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ABSTRACT

Conservation depends on acquiring timely knowledge on species' ecology to alleviate the risks of biodiversity loss driven by anthropogenic stressors. Himalayan freshwater ecosystems are exceedingly threatened by the compounding effects of rising developmental pressure and climate change, jeopardizing biodiversity nested within this imperilled landscape. Riverine ecosystems of the Himalayan foothill forests of India are a stronghold of the vulnerable smooth-coated otter populations. This study entails the understanding of resource utilisation by the smooth-coated otter (*Lutrogale perspicillata*) in terms of habitat use and dietary composition in seven rivers along the Himalayan foothills in India. We surveyed 121.09 km of rivers for otter signs and associated habitat variables. Using Generalised Linear Models, we assessed the factors influencing otter habitat use. We estimated the relative abundance and catch per unit effort of fish species and evaluated otter diet based on spraint samples ($n = 120$) using frequency of occurrence and score-bulk estimate methods. Habitat use by otters is governed by a combination of habitat components, which are intricately linked to different requirements such as feeding, grooming, and denning. We found that habitat use was positively associated with channel depth, moderate vegetation, and bank substrate types – bedrock, boulders, sand, and grass. Whereas, increasing distance to escape cover, sparse vegetation, channel width, and anthropogenic disturbance negatively influenced habitat use. Dietary analyses revealed that relatively abundant fish species *viz.*, *Tor putitora* and *Barilius vagra*, predominated the diet of otters. Echoing the principles of optimal foraging theory, our results indicated that small-medium sized fishes of the size range 79.05–199.92 mm, were consumed more often, and larger fishes (> 263.24 mm) were consumed opportunistically. Our findings provide important conservation insights on the status of the smooth-coated otter, their interactions with different habitat components, and dietary spectrum in rivers of the Himalayan foothills. Overall, our study gives cognizance to the importance of preserving freshwater and riparian habitats to ensure the persistence of otters and their prey in the region.

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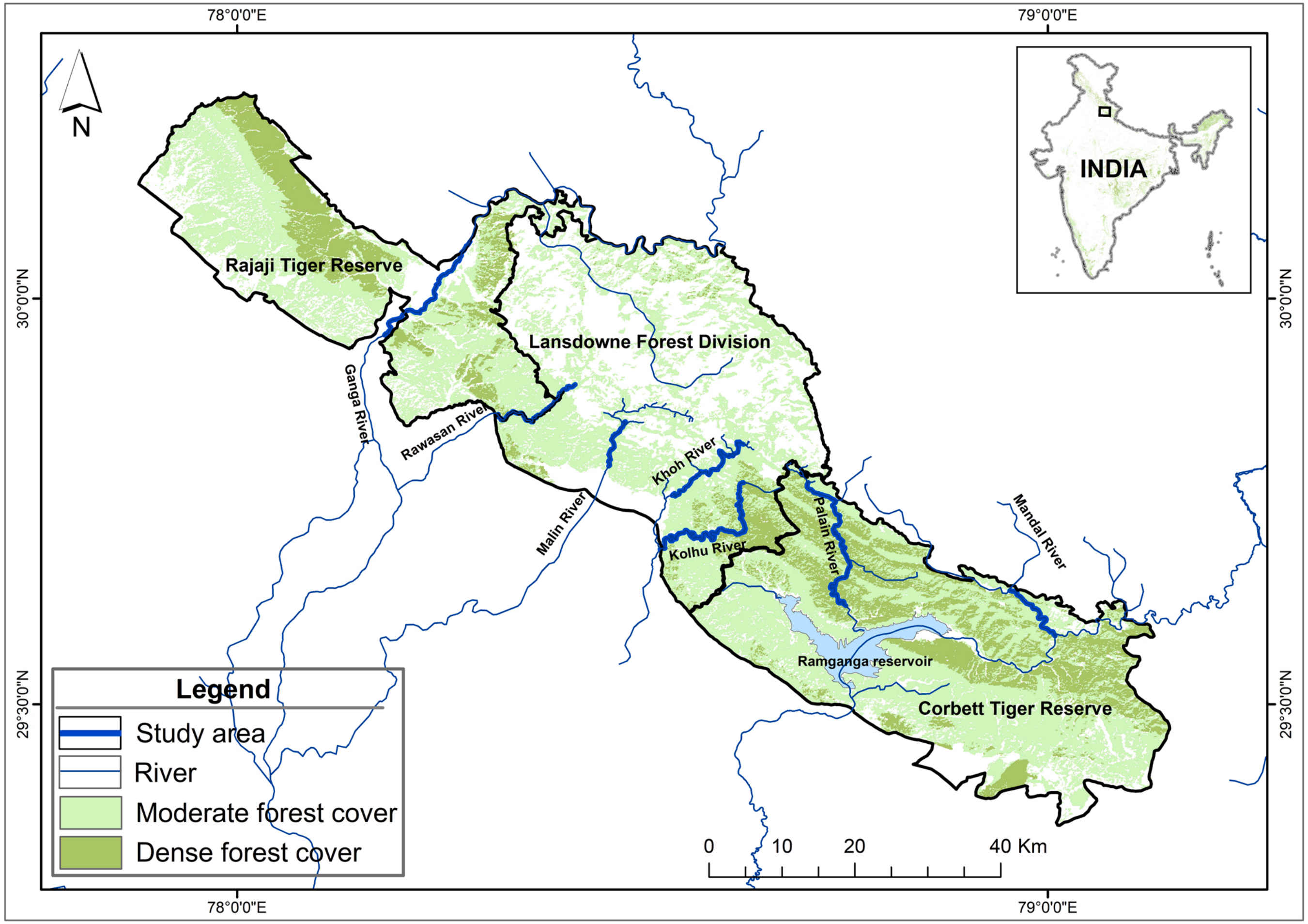

Fig. 1. Distribution of rivers surveyed for smooth-coated otter in the Himalayan foothills region of India encompassing Rajaji Tiger Reserve, Lansdowne Forest Division, and Corbett Tiger Reserve.

