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Multi-scale habitat influences sprainting and group size of a freshwater-obligate smooth-coated otter (*Lutrogale perspicillata*) in Tungabhadra Otter Conservation Reserve, India

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Abstract

Background The impact of changing land-use patterns and associated anthropogenic threats on scale-dependent habitat use of semi-aquatic mustelids in scent-marking and social behaviour can provide important insights into the habitat ecology of smooth-coated otters (*Lutrogale perspicillata*).

Methods We sampled 180 stream segments (100–400 m) as spatial replicates of 60 1-km² sites to record indirect evidence (i.e. spraints and mass latrine sites) and group sizes of smooth-coated otters along the Tungabhadra Otter Conservation Reserve (TOCR) during the dry season. To quantify habitat, we recorded stream characteristics, riparian vegetation, and anthropogenic disturbances at the local scale, and hydro-environmental characteristics and land uses at the landscape scale. Using Markovian-chain detection and occupancy models, we assessed the multi-scale habitat use of otters in their selection of suitable areas for scent-marking based on repeated presence-absence data on spraint/latrine locations along the TOCR. We further used linear regression techniques to explore relationships between the number of individuals in smooth-coated otter group and hydro-environmental characteristics, spraint/latrine encounter rate, anthropogenic pressure, land cover, topography, and vegetation.

Results At the local scale, the probability of spraint deposition and group size decreased with anthropogenic disturbance while the probability of spraint detections decreased with grass cover. At the landscape scale, the probability of otter site use for spraint deposition and group sizes increased in southeast flowing streams. Spraint deposition increased with the proportion of sugarcane fields, whereas in contrast, group size decreased with proportion of sugarcane fields.

Conclusions Our findings highlight the first empirical evidence on multi-scale habitat use of a southern Indian population of smooth-coated otters in an inland freshwater ecosystem surrounded by the scrub jungle–agriculture matrix. We suggest that habitat models built from analytical approaches that account for correlated detections can avoid biased predictions when estimating occupancy and detection probability of semi-aquatic or riparian mammal communities with linear distributions. Our findings indicate that human activity can impose constraints on the choice

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of sites used for spraint deposition and preliminary patterns in otter groups. The study provides some crucial evidence on the need to maintain areas with minimal human interference for sustainability of freshwater reserves.

Keywords Presence-absence modelling, Inland river, Freshwater ecosystem, Semi-aquatic mammal, Smooth-coated otter

Background

Morphological degradation of river channels from sand mining, hydropower projects, tourism activity, and contamination from agricultural effluents threaten freshwater ecosystems globally (World Wildlife Fund 2018). Riparian areas play a crucial ecological role due to various characteristics, including their ability to provide moisture, offer structural complexity, maintain linear continuity, create distinct microclimates, offer diverse food resources, and influence aquatic habitats (Kondolf et al. 1996). However, these features constitute a small proportion of the total area relative to the adjacent terrestrial ecosystems (National Research Council 2002). The seasonality of streams from confounding changes in climate, the interactive nature of ecotonal habitats or edge habitats at riparian buffers, and the fluvial effects from ecohydrological regimes play a crucial role in shaping the habitat ecology of semi-aquatic mammals (Crowley et al. 2012; Holland et al. 2019; Hussain and Choudhury 1997). Particularly, inland rivers at low elevations have a greater risk of fragmentation from increasing land transformation and seasonal droughts. Riparian or semi-aquatic species in freshwater habitats are often prone to faster rates of local extinctions from climate change risks (Conroy et al. 1998; Khan et al. 2010; Suthar et al. 2017) relative to terrestrial or marine species (Collen et al. 2014; Wiens 2016). India has the greatest freshwater withdrawals in the world with over 760 billion cubic metres withdrawn per year followed by China and the United States (Ritchie and Roser 2020). In India, 91% of freshwaters are used in the agricultural sector (FAO 2016), which is protected through the 2010 National Wetland Rules and the 2012 National Water Policy (Iyer 2009). Additionally, waters are protected if they lie within the Protected Area Network (Gupta et al. 2014). However, the designation of Freshwater Key Biodiversity Areas traversing multiple Indian states outside of Protected Area networks also conserves many endangered and endemic freshwater species (Molur et al. 2011, 2014).

The smooth-coated otter *Lutrogale perspicillata* (SCO) is an emblematic species for freshwater biodiversity conservation in a broad societal context as they are an effective model species that could be linked with human health and well-being (Bedford 2009; Ben-David et al. 1998; Nawab et al. 2016; Wainstein et al. 2022). It is one of the apex predators (Mason and Macdonald

1986; Nawab and Hussain 2012); an ecological indicator of anthropogenic stress (Shenoy 2003; Shenoy et al. 2006), freshwater connectivity (Carranza et al. 2012), and freshwater ecosystem health (Bedford 2009); and a model species that provides valuable ecosystem services (Ben-David et al. 1998; Nawab et al. 2016). The species has a wide global distribution in south and southeast Asia (Foster-Turley and Santiapillai 1990). However, their global population has declined by > 30% during the last three decades (de Silva et al. 2015). In India, frequent reports of SCO in urban and rural settings increases risks to their long-term persistence (Dias et al. 2022; Raman et al. 2019; Tamarapalli and Kolipaka 2022). Throughout the species distribution range, the population connectivity is threatened by hydrological barriers mainly hydrological projects. Additionally, increasing anthropogenic developmental pressure in the form of linear infrastructure has led to the loss of high-quality in-stream, riparian, and riverine-edge habitats due to agricultural expansion, sand mining, and human settlements (Dudgeon 2000; Shenoy 2003; Shenoy et al. 2006; Suthar et al. 2017). Otters are subject to persecution for their pelts, meat, and body parts, with retaliatory hunting by fishermen in response to fish thefts and fishing net damages (Meena 2002; Nagulu et al. 1999). Otters in the river system of Karnataka including Tungabhadra are susceptible to various threats, including poaching, attributed to the absence of a robust conservation strategy (Shenoy 2003; Shenoy et al. 2006). The species is listed as 'Vulnerable' by the IUCN Red List of Threatened Species and included in Appendix I of CITES (Khoo et al. 2021). In India, SCO is protected and categorized under 'Schedule I' in the 1972 Indian Wildlife Protection Act due to poaching, hunting, and illegal trade.

Studies indicate that determining the scale at which management interventions are required for the protection of otter species and their freshwater habitats is much needed as many of their habitat use patterns and ecological processes are scale-dependent (Crowley et al. 2012; Holland et al. 2019; Lundy et al. 2010; Pimenta et al. 2018). There are a number of recent studies indicating multi-scale responses of semi-aquatic mammals to stream characteristics, river connectivity, land cover, riparian habitat, vegetation, and sediment chemistry (Crowley et al. 2012; Holland et al. 2019; Lundy and Montgomery 2010; Pimenta et al. 2018). At the local

scale, SCO use sites with higher-quality riparian vegetation and adequate ground substratum for choosing appropriate holt locations and feeding/hunting prey whereas sandy and muddy banks are more suitable for grooming and basking (Khan et al. 2014). At the landscape scale, SCO prefers large, slow-flowing rivers with greater inter-reach connectivity (Khan et al. 2014; Raha and Hussain 2016). Therefore, SCO are likely to use certain sites more than others within their home ranges at multiple scales depending upon their perception of the environment, their hierarchical order of habitat selection, and the interactive effects of local-scale and landscape-scale features (Johnson 1980).

Our objectives aimed to predict the probability of SCO site use as defined by spraint deposition (henceforth termed “site use”) and spraint detection along the riverine stretch of the Tungabhadra Otter Conservation Reserve (TOCR) by applying single-season Markovian-chain presence/absence habitat models built from local-scale (100–400 m) factors (i.e. stream characteristics, riparian habitat features, and anthropogenic activities) and its surrounding landscape-scale (1-km²) factors (i.e. land-use patterns and hydro-environmental characteristics). Based on our knowledge of the study area and patterns of habitat associations from literature, we tested relationships between SCO site use and local-scale and landscape-scale factors. We also explored relationships among the effects of multi-scale factors on the number of individuals in SCO groups (henceforth termed “group size”) using linear regression techniques. We hypothesized that site use and SCO group size would be positively associated with hydrological characteristics (e.g., Raha and Hussain 2016; Narasimmarajan et al. 2021; Nawab and Hussain 2012) and negatively associated with certain types of crop fields (e.g., Kantimahanti and Allaparthi 2017; Kamjing et al. 2017), poor water quality (e.g., Bedford 2009; Hong et al. 2020; Dias et al. 2022), and degrees of anthropogenic threats (e.g., Shenoy 2003; Prakash et al. 2012). We hypothesized that the probability of SCO spraint detection would be positively associated with stream substratum (Gupta et al. 2020) and negatively associated with weed and grass cover (Acharya and Lamsal 2010; Shenoy et al. 2006).

