−1774.

Santos LB, dos Reis NR. 2012. Use of shelters and marking sites by *Lontra longicaudis* (Olfers, 1818) in lotic and semilotic environments. *Biota Neotropica*, **12**(1): 199−205.

Scorpio V, Loy A, Di Febbraro M, Rizzo A, Aucelli P. 2016. Hydromorphology meets mammal ecology: river morphological quality, recent channel adjustments and otter resilience. *River Research and Applications*, **32**(3): 267−279.

Sergio F, Caro T, Brown D, Clucas B, Hunter J, Ketchum J, et al. 2008. Top predators as conservation tools: ecological rationale, assumptions, and efficacy. *Annual Review of Ecology, Evolution, and Systematics*, **39**: 1−19.

Sun XH, Ma Z, Su WG. 2019. Analysis on the interference characteristics of borehole strain rainfall in yushu of Qinghai province. *Plateau Earthquake Research*, **31**(1): 31−36. (in Chinese)

Taylor MFJ, Sattler PS, Evans M, Fuller RA, Watson JEM, Possingham HP. 2011. What works for threatened species recovery? An empirical evaluation for Australia. *Biodiversity and Conservation*, **20**(4): 767−777.

Venables WN, Ripley BD. 2002. Modern Applied Statistics with S. 4th ed. New York: Springer.

Weinberger IC, Muff S, de Jongh A, Kranz A, Bontadina F. 2016. Flexible habitat selection paves the way for a recovery of otter populations in the European Alps. *Biological Conservation*, **199**: 88−95.

You ZQ, Hu JH, Wei Q, Li CW, Deng XF, Jiang ZG. 2018. Pitfall of big databases. *Proceedings of the National Academy of Sciences of the United States of America*, **115**(39): E9026−E9028.

Zhang HH, Zeng Y. 2015. Variation of fish fauna and status of fish resources in Tangjiahe Nature Reserve. *Freshwater Fisheries*, **45**(1): 42−45. (in Chinese)

Zhang L, Turvey ST, Chapman C, Fan PF. 2021. Effects of protected areas on survival of threatened gibbons in China. *Conservation Biology*, **35**(4): 1288−1298.

Zhang L, Wang QY, Yang L, Li F, Chan BPL, Xiao ZS, et al. 2018. The neglected otters in China: distribution change in the past 400 years and current conservation status. *Biological Conservation*, **228**: 259−267.

Zhang T, Li YX. 2020. Spatial distribution, fractions and risk assessment of five heavy metals in the sediments of Jialing River: a tributary of the Yangtze. *Environmental Earth Sciences*, **79**(19): 464.

Zilio MI, Bohn VY, Piccolo MC, Perillo GME. 2021. Land cover changes and ecosystem services at the Negro River Basin, Argentina: what is missing for better assessing nature's contribution?. *International Journal of River Basin Management*, doi: 10.1080/15715124.2021.1901727.