1. Introduction

The Anthropocene has brought upon the world, unprecedented development, propelling biodiversity loss at an accelerated rate (Ceballos et al., 2020). Freshwater ecosystems, which constitute only 0.8% of the earth's surface (Gleick, 1996), are among the world's most threatened ecosystems, disappearing three times faster than their terrestrial counterparts (Dudgeon et al., 2006; Gardner and Finlayson, 2018). A combination of the prevalent threats *viz*., habitat loss and degradation, flow modification, water pollution, overexploitation, and invasive species, compounded by the global impacts of climate change, have resulted in severe biodiversity loss in freshwater ecosystems, as compared to the most critically threatened terrestrial ecosystems (Sala et al., 2000; Dudgeon et al., 2006; Vörösmarty et al., 2010). The general paucity of knowledge and global awareness on biodiversity of freshwater ecosystems has further escalated the issues pertaining to freshwater-centric conservation and management practices (Dudgeon et al., 2006). The ubiquitous conservation strategies applied to terrestrial ecosystems are usually not focussed on freshwaters, although, some sections of rivers and streams may come within the ambit of the protected area network (Abell et al., 2017; Bastin et al., 2019). These practices are not adequate as around 1/3rd of the global vertebrate species reside in freshwater ecosystems (Dudgeon et al., 2006). In India, the protected area network, covering around 5% of the total geographical area of the country, is largely focussed on terrestrial ecosystems (Ghosh-Harihar et al., 2019). Conservation of riverine biota especially poses a unique challenge as rivers are open, directional systems, with species occupying various zones of habitat, including aquatic species (*e.g.*, fish, river dolphin), and semi-aquatic species (*e.g.*, turtles, crocodiles, otters) (Welcomme, 1979; Dudgeon et al., 2006). Planning effective conservation measures can be incredibly challenging if the species' ecological requirements are unknown (Kerley et al., 2012), which is a major pitfall in case freshwater species. Thus, the need of the hour is to understand how freshwater species interact with their environment, which can help shape effective conservation practices, particularly as undisturbed habitats are becoming increasingly scarce and fragmented.

Otters are carnivorous mammals of the family Mustelidae, sub-family Lutrinae, distinguished by their unique array of semi-aquatic adaptations (Kruuk, 2006). Physiological and morphological adaptations of otters, have enabled them to cope with the energetic costs of living in semi-aquatic conditions (Williams, 1999). Concordant to their unique adaptations, otters have been able to colonize a wide variety of habitats, ranging from open seas to peat swamp forests, high altitude lakes and streams to river basins and marshes, and even occur in urbanised landscapes such as Singapore (Mason and Macdonald, 1987; Ruiz-Olmo et al., 1998a, 1998b; Khoo and Lee, 2020). Otters use available habitats to meet various requirements such as movement, foraging, denning, grooming, and social interactions (Hussain, 1993). Ideally designated as "*wetland ambassadors*", otters regulate aquatic food chains, aid in nutrient transfer, and are sensitive to the degradation of these threatened ecosystems (Foster-Turley et al., 1990; Hammerschlag et al., 2019). As apex predators of aquatic ecosystems, otters are highly susceptible to environmental perturbations due to anthropogenic stressors (Peterson and Schulte, 2016). The Red List Index of the world's mammals indicates a global declining trend, with exceptionally high deteriorations in South and Southeast Asia (Hoffmann et al., 2010). All the Asian otter species included in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species are undergoing severe population decline. Of the 13 species of otters found globally, India is home to three species *viz*., smooth-coated otter (*Lutrogale perspicillata*), Eurasian otter (*Lutra lutra*) and small-clawed otter (*Aonyx cinereus*) (Pocock, 1949; Hussain, 1993). The smooth-coated otter has the widest distribution range in the country, occurring southward from the Himalaya, except the arid regions of western India (Prater, 1971; Hussain and Choudhury, 1997). Smooth-coated otters occur in a wide range of habitats ranging from forested rivers and freshwater wetlands to mangroves (Hussain and Choudhury, 1995). Being a piscivorous species, it is entirely dependent on the aquatic environment for its dietary needs, however, it also opportunistically consumes birds, amphibians, and crustaceans to meet additional energy requirements (Hussain and Choudhury, 1998). Despite having a wide distribution range, the species is facing extensive decline owing to habitat loss and degradation, depletion of prey base, poaching and exploitation, earning it the Vulnerable category in the IUCN Red List (de Silva et al., 2015). The intensity of the prevalent threats is further aggravated by the complex life-history traits of the species, as most freshwater otters are habitat specialists, found in low densities, requiring large extents of suitable interconnected freshwater habitats (Hussain, 1997; Bonesi and Macdonald, 2004).

The Himalayan biodiversity hotspot (Mittermeier et al., 2004) is becoming increasingly threatened, as the sub-tropical and tropical forests are undergoing severe biodiversity loss due to high anthropogenic pressure combined with climate change impacts (Pandit et al., 2007; Grumbine and Pandit, 2013; Dimri et al., 2018). Perceiving how an apex freshwater carnivore interacts with its environment in the forested catchments of the Himalayan foothills will significantly aid in elevating the existing knowledge about the species' ecology. In this study, we attempted to assess the factors influencing the habitat use of smooth-coated otter in seven Himalayan foothill rivers *viz*., Ganga, Kolhu, Palain, Rawasan, Mandal, Malin and Khoh. We also evaluated the dietary spectrum of the species in the landscape. We were interested in understanding the predominant factors that significantly influence otter habitat use and assessing their dietary composition.