Methods

Study area

TOCR is the first otter conservation reserve in India, being founded in 2015 by the Karnataka Government under the 1972 Indian Wildlife (Protection) Act. The reserve is dedicated to the conservation of Rare, Endangered and Threatened keystone freshwater species. In TOCR, the SCO shares its freshwater habitats with the IUCN Red Listed ‘Vulnerable’ mugger crocodile

(*Crocodylus palustris*), ‘Near Threatened’ Indian black turtle (*Melanochelys trijuga*), and the ‘Endangered’ Deccan mahseer (*Tor khudree*) (Devi and Boguskaya 2007). Thus, TOCR is an important freshwater reserve for a range of freshwater-obligate species. The study area spans between 15°15′44.01″ N, 76°20′17.67″ E to 15°26′27.90″ N, 76°36′58.84″ E (Fig. 1), which begins from Mudlapura village to Kampli in Bellary district, North Karnataka. TOCR lies at the boundary of Koppal and Bellary districts in the Krishna River Basin (KRB), which is India’s fourth largest drainage system, with a catchment area of 258,948 km². Unlike other river systems of India, KRB has undergone severe modification in the hydrologic regime due to the agricultural development coupled with the construction of major and minor irrigation structures and other water diversion structures. In fact, KRB is one of the nine river basins in India categorized as “strongly affected” by flow fragmentation and regulation (Groombridge and Jenkins 1998). The mainstream of the Tungabhadra River is formed by the confluence of the Tunga and Bhadra rivers, joining with the Krishna River 531 km downstream (Tungabhadra Board 2024). The mean width of the Tungabhadra River varies from 359 to 4312 m and increases downstream due to increasing discharges. The surrounding forests comprise dry deciduous and southern thorn forests (Champion and Seth 1968). A total of 14 ancient check dams (anicut) built along the Tungabhadra River during the Vijayanagara Empire (Middle Period) 500 years ago provide supplementary water to irrigated dry-crop subsistence farms (Morrison 2010). Of these check dams, nine still exist today in TOCR.

The average annual rainfall recorded over the Tungabhadra River region is around 1200 mm (Lo Porto et al. 2010; Venkatesh and Ramesh 2018). Most of the rainfall occurs during the southwest monsoon (average 456 mm from June through October) followed by the northeast monsoon (average of 127 mm from October through December). However, TOCR received very low rainfall (average of 68 mm) during the study period (Indian Water Resource Information System Web Portal <https://indiawris.gov.in/wris/#/rainfall>). Elevation in the study area ranges from 450 to 750 m msl and slopes eastward (Ramachandra et al. 2015).

The Tungabhadra River is utilized for commercial fishing, and in recent years, the state of Karnataka has promoted the production of carp *Catla catla*, *Labeo rohita*, and *Cirrhinus mrigala* and several exotic fish species *Cyprinus carpio*, *Hypophthalmichthys molitrix*, and *Ctenopharyngodon idella* (Gowda et al. 2015). Despite the conservation significance of TOCR, it is exposed to a high degree of anthropogenic pressure from farmlands, stone quarrying, sand mining, waterlogging, salinization,

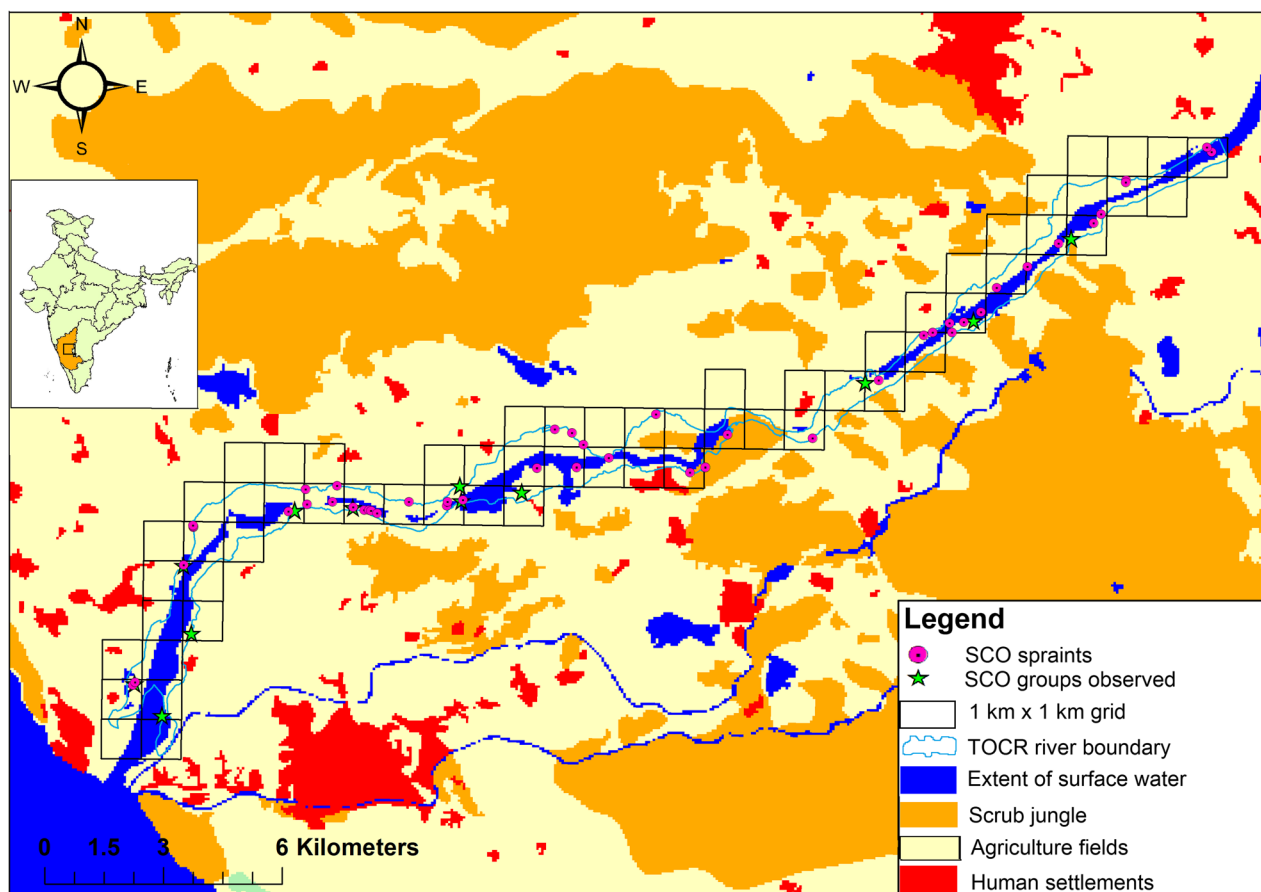


Fig. 1 Sampling sites for smooth-coated otter (SCO) surveys along the Tungabhadra Otter Conservation Reserve

and poly-fibre industries, thereby creating seasonal and spatial variation in water quality (Janmat 2004; Shepur et al. 2020). Additionally, certain reaches of TOCR are experiencing intense eutrophication from the weed-infested water hyacinth (*Eichhornia crassipes*) and pink morning glory (*Ipomoea carnea*). TOCR also is under enormous pressure from tourism as it passes through the historical city of Hampi, which is a UNESCO World Heritage site. This city is visited by local and international tourists for its ancient and holy sites within the ruins of the Vijayanagara dynasty that still exist.

Smooth-coated otter field survey

We overlaid 1-km × 1-km polygons as sampling sites along TOCR using ArcGIS 10.1 (ESRI 2012; Fig. 1). Before initiating the recording of data, we first conducted a thorough preliminary survey of the TOCR over 15 days to identify SCO activity areas through evidence of spraints, holts, and direct group sightings. A site was defined as a 1-km² grid each having three spatial replicates ranging in length from 100 to 400 m. The average distance between survey segments within a site was 314.86 m, with an average

distance between sites of 997.63 m. Most of the stream segment-based surveys have employed stream routes of 100–600 m for surveying semi-aquatic mammals, including other Asian otter species (Prakash et al. 2012; Raha and Hussain 2016), Eurasian otters (*Lutra lutra*) (Hong et al. 2018; Bedford 2009), and Pyrenean desman (*Galemys pyrenaicus*) (Charbonnel et al. 2014). These segment lengths are within the range of the small-scale movement distances (250–1500 m) reported from radio-tagged SCO individuals in the National Chambal Sanctuary (Hussain 1993). Thus, considering the reported home range sizes of adult males and females with pups, SCO home ranges could potentially range from 2.13 to 6.57 km² (Hussain 1993; Kruuk 1995), which is larger than the 1-km² sites used in our study. Therefore, we considered the occupancy term as ‘habitat use’ of the species given that SCO likely has home ranges larger than our sampling sites in which case the same SCO individual/group could use multiple sampling sites within a short survey duration. Thus, we interpreted our results in terms of the site used (i.e. habitat use for sprainting), and not the area occupied at sampling sites.

We collected data between February and May 2019 during the dry/summer season. All segments were surveyed by foot or coracle (circular bamboo boat) in the early mornings (06:00–09:00) when SCO are most active. We searched for indirect evidence (e.g., mass-latrines, spraints), active holts (e.g., large gaps among boulders used as breeding refugia), and claw marks that were recorded within the 15-m buffer along rocky, sandy, or vegetated banks of survey segments. We also opportunistically recorded direct sightings of SCO groups during these surveys. The majority of the spraint deposition sites were in communal latrine sites. We recorded all direct or indirect evidences of SCO using a handheld GARMIN 20×GPS (Garmin Ltd., Olathe, Kansas, USA) and Locus mobile mapping app (Asamm software, Krhanická, Czech Republic). Each instance of direct observation and the count of indirect signs were treated independently. Communal latrine sites were also considered, with the criterion that spraints more than 5 m apart were treated as distinct evidence (Basak et al. 2021; Kruuk et al. 1986). We identified fresh SCO spraints based on the shape, diameter, and length (Khan et al. 2014), and estimated the age of the spraints as fresh (<2 days) or old (>2 days) based on the texture, condition, moisture, and odour. Additionally, tracks of the Asian small-clawed otter (*Aonyx cinereus*) are distinct from SCO and can be inferred from the absence of claw marks and reduced webbing in the latter (Mohapatra et al. 2014; Raha and Hussain 2016). For further analysis, we considered only the fresh spraints and tracks of SCO.

Multi-scale habitat measurements

We conducted a thorough literature review on studies reporting the ecological requirements of SCO, and other otter species and semi-aquatic mammals to identify potential local-scale and landscape-scale variables for modelling SCO habitat use in TOCR (see Additional file 2: Table S1). We also measured additional local-scale habitat variables in the region based on our field knowledge in TOCR. We recorded local-scale habitat variables in a 15-m×15-m plot delineated at every 50-m distance in each segment. Depending on the length of the segment, we laid 2–8 plots alternatively on the riverbank side to measure each habitat variable. We then calculated the average for the continuous variables and assigned them to the sampled segment or site, whereas for categorical variables, we assigned the most frequent category to the site. Additional file 2: Table S2 contains additional details on each local-scale measurement.

For landscape-scale measurements, we considered 1-km×1-km polygons along the riverine extent of TOCR using ArcMap 10.1 (ESRI 2012). This approach for measuring landscape-scale factors for semi-aquatic

small carnivores has been applied previously to quantify land-uses surrounding rivers/streams in otter ecological studies (e.g., Loy et al. 2009). We measured high-resolution, hydro-environmental attributes and land uses at 1-km×1-km grids along 60 sample sites. The hydro-environmental variables utilized in this study were sourced from the Global hydro-environmental sub-basin and river reach characteristics dataset (Additional file 2: Table S2), offering high spatial resolution. These variables encompass elements from seven categories: hydrology (including discharge, runoff, wetland inundation, and groundwater table depth), physiography (encompassing elevation, slope, and landform), climate, land cover, soil, geology, and anthropogenic influences (as detailed in Linke et al. 2019). Additional file 2: Table S2 and Additional file 1: Fig. S1a–o contains additional details on the measurements of landscape-scale variables, their definitions, and calculations using GIS processing tools.

Principal component analysis of hydro-environmental characteristics

We z-transformed all continuous local-scale and landscape-scale variables for standardization. We conducted principal component analysis (PCA) to reduce nine hydro-environmental variables (total stream power, distance to the most downstream pixel of the reach, catchment area, river geometry, river area, terrain slope, stream gradient, soil erosion, and order strata) into three components (PC1, PC2 and PC3) that would describe the stream structure and hydrology. We conducted all analyses using program R packages (R Core Team 2019). We used the package “factoextra” (Kassambara 2015) to first plot the eigenvalues and percentage of variance in a scree plot and identify the number of dimensions needed to explain variation. We concluded that three dimensions were sufficient to summarize the variation and then created biplots of variable contributions. PCA was followed by a Hierarchical Agglomerative Clustering (HAC) where we applied gap statistics to identify the optimum number of clusters by comparing the total within intra-cluster variation for different values of k (# of clusters) with their expected values under the null data distribution using the package “cluster” (Tibshirani et al. 2001). We then applied the Euclidean distance (from PCA) and Ward’s criterion to group the sampled sites into clusters characterized by the nine hydro-environmental variables using the *HPCP* function in package “FactoMineR” (Lê et al. 2008). We described each cluster by variables and their significance using the *v.test* associated with a *p*-value (Husson et al. 2010). We further tested correlations among local-scale and landscape-scale variables using Pearson correlation coefficients (Additional file 1: Fig. S2) from the package “mosaicdata” (<http://www.mosaic-web.org/about.html>,

Pruim et al. 2017), “ggcorrplot” (Kassambara 2019), and “ggplot2” (Wickham 2016).

Modelling site use and detection probability

We assessed the multi-scale habitat use of SCO by fitting Markovian-chain models to the presence/absence data (Hines et al. 2010). This model accounts for the lack of spatial independence in replicate surveys by including segment-level occupancy and detection probability conditional on adjacent segment-level occupancy. This model has been successfully applied when surveys are conducted along linear features (Charbonnel et al. 2014; Srivathsa et al. 2014; Thorn et al. 2011), and when target species have linear territories (Hussain 1993; ÓNeill et al. 2009; Sauer et al. 1999). However, this model has been rarely applied to assess habitat use of semi-aquatic species (Charbonnel et al. 2014, 2015). Hines et al. (2010) reported that standard single-season models considerably under-estimated occupancy when spatial autocorrelation was not accounted for. Spatial replicates are a cost-effective approach when sites are surveyed within short durations. In our study, 100–400 m survey segments were spatial replicates for 60 1-km² sites. In this manner, we built detection histories for 60 1-km² sites, with each having three spatial replicates. Hines et al. (2010) spatial dependence model estimates ψ , which denotes the probability of SCO at a site. The model captures spatial dependence in segment-level occupancy (θ) through θ^0 , which is the probability of SCO being present at a replicate (i.e. segment) given the previous replicate was not occupied by SCO; θ^1 , the probability of SCO being present at a replicate given the previous replicate was occupied by SCO; and $\theta\pi$, represents the first replicate where there is no prior information for segment-level occupancy. Additionally, p indicates the probability of detecting SCO in a segment. The detection parameters θ^0 and θ^1 express the magnitude of spatial dependence between continuous segments, with $\theta^0 = \theta^1$ indicating complete independence of segments.

We created SCO detection histories for each of the three spatial replicates that constituted segments such that each of the 60 sites had three sampling occasions, resulting in a sampling effort of 180 survey segments. The detection history consisted of binary values with ‘1’ indicating SCO detection during the sampling occasion and ‘0’ indicating non-detection based on direct and indirect evidence such as fresh spraints/latrines along a segment (Newman and Griffin 1994; Khan et al. 2014). Thus, the resulting detection histories were created as 110, 001, 111, 101, 000, 010, 011, or 100. We analysed detection histories for the 180 segments covering 60 1-km² grids (henceforth termed “sites”) with multi-scale covariates by fitting single-season Markovian models in the program