2. Materials and methods

2.1. Study area

The study was conducted in seven rivers *viz*., Ganga, Kolhu, Palain, Rawasan, Mandal, Malin and Khoh of the Himalayan foothills region in the state of Uttarakhand, India (Fig. 1) from December 2018 to June 2019. The study area encompassed the above-mentioned rivers within the Rajaji Tiger Reserve (RTR), Corbett Tiger Reserve (CTR), and Lansdowne Forest Division (LFD), a crucial wildlife corridor connecting the RTR and CTR (Johnsingh and Williams, 1999). The CTR and RTR are classified as protected under the Wild Life (Protection) Act, 1972, whereas the LFD is a reserve forest, classified under the Indian Forest Act, 1927 and has some degree of protection. The surveyed rivers were perennial, except Malin (Bhutiani et al., 2018). Contiguous tracts of the forested landscape in this protected area network are crucial to the survival of megafauna such as the tiger (*Panthera tigris*) and the Asian elephant (*Elephas maximus*) (Johnsingh and Williams, 1999; Harihar et al., 2009). The study area falls within the Himalayan foothills region, which is characterised by rugged terrain, conspicuous flat-bottomed valleys known as "*duns*", and rocky seasonal streams called "*raus*" (Karan, 1966; Mani, 1974; Rawat and Mukherjee, 2005; Jerath et al., 2006). High biological productivity of the riverine ecosystems of this region is attributed to characteristics of the rivers such as moderate temperature, low current, and the prevalence of deep pools (Joshi, 1994). The region experiences a subtropical climate, with three distinct seasons – winter, summer and monsoon (Sati, 2020). The elevation of the surveyed river stretches ranges between 270 and 780 m. Vegetation in the study area is comprised of Northern Indian Moist Deciduous Forest and Northern Tropical Dry Deciduous Forest (Champion and Seth, 1962). Dominant vegetation includes *Shorea robusta*, with associate species *viz.*, *Mallotus philippensis, Terminalia tomentosa, Butea monosperma, Adina cordifolia,* and *Schleichera oleosa.* Riparian species include *Syzigium cumini, Ficus saemocarpa,* and *Syzigium heyneanum.* Grasses in the extensive plains known as "*chaurs*" comprise species such as *Apluda mutica, Cynodon* spp.*, Saccharum* spp.*, Vetiveria zizanioides,* and *Chrysopogon* spp. Other rare species of flora are *Wallichia densiflora, Schefflera venulosa,* and *Diplomeris hirsuta.*

2.2. Factors influencing habitat use

2.2.1. Field methods

We conducted continuous foot surveys along both banks of the rivers traversing a total of 121.09 km (Ganga: 19.23 km; Kolhu: 29.59 km; Palain: 26.11 km; Rawasan: 14.28 km; Mandal: 10.95 km; Malin: 4.5 km; and Khoh: 16.43 km) to record otter signs and habitat variables (Table 1). The track surveyed for otter signs extended up to 25 m from the shoreline (Hussain and Choudhury, 1997). In order to ascertain the presence of otters in an area, we used both direct sightings and indirect signs (spraints, tracks, dens, grooming signs). Each direct sighting and number of indirect signs in a location were considered as a single entity. Wherever we observed communal latrine sites, we considered spraints more than 1 m apart as distinct (Kruuk et al., 1986). We conducted three replicate surveys with an interval of at least seven days between each survey. We recorded habitat variables at every 250 m intervals, including the locations where otter signs were observed. We selected seven habitat variables, *a priori* based on literature and by conducting reconnaissance survey (Anoop and Hussain, 2004; Nawab and Hussain, 2012a). The variables included mean channel depth, mean width, and mean velocity as stream characteristics, and vegetation cover, distance to escape cover (hereafter, escape distance), percentage cover of bank substrate types *viz.*, sand, gravels, pebble, boulder, bedrock, mud and grass, and anthropogenic disturbance were recorded as bank characteristics (Table S1). We categorised vegetation cover, using ocular estimation, as dense/moderate/sparse, and anthropogenic disturbance was categorised as presence/absence. Escape distance was measured as the distance between the shoreline and the nearest vegetation cover or rock pile, which provide shelter to otters (Nawab and Hussain, 2012a). We construed anthropogenic disturbance as any form of human activity that caused degradation, loss, or fragmentation of suitable otter habitat at 250 m from the shoreline; these included construction activities, sand and boulder collection, illegal fishing, settlements of the pastoral *gujjar* community, vehicular road, river channelisation, bank concretization, dams, barrages, and pollution.

2.2.2. Analytical methods

Each river was divided into 1 km segments in ArcGIS 10.3 (ESRI, Redlands, USA). Habitat variables collected at 250 m intervals were averaged for each segment. We selected the category falling in a maximum number of 250 m points within each 1 km segment for the categorical variables – vegetation cover and disturbance. We used the total number of signs observed in each segment as the dependent variable and all the seven variables described above as explanatory variables, including categorical and continuous data. We used Spearman's rank correlation to test for multicollinearity among variables. Correlated variables with Spearman's rank correlation coefficient (Spearman's ρ) > 0.7, were excluded. We evaluated the factors affecting habitat use of otters with Generalized Linear Model (GLM) using the package MuMIn (Barton and Barton, 2015) in freeware R version 4.0.3 (R Core Team, 2020). Quantitative habitat variables were Z-transformed before performing the GLM analysis to bring data to the same scale. The data was tested for overdispersion and suitable error distributions were used accordingly (negative binomial). For model selection, we used Akaike's

Table 1
Baseline details of the seven rivers surveyed in the Himalayan foothills region.

Area	River	Mean elevation ± SE (m)	Length surveyed (km)	Total 1 km segments	Otter positive segments	Otter positive segments (%)
Rajaji Tiger Reserve	Ganga	293.60 ± 2.29	19.23	18	4	22.22
Lansdowne Forest Division	Kolhu	406.71 ± 6.24	29.59	30	30	100
Corbett Tiger Reserve	Palain	423.05 ± 5.53	26.11	25	14	56
Lansdowne Forest Division	Rawasan	474.76 ± 8.03	14.28	13	5	38.46
Corbett Tiger Reserve	Mandal	496.73 ± 3.35	10.95	11	10	90
Lansdowne Forest Division	Malin	516.33 ± 17.06	4.5	5	0	0
Lansdowne Forest Division	Khoh	590.65 ± 10.81	16.43	16	9	56.25
		Total	**121.09**	**118**	**72**	**61.02**

information criterion adjusted for small sample sizes (AICc; Burnham and Anderson, 2002), and considered the models with ΔAICc < 2 as the best model.

2.3. Relative abundance and catch per unit effort (CPUE) of fish species

We conducted catch and release fishing in three sites along the upper, middle and lower courses of each river using cast net (10 mm mesh size; diameter of 4 m), gill net (15 – 34 mm mesh size; panel length of up to 5 m), and drag net (fine mosquito net). We evaluated the relative abundance of each species to assess the commonly occurring species in the area. The number of individuals of each species and time invested for every catch was recorded. CPUE for each species was estimated as the number of individuals captured per hour in one net, where 10 nets deployed in a standardised time of one hour constituted as a unit effort. The time of net deployment was standardised in hours.

2.4. Diet composition

2.4.1. Preparation of reference material

We prepared reference material for identifying fish remains in otter spraints by (a) using available specimens of species from the study area preserved in the National Repository at Wildlife Institute of India and (b) by collecting dead fish found during the survey. The scale shape and patterns (circuli, radii, foci) were observed under 4 X magnification of compound microscope, and the signature patterns of each species were recorded (Webb, 1975; Bräger and Moritz, 2016).

2.4.2. Spraint collection and sample preparation

We collected 182 spraint samples during the survey. Fresh spraints were characterised by dark grey colour, odour, sliminess, and high moisture content (Bas et al., 1984). Samples were stored in 70% ethanol-filled vials at room temperature. For dietary analyses, the samples were soaked in sodium carbonate (Na_2CO_3) solution overnight, washed under tap water using 1 mm sieve, then dried in a hot air oven at 50 °C, and weighed individually.

We identified prey remains by comparing them with references prepared during the study, and categorized items into major prey categories (fish/crab/bird) following the methodology described by Anoop and Hussain (2005). Ten scales were randomly examined covering all the grids of a petri-dish. In case the examined scales belonged to the same species, no further scales were chosen from that sample. If different species were identified from the first ten scales, another ten scales were examined. We repeated this procedure as the number of species increased until asymptote was achieved (Hermsen and Maarseveen, 2011). Scales were stained using methylene blue and examined under a compound microscope with 4 X magnification. Effort was made to identify prey up to species level, but due to uncertainty in some cases, we identified prey up to the genus level only. To ascertain the adequate sample size for dietary analysis, we plotted cumulative frequency graph of prey species found and the number of samples analysed following Hussain (1993). An asymptote was achieved at 22 samples (Fig. S1). We analysed 120 samples of the total 182 samples collected for dietary study.

2.4.3. Dietary analyses

We quantified dietary spectrum following two approaches: frequency of occurrence (FO) and score-bulk estimate (SBE). In FO, the number of occurrences of a prey category was expressed as a percentage of occurrences of all prey categories. SBE minimizes the discrepancy of over-representation of minor items and underrepresentation of major items consumed. In this method, the proportion of each prey item was estimated and scored from 1 to 10, with 10 being the total score for one spraint. The score for each category was then multiplied by the dry weight of the spraint and the resulting figures were expressed as a percentage of the sum of scores for each prey category (Wise et al., 1981; Hussain and Choudhury, 1998).

2.4.4. Estimation of fish size

A positive correlation occurs between vertebrae length and fish length (Wise, 1980; Anoop and Hussain, 2005). Fish vertebrae were obtained by boiling specimens belonging to different size classes and washing off the digestible parts using a sieve under running water. We measured the length of 202 vertebrae belonging to 30 individuals of different fish species of known total length by randomly selecting and measuring ten vertebrae from each sample using digital Vernier calliper and segregating them into 11 different size classes: 0.5–1 mm, 1–1.5 mm, 1.5–2 mm, 2–2.5 mm, 2.5–3 mm, 3–3.5 mm, 3.5–4 mm, 4–4.5 mm, 4.5–5 mm, 5–5.5 mm, and 5.5–6 mm. We evaluated the relationship between vertebrae length and fish length using linear regression (Fig. S2). The proportions of vertebrae size classes will provide an estimation of the corresponding size classes of fish consumed. Vertebrae length is related to total fish length by the linear relationship:

Total fish length= 61.56 x Vertebrae length – 0.325

3. Results

3.1. Habitat use

Habitat characteristics from 118 segments (712 sampling points) including 72 segments (301 sampling points) with otter presence were utilised in the analyses. We surveyed a combined length of 121.09 km along the seven rivers and found signs of otter presence in 61.02% of the 118 surveyed sites (Table 1). Of the total surveyed sites within the protected areas (CTR and RTR) ($n = 54$), 51.85% sites ($n = 28$) were positive for otter presence, whereas among the total surveyed sites in the non-protected area (LFD) ($n = 64$), 68.75% were otter positive sites ($n = 44$), indicating that suitable otter habitats occur outside the protected areas as well. The encounter rate (signs/km) of smooth-coated otter, in decreasing order, for each river was (mean ± SE): 7.67 ± 1.60 (Kolhu), 6.73 ± 2.29 (Khoh), 5.7 ± 1.09 (Palain), 5.38 ± 1.43 (Mandal), 0.93 ± 0.51 (Ganga), 0.55 ± 0.11 (Rawasan) (Fig. 2). Otter signs were not recorded from the Malin River, hence, habitat data obtained from this river was excluded from the analyses.

Spearman's rank correlation test indicated that none of the variables were strongly correlated (Spearman's $\rho < 0.7$ for all pairs) (Table S2), hence we used all the variables in the same model. Overdispersion test performed on the Poisson model indicated that the data was over-dispersed ($P < 0.001$), therefore we used negative binomial to fit models to the data. Negative binomial models are better suited to fit count data that are skewed and over-dispersed with wide-ranging values (Anscombe, 1949; Bowden et al., 1969). The top-ranked model (ΔAICc = 0) explaining habitat use of otters included channel depth and width, vegetation cover, escape distance, percentage cover of bedrock, boulder, sand and grass, and anthropogenic disturbance (Table 2), with an Akaike weight (ω_i) = 0.55, implying a 55% chance of being the best among the evaluated models. The second-best model with ΔAICc = 1.9 and Akaike weight (ωi) = 0.22, included the variable channel velocity in addition to the variables included in the best-fit model (Table 2). Variables in the top-ranked model showing a significantly strong positive association with otter habitat use were channel depth ($\beta = 0.496$, $P < 0.001$), moderate vegetation cover ($\beta = 0.861$, $P < 0.001$), percentage cover of bedrock ($\beta = 0.493$, $P < 0.001$), boulders ($\beta = 0.417$, $P < 0.001$), sand ($\beta = 0.626$, $P < 0.001$), and grass ($\beta = 0.275$, $P < 0.001$) (Table 3). Whereas the negatively associated habitat variables were escape distance ($\beta = -0.381$, $P < 0.001$) sparse vegetation cover ($\beta = -1.345$, $P = 0.01$), channel width ($\beta = -1.186$, $P < 0.001$), and anthropogenic disturbance ($\beta = -0.642$, $P < 0.001$).