PRESENCE v 13.11 (Hines 2006). During modelling, we used the z-transformed values of continuous covariates. For modelling, we did not combine variables into a single model when they were correlated ($r \geq 0.5$) using Pearson’s correlation test (Additional file 1: Fig. S2). Rather, we grouped all covariates for each scale into six categories: habitat, vegetation, topography, hydrology, land use, and anthropogenic disturbance. First, we calculated the naïve occupancy estimate without accounting for false absences (i.e. number of sites where SCO presence was detected at least once/total number of sites surveyed) (MacKenzie et al. 2018). To construct a set of candidate models, we followed a common practice of first modelling the detection probability by selecting the best detection covariate ($< 2 \Delta AIC$) while keeping site occupancy constant. This involved taking seven detection covariates, of which stream substrate failed to converge (Additional file 2: Table S3). Then, by holding the best detection covariate, we constructed models with seven local-scale covariates (Additional file 2: Table S4) and then with 24 landscape-scale covariates under each broad category in a univariate fashion (Additional file 2: Table S5). At this stage, we selected the best local-scale and landscape-scale variables under each of the six categories to identify the most important predictors of SCO site use. This further allowed us to assess whether site occupancy was driven by local-scale or landscape-scale variables, or combinations of variables from both scales (Additional file 2: Table S6; Burnham and Anderson 1998; MacKenzie et al. 2018). We eliminated those models that did not converge (Cooch and White 2005). The relationship between the probability of SCO site use and covariates at both spatial scales was established using a logistic model (logit link) in the program PRESENCE v 13.11 (Hines 2006). For the best models, we averaged the untransformed beta coefficients and standard errors (β , $SE(\beta)$) to determine the magnitude and direction of influence of individual covariates on the probabilities of site use, the detection of SCO, and infer relationships (whether positive or negative) between covariates and parameters. We further assessed how well the top-ranked models ($\Delta AIC < 2$) fit the data with a ‘goodness-of-fit’ test using 10,000 bootstrapping iterations (MacKenzie and Bailey 2004) to obtain P values of the model’s fit. The overdispersion (\hat{c}) was estimated by calculating the χ^2 ‘goodness of fit’ statistic for a model divided by the mean test statistic of 10,000 bootstrapped samples. We considered parameters with a 95% confidence interval not overlapping 0 to be informative. The Akaike weights (ω_i) also were calculated for each model. A final prediction map was produced from the top models by plotting the average site using ψ and detection probability p of SCO from the top models. Figure 2 contains a complete schematic

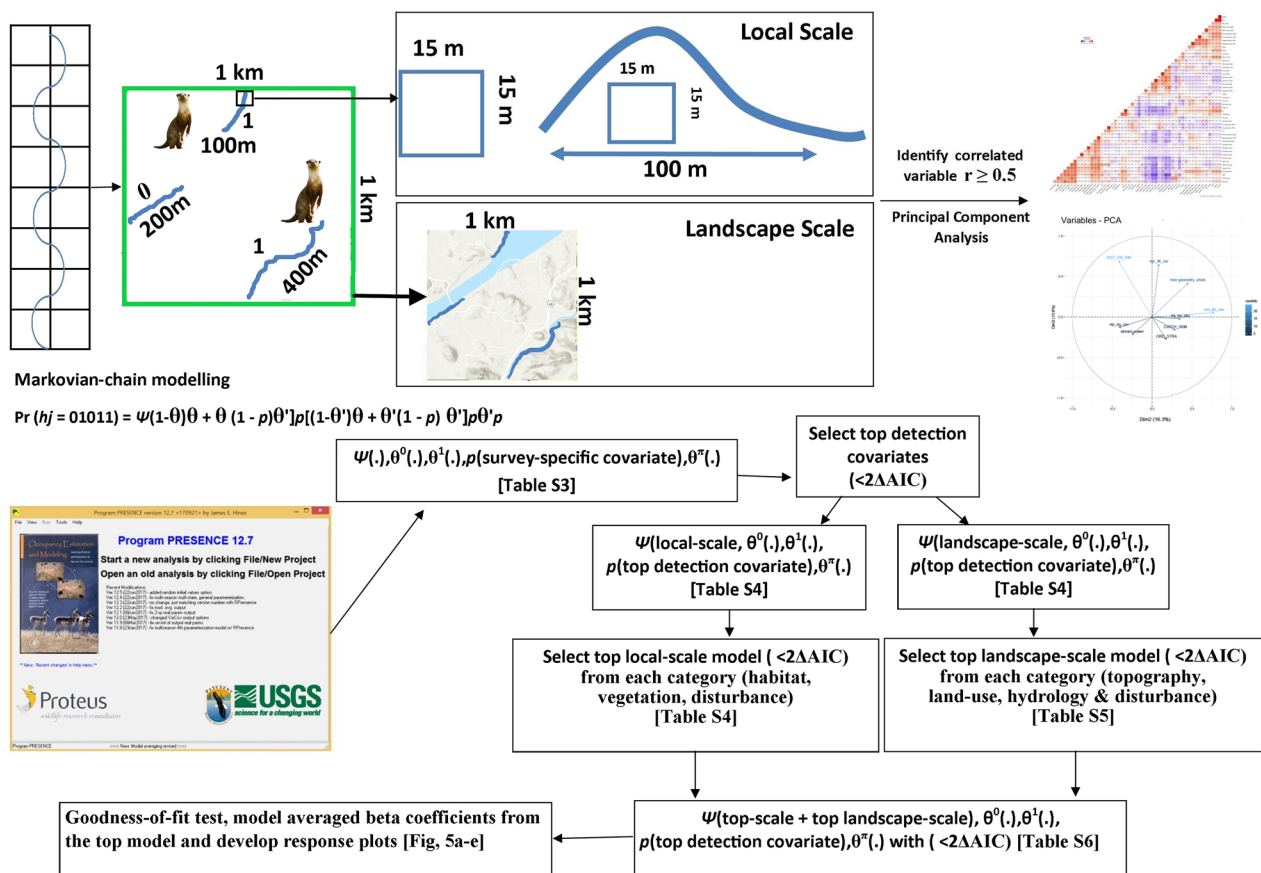


Fig. 2 A schematic representation of the workflow involving the sampling procedure for smooth-coated otter surveys, local- and landscape-scale measurements of variables, correlations, principal component analysis and a decision tree-based procedure to predict smooth-coated otter habitat use in Tungbhadra Otter Conservation Reserve

workflow of the steps involved from field data collection to analysis.

Group size relationships with habitat factors

SCOs are highly social, semi-aquatic carnivores, and thus, we expected that certain local-scale and landscape-scale habitat features would be associated with both high and low group sizes. To associate group-size relationships with local-scale and landscape-scale factors, we considered the z -transformed values of hydro-environmental characteristics, vegetation, land cover, hydrology, and topography. We applied box plots to compare group sizes between categorical or binary factors such as the presence/absence of check dams, islands, sand banks, and flow direction. We conducted univariate linear regression modelling using ordinary least-squares regression techniques from the 'olsrr' package (Hebbali 2023) in R studio (Rstudio Team 2020). Specifically, we used PC1, river depth, river width, the proportion of sugarcane and banana fields, island size, anthropogenic pressure, and grass cover as potential predictors. For each model, we

tested for significant relationships, residual diagnostics, homoscedasticity, and normal distribution.

Overall, we chose these potential variables as we expected large SCO group sizes to be associated with PC1, wider river widths, greater river depths, increasing island sizes, and greater grass coverage. We further expected that smaller groups would be sensitive to high anthropogenic pressure and thus avoided disturbed sites thereby exhibiting negative relationships with increasing SCO group sizes. Given the territorial nature of otters, we expected the larger groups to displace the smaller ones to highly modified landscapes, as these areas provide suboptimal conditions. This displacement is anticipated to compel smaller groups to river buffers having high proportion of sugarcane for foraging and hunting.

Results

Smooth-coated otter sign evidence and groups

We recorded evidence of SCO in the form of spraints 48 out of 180 sampling segments. Other evidences such as direct sightings, claw marks, and holts were recorded

at 15 sampling sites. Overall, SCO signs were recorded at 31 of 60 sampling sites yielding a naïve occupancy of 0.52. During the study period, we encountered a total of 69 SCOs in 12 different groups, each consisting of 1–13 individuals including both adults and sub-adults. The mean SCO group size in TOCR was 5.75 ± 3.41 (mean \pm SD). Various activities like basking over boulders, grooming, travel groups, individuals huddling over each other while resting, and large hunting and foraging groups along with at least two sub-adults were observed. Six of the 12 groups were hunting/foraging groups (mean group size = 6.5), two groups had loners for which behavioural information could not be recorded as they were brief encounters, one group was observed resting over boulders on islands and near sugarcane banks, two groups were observed travelling from either side of the riverbank, and one group was observed escaping from fishermen during fishing activity. The mean SCO sign encounter rate (number of signs/km) in TOCR was 1.40 ± 0.20 signs/km. Sign encounter rate was the greatest in the river reach surrounded by barren rocky stretches and rock outcrops broadly categorized here as barren land (1.84 ± 0.20 signs/km) followed by agriculture fields (1.39 ± 0.20 sign/km), with human settlements having the lowest encounter rate (0.89 ± 0.20 signs/km).

Stream structure and hydrology

The PCA of stream attributes across all sites created three principal components. PC1 explained 25% of the total variance with PC2 explaining 16% of the variance (Table 1). The varimax rotation revealed a major gradient for PC1 (Additional file 1: Fig. S3a) that was largely explained by stream order and river area with greater values towards the right end of the first axis, and slope and catchment area with greater values towards the left end of the first axis. The second PC2 (Additional file 1: Fig. S3b) was explained largely by soil erosion and river geometry with greater values towards the right end of the axis and the most downstream pixel of reach and slope towards the left end of the axis. The third PC3 (Additional file 1: Fig. S3c) was mainly related to stream gradient and river geometry, which was towards the left end of the axis and the distance to the most downstream pixel of the reach had greater values towards the right end of the axis. The HAC analysis generated a dendrogram (Additional file 1: Fig. S4a) and partition plot (Additional file 1: Fig. S4b) representing nine site clusters (Additional file 1: Fig. S4c).

Probability estimates of site use and detection and model fit

The bootstrap χ^2 goodness-of-fit test showed that the three top-ranked models fitted the data well (model 1

Table 1 Principal component loadings from 60 sites for stream attributes in Tungabhadra Otter Conservation Reserve

Stream attribute	PC1	PC2	PC3
Total stream power	0.52	− 0.25	− 0.22
Distance to the most downstream pixel of the reach	0.32	− 0.42	0.69
Area of catchment	− 0.48	0.29	− 0.16
River geometry	− 0.009	0.45	0.42
River area	0.68	0.35	− 0.020
Slope	− 0.72	− 0.41	− 0.13
Stream gradient	− 0.05	0.08	0.65
Soil erosion	− 0.34	0.77	0.05
Order strata	0.75	0.18	− 0.28
Variance	2.27	1.46	1.25
Percentage of variance	25.31	16.27	13.92
Cumulative percentage of variance	25.31	41.58	55.51

Bold font indicates the loadings used to interpret the meaning of the principal component

bootstrapped P value = 0.90 for $\psi(\text{sugarcane} + \text{anthropogenic pressure} + \text{flow direction south-eastwards}), \theta^0(.,) \theta^1(.,) p(\text{grass cover}), \theta^\pi(.,)$; model 2 bootstrapped P value = 0.93 for $\psi(\text{sugarcane} + \text{anthropogenic pressure} + \text{flow direction southwards}), \theta^0(.,) \theta^1(.,) p(\text{grass cover}), \theta^\pi(.,)$; model 3 bootstrapped P value = 1.06 for $\psi(\text{sugarcane} + \text{anthropogenic pressure}), \theta^0(.,) \theta^1(.,) p(\text{grass cover}), \theta^\pi(.,)$. The average predicted site use (0.77 ± 0.19 ; 95% CIs 0.29–0.96) and detection probability (0.84 ± 0.13 ; 95% CIs 0.27–0.97) was relatively high in TOCR and greater than naïve occupancy (0.52). The average probability of site use ranged from a minimum of 0.48 ± 0.28 to 0.98 ± 0.03 (Fig. 3), suggesting sites with moderate to high SCO habitat suitability and also that SCO selectively used certain sites more than others. Average detection probability for each survey segment ranged from 0.41 ± 0.22 to 0.97 ± 0.04 (Fig. 4). The top spatial autocorrelation models indicated that the probability of SCO presence was lower when there was no spraint detected on the previous segment than when spraints had been detected on the previous segment ($\theta^0_{\text{average of top 3 models}} = 0.33 \pm \text{SE } 0.14$ and $\theta^1_{\text{average of top 3 models}} = 0.48 \pm 0.12$).

Influence of multi-scale covariates on the probability of SCO site use and detection

The top survey-specific covariate contained weed cover and grass cover in the lowest-rank models ($< 2 \Delta\text{AIC}$). Other survey-specific covariates such as river depth, river width, survey effort, and proximity to natural vegetation had generally greater ΔAIC rankings (Additional file 2: Table S3). The univariate analysis of the local-scale occupancy covariates after accounting for detections

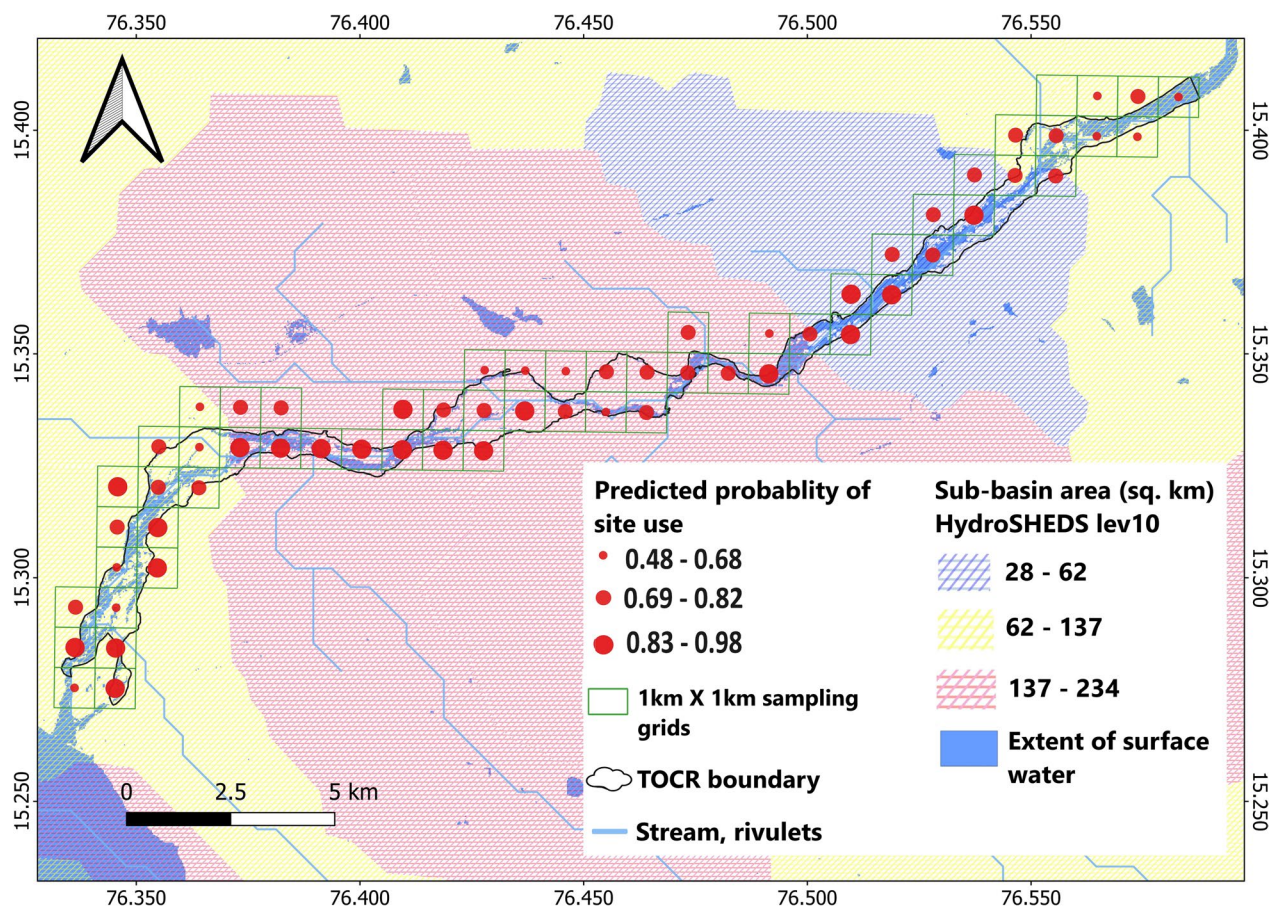


Fig. 3 Map showing the average predicted probability of smooth-coated otter site use along 60 sites in Tungabhadra Otter Conservation Reserve

suggested that variables $< 2 \Delta AIC$ included the presence of islands, sand banks, bank vegetation, canopy cover, and anthropogenic pressure (Additional file 2: Table S4) while the univariate results of landscape-scale covariates included elevation, island size, flow direction, proportion of sugarcane fields, area of roads, and area of settlements (Additional file 2: Table S5). These univariate models contained lower AIC values than the null models for each covariate group. The combination of local-scale and landscape-scale covariates into a single model had a lower AIC than either local-scale or landscape-scale models done separately (Additional file 2: Table S6). Hence, the final top three models explaining SCO site use included the additive effects of the proportion of sugarcane fields, anthropogenic pressure, flow direction (south-eastwards and southwards), and with grass cover as the top detection covariates (Additional file 2: Table S6). The proportion of sugarcane fields ($\beta_{\text{average of top 3 models}} = 0.71 \pm 0.23$) had a positive relationship with SCO site use as indicated by the positive β coefficients (Fig. 5a). Similarly, SCO site use increased in streams flowing south-eastwards ($\beta_{\text{top model 1}}$

$= 0.68 \pm 0.38$) more so than southwards ($\beta_{\text{top model 2}} = -0.67 \pm 0.39$) and south-westwards (Fig. 5b). Conversely, the probability of SCO site use decreased with increasing anthropogenic disturbance ($\beta_{\text{average of top 3 models}} = -0.42 \pm 0.19$; Fig. 5c). The probability of SCO detection had a strong negative relationship with increasing grass cover ($\beta_{\text{average of top 3 models}} = -1.24 \pm 0.78$; Fig. 5d). Additionally, SCO spraint locations appeared to be non-random and clustered within sites with some adjacent stream segments marked with more spraints than others. SCO also occurred at more or less regularly spaced sites across TOCR, with apparent marked preferences for specific sites during the dry season.