3.2. Relative abundance of fish species

We recorded 388 individuals of fish belonging to 22 species and representing six families (Table S3). Species belonging to the family Cyprinidae were the most commonly recorded, followed by the families Danionidae, Gobiidae, Channidae, Mastacembelidae, and Sisoridae. Intensive sampling for capturing and identifying all fish species was not possible due to logistic constraints. We invested 50.65 hrs in fish sampling and observed that mean individuals captured was highest using gill net (6.89 ± 1.59), followed by cast net (3.52 ± 0.68), and lowest for drag net (1.5 ± 0.75) (Table S4). We observed that *Garra gotyla* was the most abundant species, followed by *Barilius vagra* and *Tor putitora* (Fig. 3).

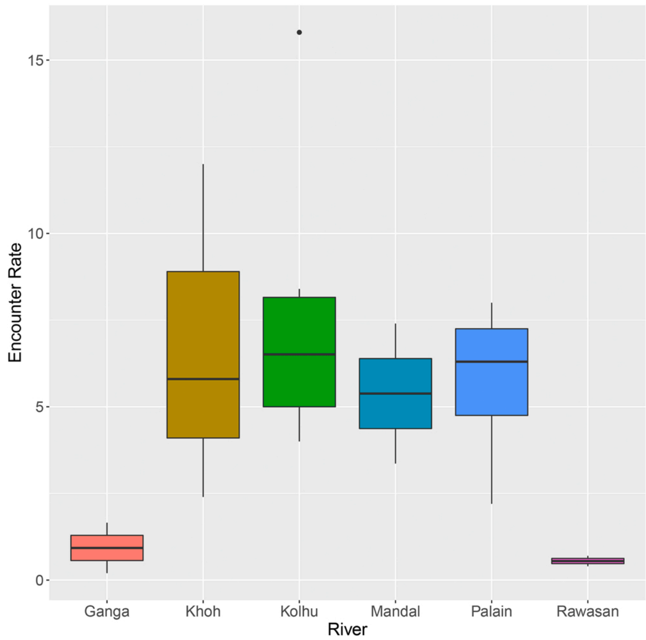

Fig. 2. Box and whiskers plot of encounter rate (otter signs/km) across the seven rivers surveyed in the Himalayan foothills in Uttarakhand, India. Boxes show median and quartiles. Whiskers show maximum and minimum defined as > 1.5 times the interquartile range, excluding outliers.

Table 2
Summary of five models examining the factors influencing otter habitat use, with each model's Aikaike information criteria adjusted for small sample sizes (AICc), difference in AICc from the top-ranked model (ΔAICc), and Akaike weight.

Response variable	Models	Predictor variables	AICc	ΔAICc	Weight
Otter signs	1	~Width+ Depth+ Vegetation cover+ Disturbance+ Escape cover+ Bedrock+ Boulder+ Grass+ Sand	676	0.0	0.551
	2	~Width+ Depth+ Velocity+ Vegetation cover+ Disturbance+ Escape cover+ Bedrock+ Boulder+ Grass+ Sand	678	1.9	217
	3	~Width+ Depth+ Vegetation cover+ Disturbance+ Escape cover+ Bedrock+ Boulder+ Mud+ Grass+ Sand	679	2.4	166
	4	~Width+ Depth+ Vegetation cover+ Escape cover+ Disturbance+ Velocity+ Bedrock+ Boulder+ Grass+ Mud+ Sand	681	4.3	0.064
	5	~Width+ Sand+ Vegetation cover+ Escape cover+ Disturbance+ Bedrock+ Boulder+ Grass	689	12.6	0.001

Table 3
Summary of variables in the top-ranked model (ΔAICc = 0.0) explaining the factors influencing otter habitat use.

Predictor variable	Estimate (β)	SE	*Z*-value	*P*-value
Width	-1.186	0.196	5.98	<0.001
Depth	0.496	0.130	3.76	<0.001
Vegetation (moderate)	0.861	0.144	5.88	<0.001
Vegetation (sparse)	-1.345	0.527	2.52	0.01
Escape distance	-0.381	0.098	3.81	<0.001
Disturbance (presence)	-0.642	0.124	5.09	<0.001
Bedrock	0.493	0.073	6.68	<0.001
Boulder	0.417	0.078	5.27	<0.001
Sand	0.626	0.067	9.30	<0.001
Grass	0.275	0.036	7.51	<0.001