Group size relationships with multi-scale habitat

SCO group size was not correlated with sign encounter rate ($r = 0.08$, $P = 0.79$) and the autocorrelation test results showed that spatial locations of SCO groups were independent (Moran's Index: -0.33 , z -score: -1.61 , $P = 0.10$), which allowed us to treat locations of group activity as unique behavioural locations independent of spraint locations. SCO group size decreased significantly

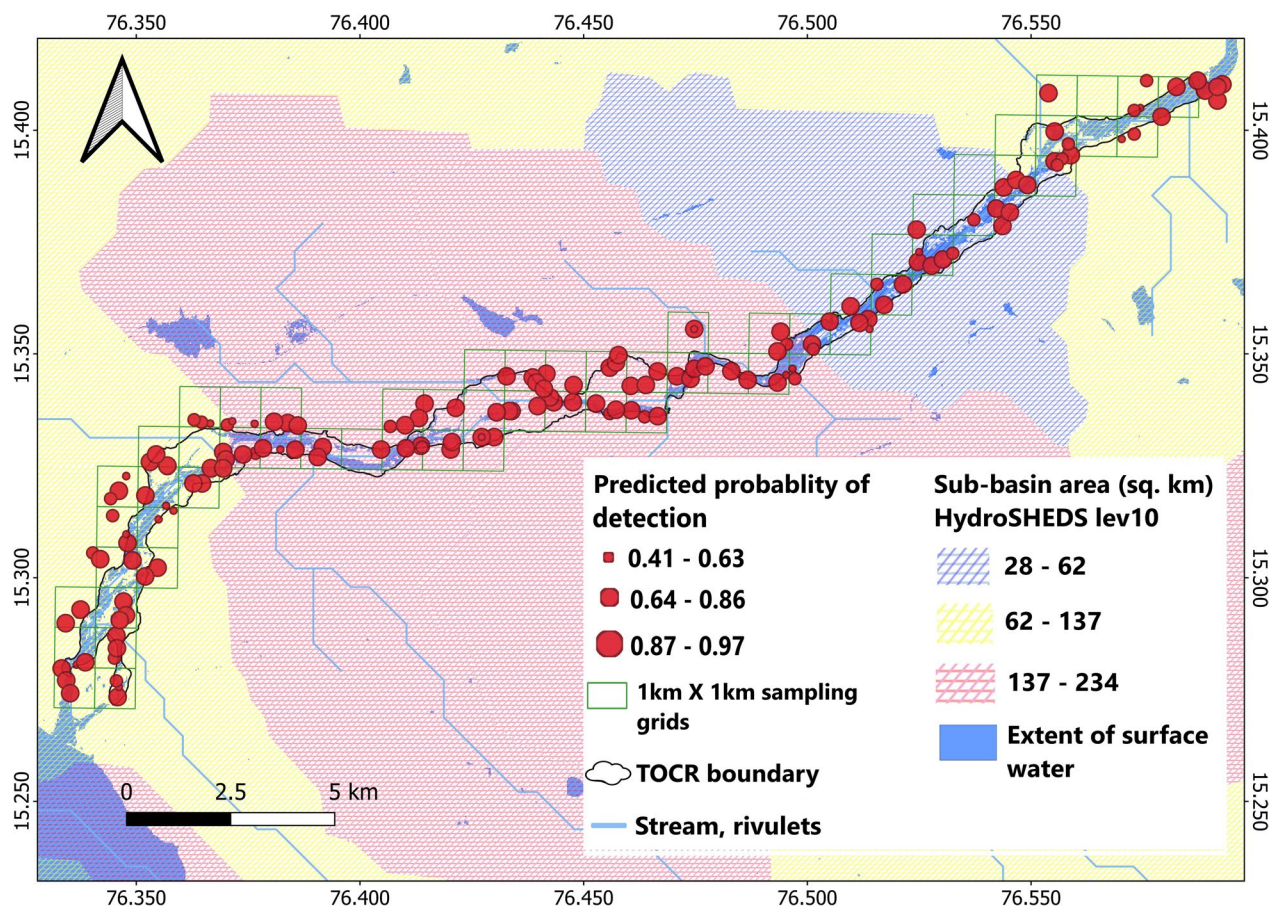


Fig. 4 Map showing the average probability of smooth-coated otter detection along 180 survey segments in Tungbhadra Otter Conservation Reserve

with increasing proportion of sugarcane fields ($\beta = -1.74 \pm 0.59$, $R^2 = 0.46$, $F = 8.62$, $P = 0.01$) while it increased with grass cover ($\beta = 2.20 \pm 1.10$, $R^2 = 0.28$, $F = 3.96$, $P = 0.074$), though only with marginal significance. Although insignificant, SCO group sizes increased with PC1 ($\beta = 0.54 \pm 0.50$, $R^2 = 0.10$, $F = 1.16$, $P = 0.31$), river depth ($\beta = 1.06 \pm 0.77$, $R^2 = 0.16$, $F = 1.86$, $P = 0.20$), and river width ($\beta = 1.66 \pm 1.17$, $R^2 = 0.16$, $F = 2.00$, $P = 0.18$) while it decreased with island size ($\beta = -2.21 \pm 1.35$, $R^2 = 0.21$, $F = 2.69$, $P = 0.13$) and anthropogenic pressure ($\beta = -1.79 \pm 1.18$, $R^2 = 0.18$, $F = 2.32$, $P = 0.15$; Fig. 6a–g). There was virtually no difference in SCO group sizes between sites with and without islands (Fig. 7a). Larger group sizes were associated with sites having south-east-flowing streams more so than southwest-flowing streams (Fig. 7b), with a similar pattern observed at sites with sand banks compared to sites without sand banks (Fig. 7c).

Discussion

This study considered high-resolution hydro-environmental characteristics, riparian vegetation, and anthropogenic threats at multiple spatial scales for determining the probability of SCO site use and group size patterns in a low-elevation, inland river surrounded by a highly modified scrub jungle–agriculture matrix in southern India. Our study applies a novel empirical method that accounts for the spatial dependency in stream survey routes covering adjacent segments to assess site use and detection probabilities of SCO. Approximately two-thirds area of TOCR was intensively used by SCO during the dry season when 80% of TOCR was shallow (0.3–2.5 m depth) until the monsoon season arrived. SCO spraint locations appeared to be non-random and clustered within sites with some adjacent stream segments marked with more spraints than others. SCO appeared to occur at regularly spaced sites across TOCR, though they did