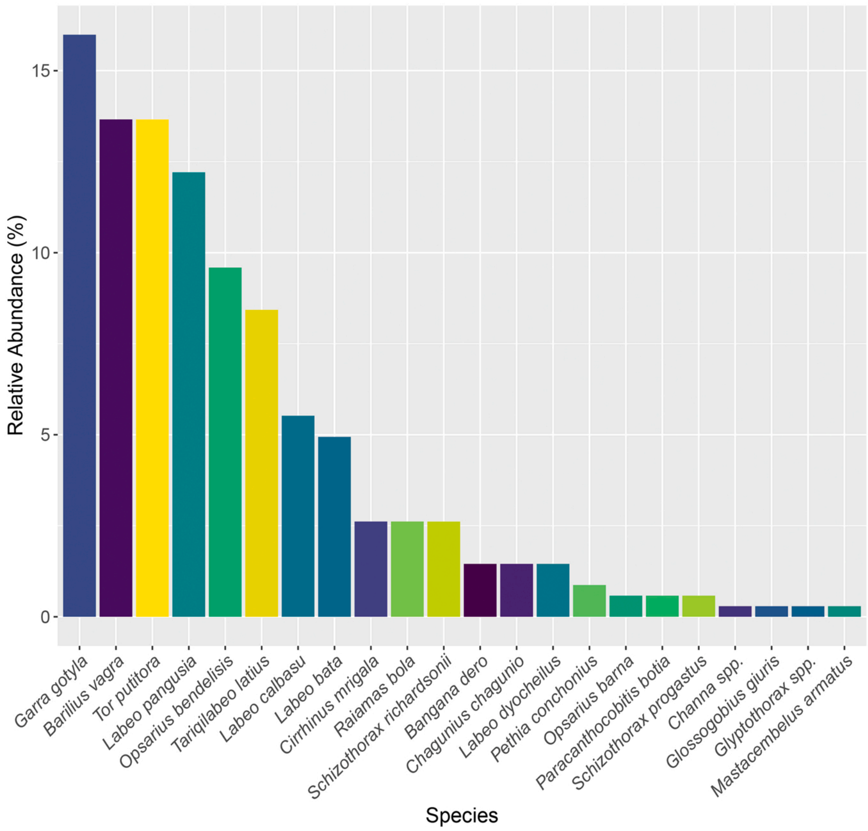

Fig. 3. The relative abundances of fish species in the seven rivers surveyed in the Himalayan foothills in Uttarakhand, India.

3.3. Diet composition

3.3.1. Proportions of prey categories

Diet of the smooth-coated otter constituted predominantly of fish (FO = 95%; SBE = 96.48%), followed by crabs (FO = 4.17%; SBE = 3.13%) and birds (FO= 0.83% and SBE = 0.39%) (Table S5). We identified 15 fish species in otter spraints (n = 120). The major proportion of otter diet was comprised of *T. putitora* (FO = 21.93%, SBE = 25.87%), followed by *Tariqilabeo latius* (FO = 15.61%, SBE = 8.41%), and *B. vagra* (FO = 12.96%, SBE = 22.44%), while *Channa* spp. (FO = 0.99%, SBE = 0.35%), *Labeo calbasu* (FO = 0.34%, SBE = 0.14%) and *Pethia conchonius* (FO = 0.33%, SBE = 0.21%) formed the least proportion (Table 4).

3.3.2. Prey size

The spraint analysis revealed a high occurrence of fishes belonging to small and medium size classes: 79.05 mm, 110.98 mm, 136.54 mm, 168.69 mm, and 199.92 mm corresponding to the vertebrae length classes 1 – 1.5 mm, 1.5 – 2 mm, 2 – 2.5 mm, 2.5 – 3 mm, and 3 – 3.5 mm respectively (Fig. 4). Representation of fishes belonging to very small (53.08 mm) and large (263.24 – 354.26 mm) size classes was low in the spraints.

4. Discussion

Smooth-coated otter populations are facing continuous decline due to habitat loss and degradation as a consequence of the pervasive anthropogenic pressure, water pollution, poaching, and illegal trade (de Silva et al., 2015). Ecological understanding of how otters interact with their environment and their role as an apex predator in the highly threatened freshwater ecosystems is imperative for planning effective conservation strategies for the species. Here, we have analysed the factors influencing habitat use and the diet of smooth-coated otter in seven rivers of the Himalayan foothills region of India. The Rajaji-Corbett landscape chosen for this study is of high conservation significance, which serves as a refuge to the biodiversity of this region. These forested tracts including the riverine ecosystems, are under tremendous pressure due to increasing developmental activities leading to accelerated deforestation, and consequent disruption of the hydrological cycle resulting in high monsoonal flow and reduced dry season flow, further aggravated by climate change, endangering aquatic biota (Ives, 1989; Grumbine and Pandit, 2013). Rivers and streams in this landscape, especially those within the limits of a protected area are strongholds of smooth-coated otter populations, as evident from the high encounter rates found in this study. High otter signs observed in the Kolhu, Mandal, Khoh and Palain rivers, evident from the sprainting intensity and the frequency with which signs were recorded (100%, 90%, 56.25%, and 56% positive sites respectively) suggested that the otter populations were utilizing the most available habitats, that had ideal conditions to support them, *viz*., intact riparian vegetation cover, available sites for denning and foraging, and absence of anthropogenic disturbance, further augmented by the protected status of the Rajaji-Corbett landscape. We found that the rivers Kolhu and Khoh, within the LFD, had a high percentage of otter signs (68.75%), indicating that these rivers, although falling outside the protected area boundaries according to the Wild Life (Protection) Act, 1972, are considerably undisturbed areas and thereby offer conducive habitats for otters. We observed that habitat use of smooth-coated otter was influenced by a multitude of factors including channel depth and width, vegetation cover, bank substrate type, escape distance, and anthropogenic disturbance. Dietary analysis revealed that otters consumed fish species that were relatively more abundant in the rivers, such as the endangered golden mahseer (*T. putitora*). Fishes belonging to the small – medium size classes were consumed more frequently in comparison to fishes of larger size class. These findings indicate towards the requirement of a holistic approach in planning conservation strategies for otters pertaining to their resource requirements in the freshwater ecosystems they inhabit.

Table 4
Frequency of occurrence (FO) and score bulk estimate (SBE) of fish species in otter spraints (n = 120) collected from the seven rivers surveyed in the Himalayan foothills in Uttarakhand, India.

Species	Occurrences	FO (%)	SBE (%)
Tor putitora	66	21.93	25.87
Tariqilabeo latius	47	15.61	8.41
Barilius vagra	39	12.96	22.44
Labeo pangusia	34	11.29	14.33
Labeo dyocheilus	26	8.64	7.08
Opsarius bendelisis	22	7.31	8.58
Garra gotyla	22	7.31	4.53
Chagunius chagunio	9	2.99	3.00
Unidentified species	9	2.99	1.47
Opsarius barna	6	1.99	2.33
Glyptothorax spp.	7	2.33	0.48
Mastacembelus armatus	5	1.66	0.32
Raiamas bola	4	1.33	0.46
Channa spp.	3	0.99	0.35
Labeo calbasu	1	0.34	0.14
Pethia conchonius	1	0.33	0.21
	Total = 301		