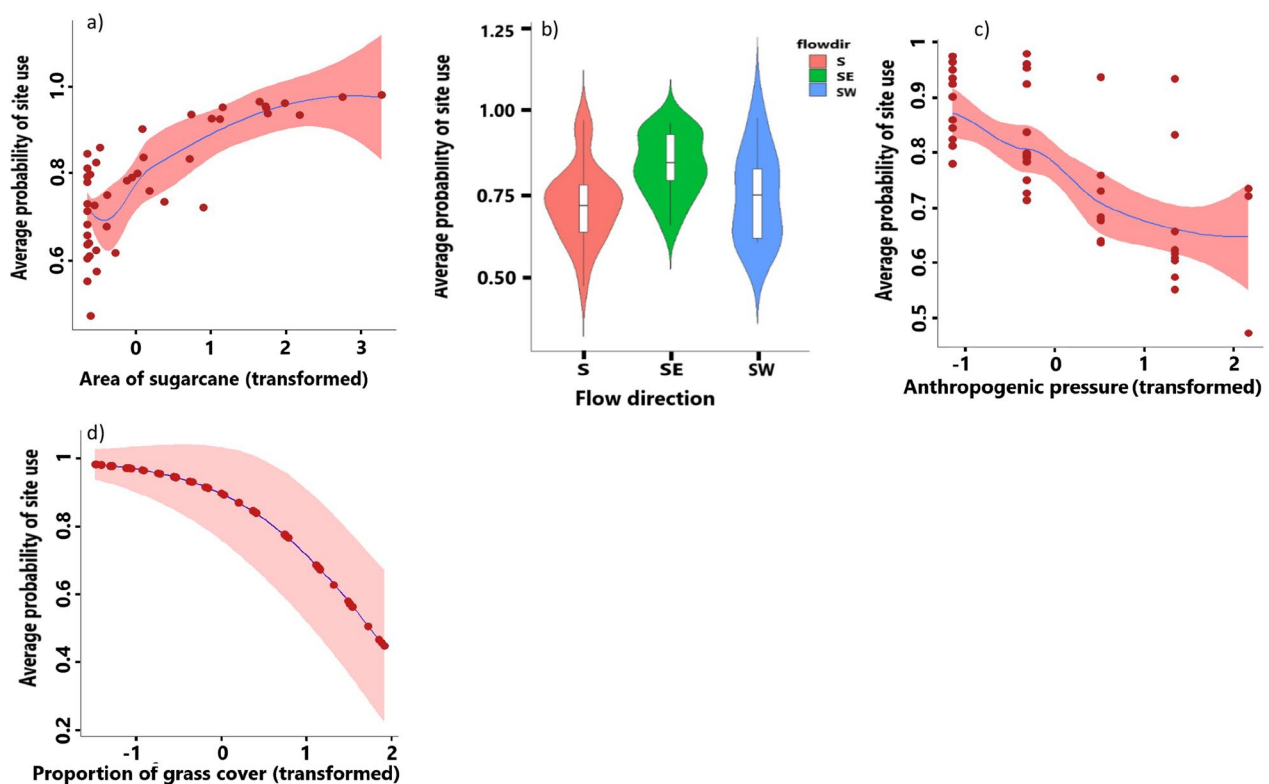


Fig. 5 Effects of multi-scale covariates on the model-averaged probability of smooth-coated otter site use and detection probability predicted by the top-ranked models. Colour shaded areas show 95% confidence intervals. Red dots represent the predicted estimates of SCO use and detection probability for each site. Predicted estimates were allowed to vary with the multi-scale covariates under consideration, while other explanatory variables present in the model were held at their mean values

exhibit marked preferences for spraint deposition as “chemical signals” and grouping patterns specific to behaviour across the TOCR during the dry season.

Site-specific preferences emphasized the impact of certain covariate combinations on SCO habitat utilization. Previous studies have shown patterns of site-specific preferences for spraint deposition and communal latrine sites of otters (Aadrean and Usio 2020; Hussain 1993). In several areas of the TOCR, we observed the species’ sensitivity to intense anthropogenic pressure, most notably in the form of solid plastic waste, excessive dynamite fishing, and the placement of poaching traps by migrant fishermen and poachers. These traps were placed near mass-latrine sites, which are easily recognized by poachers as frequent SCO activity centres. Sand mining was observed at nine sites in the middle section of TOCR. This mining covered approximately 15% of TOCR and is illegally performed near the major cities of Hospet and Kampli in Bellary district. The presence of islands in a specific length may prove to be a significant influence since they may offer secure denning locations and refugia, especially if they are vegetated and challenging to access from the banks (Prakash et al. 2014; Shenoy

et al. 2006). In this study, however, SCO groups with more members appeared to avoid larger islands because of human pressures. While smaller islands were largely devoid of human disturbance, larger islands were heavily utilized for leisure activities by tourists. According to other research, SCO were reportedly less sensitive to human presence (Anoop and Hussain 2004; Shariff 1985), but also have shown to be negatively affected by human presence outside and inside protected areas (de Silva 2011; Juhász et al. 2013; Khan et al. 2014; Prenda et al. 2001; Shenoy 2003; Shenoy et al. 2006). It appears that the sensitivity of SCO towards human activities varies across sites within its range in India.

Otters have a natural preference for emergent tall grass along riverbanks since it provides access to dens, resting areas, and hidden pathways (Helon et al. 2004; Nawab and Hussain 2012; Newman and Griffin 1994; Reed-Smith et al. 2014; Verbeek and Morgan 1978). The TOCR lacks both natural and planted woodland vegetation along the river buffer, leaving only emergent shoreline grass (mostly *Typha angustifolia* and *Scirpus validus*) as the only naturally occurring vegetative cover in this heavily altered terrain that was frequented by larger SCO

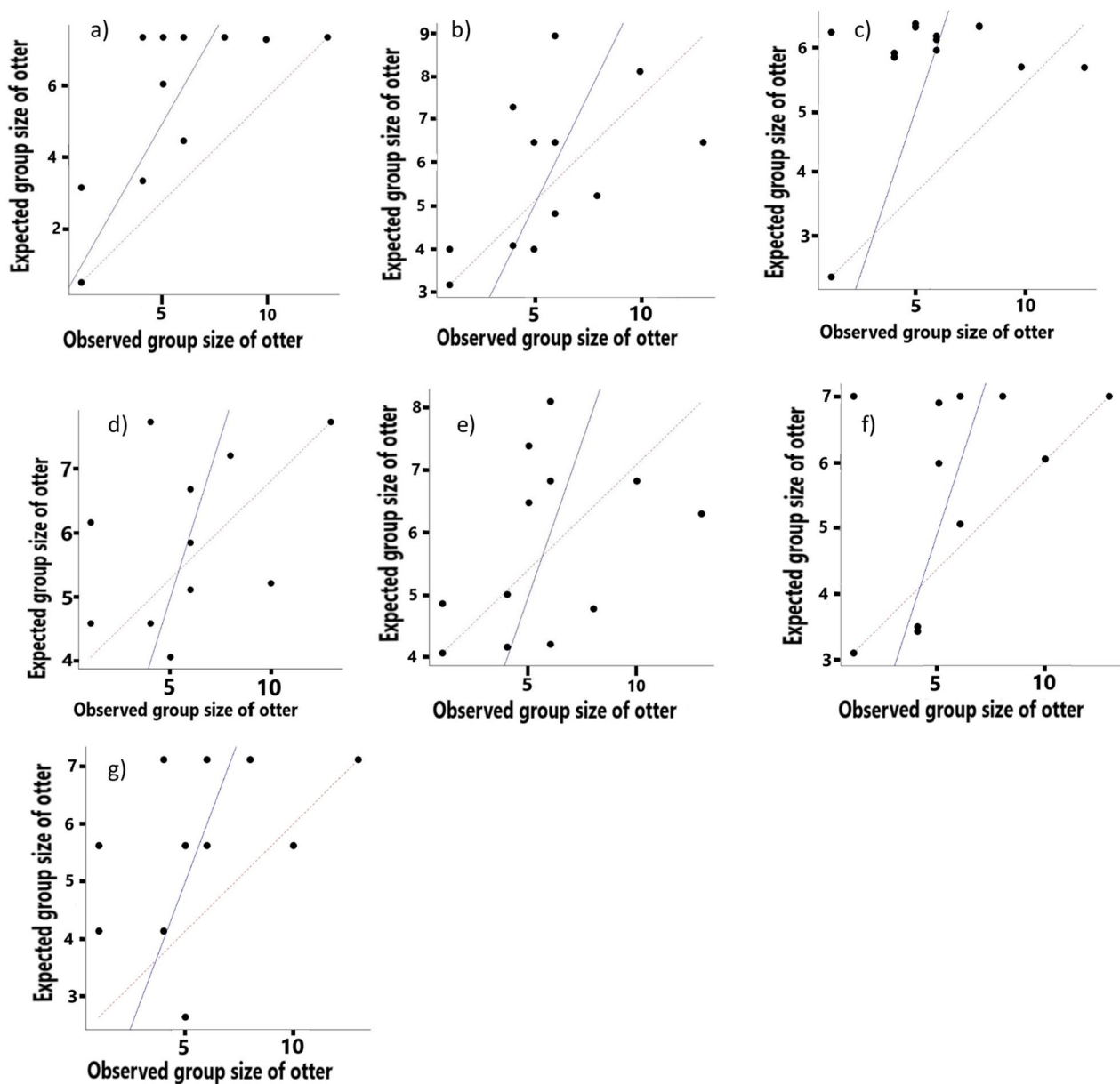


Fig. 6 Simple linear regression plots of expected and observed group sizes from univariate models for **a** proportion of sugarcane fields, **b** grass cover **c** PC1 **d** river depth **e** river width **f** island size, and **g** anthropogenic pressure