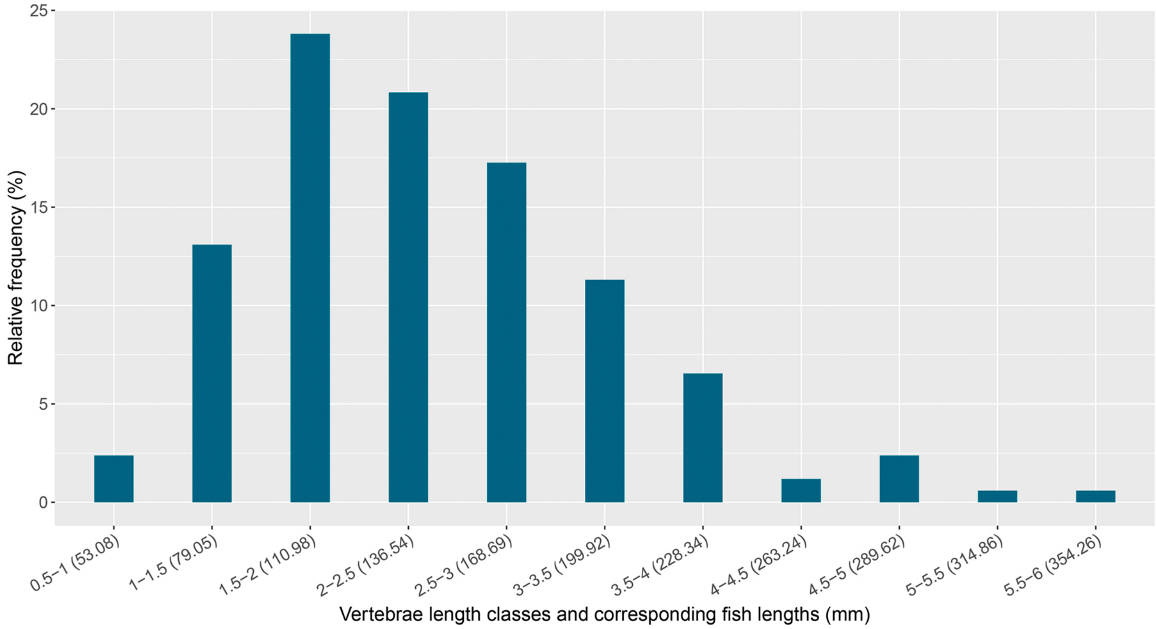

Fig. 4. Fish size classes found in otter spraints ($n = 120$) collected from the seven rivers surveyed in the Himalayan foothills in Uttarakhand, India. Numbers within parenthesis are the corresponding fish lengths (mm).

4.1. Habitat use

The distribution and availability of resources are the deciding factors of how a species interacts with its habitat (Morris, 1987). Various factors such as river width and depth, vegetation cover, bank substrate type, prey availability, and anthropogenic disturbance influence the habitat use of otters in a landscape (Madsen and Prang, 2001; White et al., 2003; Anoop and Hussain, 2004; Nawab and Hussain, 2012a, 2012b). As observed in this study, the positive association of channel depth with otter habitat use, can be attributed to otters foraging in pools, characterised by deep and slow-moving waters. Pools sustain a higher abundance of fish as they provide greater habitat complexity and diversity of micro niches for fishes to exploit (Gorman and Karr, 1978; Langeani et al., 2005), thereby providing otters with adequate prey in a localised area and enabling them to forage efficiently with minimum energy expenditure. Moreover, it was observed that during the dry winter season, when water level recedes, pools provide refuge for fishes, hence serving as ideal foraging grounds for otters. Otters consume small prey under water, but medium to large-sized prey are mostly carried to the nearest bank, island, or rock for consumption, a behaviour observed in the Eurasian otter (*L. lutra*) (Kruuk, 1995; Ruiz-Olmo et al., 1998a, 1998b). Otters being negatively influenced by river width can be explained by the scarcity of resting or feeding grounds and the dispersed nature of prey, which may be energetically demanding, thereby precluding otters from foraging efficiently in wider river channels.

River otters avoid areas which lack resting sites and escape cover, despite those areas being suitable in other aspects (Melquist and Hornocker, 1983). Moreover, the availability of suitable escape cover also determines the extent to which otters can tolerate disturbance in a given habitat (Foster-Turley, 1990). Similarly, our study indicated that the smooth-coated otter had a negative association with increasing distance to escape cover. Otters have a proclivity to use areas with moderate to dense riparian vegetation (*Pteronura brasiliensis*: Duplaix, 1980; *L. lutra*: Jenkins and Burrows, 1980; *L. canadensis*: Bowyer et al., 1995; *Lontra provocax*: Medina-Vogel et al., 2003; *Lutrogale perspicillata*: Nawab and Hussain, 2012a; *Aonyx cinereus*: Raha and Hussain, 2016). Vegetation along rivers and streams serves as an escape cover for otters during foraging or movement, with potential resting and denning sites, as otters often use cavities among tree roots for denning (Nawab and Hussain, 2012a). In corroboration with former studies, we found a significant positive association of otter signs with moderate riparian vegetation cover, while sparse vegetation cover showed a negative influence. During many instances throughout the study, otters were seen foraging in pools with moderate riparian vegetation along the banks, which they used as an escape cover. Although, bare banks with sparse vegetation had seemingly low otter signs, we assume that otters might have taken to water to travel through such areas to reach suitable habitats for their sustenance; therefore, it should not be concluded that these habitats are entirely unusable by otters. These suboptimal habitats may function as corridors, facilitating the movement of otters across optimal habitat patches with abundant resources.

We observed that a combination of bank substrates such as bedrock, boulders, sand and grass have a positive influence on otter habitat use, indicating that otters use different substrate types according to their requirements of grooming, denning, and travelling. In the study area, smooth-coated otters constructed dens in rock crevices and clayey banks sheltered with vegetation cover. The species is known to prefer rocky stretches along rivers that provide them with shelter and denning opportunities, and sandy stretches for grooming, an affiliative behaviour that serves otters to maintain their fur texture for thermoregulation and also as a means of bonding among conspecifics (Hussain and Choudhury, 1995; Anoop and Hussain, 2004; Nawab and Hussain, 2012a; Liwanag et al., 2012). We observed that otters showed strong fidelity towards some of the grooming and sprainting sites, a behaviour previously reported in otter species (Anoop and Hussain, 2004; Gorman et al., 2006). Site fidelity behaviour provides an insight into suitable habitats with stable resources and species' familiarity with their environment (Phillips et al., 1998; Powell, 2000). Our findings indicate that habitat heterogeneity is crucial for otters, as they choose to interact with different habitat characteristics according to their requirements.

Escalating anthropogenic pressure on freshwater resources has led to extensive loss of biodiversity in these critical ecosystems (Dudgeon et al., 2006). As an elusive carnivore, otters have been reported to show temporal or spatial avoidance of areas with human disturbance, although some species of otters, including the smooth-coated otter, are adapting to modified habitats and human presence (Khoo and Lee, 2020; Macdonald, 1983; Weinberger et al., 2016). Otters in this landscape showed avoidance of areas with anthropogenic disturbance, with habitat use being clustered in areas least accessible to humans. Rivers and streams often serve as boundaries to delineate different zones of protected areas, hence are prone to certain levels of anthropogenic disturbance. Incidences of disturbance such as illegal fishing, canalisation and concretisation of banks, sand and boulder collection, water abstraction, proximity to roads, *gujjar* and other settlements, were prevalent along the peripheries of the protected areas. Habitat fragmentation caused by these intermittent disturbed stretches are an impediment to the movement of specialised narrow-niche species like otters that depend on linear networks of river and stream habitats.

4.2. Diet composition

Prey choice among otters largely depends on the most abundant resources in their environment (Kruuk, 1995; Hussain and Choudhury, 1998). Concordant to previous findings, our study reveals that fishes constitute the major prey item (> 95%) in the diet of smooth-coated otter (Hussain and Choudhury, 1998; Anoop and Hussain, 2005; Nawab and Hussain, 2012b). Of the 15 species of fishes recorded in the diet of smooth-coated otter, we observed that species of the family Cyprinidae constitute a major proportion. Species with higher relative abundance in the environment accounted for a larger proportion of otters' diet. For instance, *T. putitora* which constituted a major proportion of otter diet, was relatively more abundant in the studied rivers. Interestingly, Nawab and Hussain (2012b) observed that although the abundance of *Tor* spp. was higher during winters, their occurrence in spraints was low. Contrary to the findings of Nawab and Hussain (2012b), our results conform to the opportunistic behaviour of the species consuming relatively more abundant prey. Other species with higher relative abundance *viz*., *Barilius vagra*, *Tariqilabeo latius*, and *Labeo pangusia*, also constituted a major proportion of otter diet. We observed that although *Garra gotyla* was the most abundant species recorded, its proportion in otter diet was considerably lower than the proportion of other species of low abundance like *Labeo dyocheilus*. This could be explained by the hiding behaviour of *G. gotyla* adhering under rocks and crevices using a sucking disc located ventrally on the mouth (Nagar et al., 2012), which prevents otters from pursuing and capturing the species. Conversely, the comparatively lesser abundant benthopelagic species *viz*., *T. latius* and *L. dyocheilus*, were consumed in higher proportions. Diet of otters may vary depending on seasonality and prey availability (Hussain and Choudhury, 1998); therefore, we suggest discretion while extrapolating our findings across seasons and landscapes. We recommend that replicable studies need to be conducted across different habitat types and biogeographic zones to augment the understanding of smooth-coated otter ecology and predator-prey dynamics.

Following the principles of optimal foraging theory, otters must choose prey that yield maximum energy with minimum expense for procurement, put simply as the most 'profitable prey' (MacArthur and Pianka, 1966). Echoing this, the smooth-coated otter selects fish depending on availability and size (Anoop and Hussain, 2005). We observed that the maximum proportion of otter diet consisted of fishes belonging to the size range 79.05 – 199.92 mm. Larger fish (> 263.24 mm), which required more energy expenditure for capturing, were consumed opportunistically as evident by the low occurrence of their remains in spraints. Similarly, otters consumed secondary prey such as crabs and birds depending on availability. Consumption of secondary prey is a strategy of this opportunistic species to meet additional energy requirements for thermoregulation and post-natal care, especially during the winter season (Hussain, 1993; Hussain and Choudhury, 1998). During seasons of low resource availability, otters may have to travel longer distances in search of suitable habitats and foraging patches with adequate prey base, adding to the risk of direct confrontation with anthropogenic stressors.

5. Conclusions

In summary, we found that the smooth-coated otter uses deeper sections of rivers having moderate vegetation along with a mosaic of substrate types such as boulders, sand and mud. Alternatively, wider stretches of rivers and areas with greater escape distance and anthropogenic disturbance are avoided. Riverine ecosystems of the Himalayan foothill forests are a stronghold of the vulnerable smooth-coated otter populations; hence these ecosystems need to be conserved to maintain their structural and functional integrity. Global climate change may impact the Himalayan ecosystems, resulting in a shift in species' ranges, especially that of specialised species such as the smooth-coated otter, which is affected by variations in the annul mean temperature (Cianfrani et al., 2018; Jamwal et al., 2021). Otters being riverine-dependent species, stretches of intact riparian forests need to be maintained so that the range shifts can be countered by the stretches of undisturbed forests, which also aid in maintaining the flow of rivers originating in and regenerated by the forests. As river ecosystems are often overlooked while designing protected area networks (Flitcroft et al., 2019), riverine fauna is seldom the centre of attention of forest patrolling, hence are subjected to anthropogenic impacts resulting in habitat degradation. These ecosystems need to be brought under the ambit of protected area network or conserved using community participation and monitored regularly. Besides, we found that otters consume fishes of the species *Tor putitora*, *Tariqilabeo latius*, *Barilius vagra*, and *Labeo pangusia* belonging to the small – medium size classes of around 79.05 – 199.92 mm; therefore, prey diversity and abundance in the rivers and streams need to be ensured. With growing demands of freshwater resources, it is pertinent that the ecological integrity of these critical ecosystems is conserved in order to ensure the long-term persistence of aquatic biota, especially predators such as otters and their prey.

Declaration of Competing Interest

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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CRediT authorship contribution statement

Sayanti Basak (SB) conceived the study and designed the methodology with support from Bivash Pandav (BP), Jeyaraj Antony Johnson (JAJ), and Syed Ainul Hussain (SAH); SB collected, analysed and interpreted the data and wrote the original manuscript. SAH, BP, and JAJ supervised the study. All the authors contributed critically to the drafts and gave final approval for submission.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01896.

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