groups as foraging sites. Emergent grass-dominated sections supported larger SCO groups, though negatively influenced SCO spraint detections. Tall-grass cover affects the detectability of otter evidence (Kamjing et al. 2017) such as scat, spraints, and tracks (Jeffress et al. 2011). However, the increase in SCO site use for sprainting coincident with the amount of sugarcane fields could imply the resemblance of sugarcane to naturally occurring vegetation in TOCR. There were instances when the smaller SCO groups were observed resting along the edge of the mud bank next to sugarcane fields. Preference of

river otters *Lontra canadensis* to sugarcane fields also has been recorded in the Florida Everglades, USA (Pearlstone et al. 2005). In peninsular India, observations of SCO have been reported in areas of the river that were transformed into sugarcane fields (Pradhan 1996; Sonawane et al. 2019). There is little knowledge on how sugarcane fields can affect the habitat ecology of small mammals associated with riparian habitats (Khan and Abbasi 2015; Paolino et al. 2018; Sunil et al. 2011). In our study area, among the other croplands, sugarcane fields were distributed around all nine ancient check dams (anicuts) to fulfil

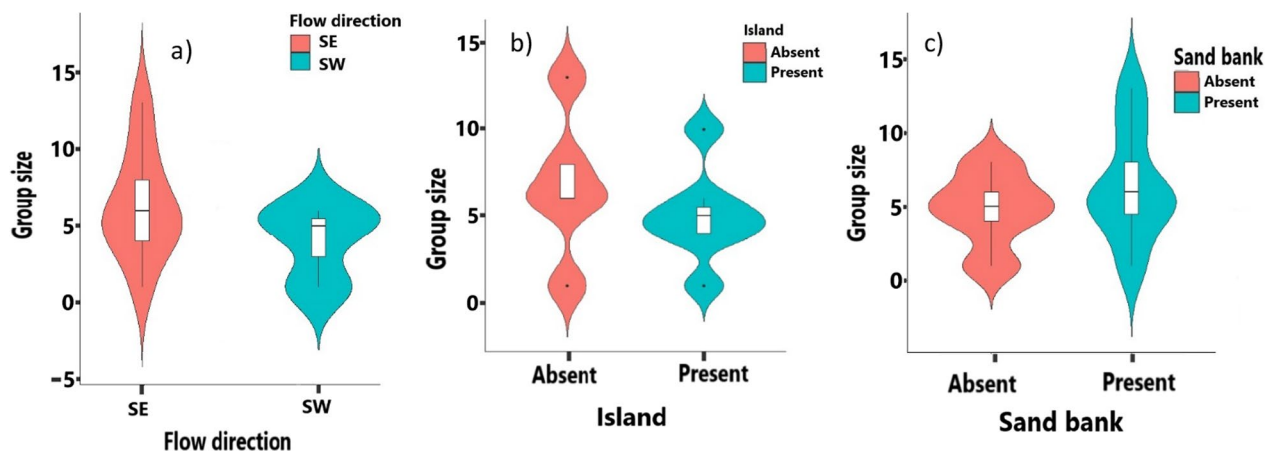


Fig. 7 Group size comparisons of SCO between **a** flow direction, **b** islands and **c** sand banks

high-water demands. Furthermore, the irrigation channels originating from these anicuts appeared to enhance stream connectivity thereby creating suitable movement routes for SCO (e.g., Latorre-Cardenas et al. 2021).

Sandbanks are extensively used by otters for grooming and basking and might be a very important feature in SCO and other otter habitats (Prakash et al. 2014). These microhabitats help regulate the body temperature, maintain fur texture, and create bonds among SCO group individuals (Basak et al. 2021). Otters groom by rolling over the sand to dry themselves after intermittent dives into the water, which is a behaviour that constitutes a large part of their daily activities. Hussain (2013) also reported that otters used sand banks extensively for marking and grooming, which is consistent with our findings that river reaches with substantial sandbank habitat supported larger SCO groups. The increasing SCO site use for sprainting and a wide range of SCO groups in southeast flowing streams was markedly linked with the greater sub-basin area. River hydrological conditions such as river direction, flow velocity, and hydromorphology have been shown to influence SCO habitat use (Khan et al. 2014; Raha and Hussain 2016).

Territoriality by otters carries costs and benefits, which are commonly affected by the spatial and temporal abundance, food availability and predictability, and pressure from intruders (Leuchtenberger et al. 2015) to gain exclusive access to essential resources (Brown and Orians 1970; Grant et al. 1992; Kruuk 1992). In TOCR, we recorded a much greater relative density of otters (1.32 individuals/km) than those reported along the Chambal and Cauvery rivers in India, which were 0.07 individuals/km, and 0.57 individuals/km, respectively (Baskaran et al. 2022; Hussain and Choudhury 1997). SCO group size is known to increase with the quality of habitat patches

(Macdonald 1983), as we reported larger groups using small islands and along riverine segments with substantial emergent grassland-dominated cover. Although our interpretations of SCO group size relationships are to be considered preliminary, it appeared that SCOs use transformed landscapes, even if they represented suboptimal habitat conditions. Due to their extensive geographical requirements, food specialization, and slow reproductive rates, these semi-aquatic carnivores are particularly sensitive to human disturbances and changes in land use (Ripple et al. 2014).

Conclusions

Our study showed that at the landscape-scale, the sugarcane-dominated river buffer of TOCR were intensively used by SCO. Although larger sub-basin areas are suitable for foraging and sprainting by SCO at the landscape scale, anthropogenic activities occurring at local scales have negative effects. The breeding females during the pup season could be highly sensitive towards disturbances from local human activities. Thus, the designation of TOCR as a Protected Freshwater Reserve may not be adequate for the sustainable conservation of SCO populations and their habitats. Primarily, the upper and lower reaches of TOCR, near the Kampli and Aneundi anicuts in particular, contain several Indo-Gangetic carps and invasive fish species (Nagabhushan 2020). SCO are remarkably adaptable species, capable of thriving in heavily modified environments like megacities and agricultural landscapes, provided there is an abundance of food and effective poaching control measures are in place (Dias et al. 2022; Khoo et al. 2021). Effective riverine-habitat management warrants improvement of riparian habitat quality for strengthening the riverbank, minimizing human

activities, reducing soil erosion, and enhancing the lateral stability of river channels along the TOCR and beyond. In order to sustain SCO populations and other freshwater apex predators over the long-term, forest department authorities might regulate rampant rock and sand mining, especially near holt locations in the TOCR. Continuous monitoring, regulating water quality, and conserving native fish fauna are crucial actions to sustain the SCO population, as agricultural landscapes pose a potential threat to local fish fauna due to the use of chemicals (Bedford 2009). This study warrants further understanding of the species' tolerance thresholds in ecotonal habitats along riverine edges as well as the extension of SCO and other otter conservation strategies in multi-land use systems across India. Furthermore, educational and awareness programmes on the habitat requirements of SCO among local villagers, fishermen, and riverside communities should be undertaken by promoting otters as ambassadors of the freshwater ecosystems.

Our study suggested that both local-scale and landscape-scale features had strong relationships with SCO site use and group size patterns. Cross-scale analyses such as these may be further extended to other riverscapes for other otter species through rigorous field-collected data on the local-scale habitat coupled with high-resolution remote-sensed variables at the landscape scale. Our models could assist decision-makers in focusing on limited resources to inform conservation and monitoring efforts for all otter species. Accounting for correlated detections and their contributing factors is essential to avoid biased predictions when building habitat use models for freshwater-dependent species. It should be taken into consideration that detection probabilities of otters and colonization of new sites may be driven by seasonally influenced hydrological dynamics (e.g., MacKenzie et al. 2002) that were not accounted for in this study. However, future seasonal surveys should emphasize tracking communal latrine sites or fresh spraint deposits in order to explain spatiotemporal shifts in otter distributions. Our novel modelling approach also could be applied towards other otter-occupied riverscapes using a larger number of sites coupled with spatial replicates as river segments within the home range (Hines et al. 2010; Thorn et al. 2011).

Abbreviations

AIC	Akaike's information criterion
HAC	Hierarchical agglomerative clustering
KRB	Krishna River Basin
PCA	Principal component analysis
SCO	Smooth-coated otter
TOCR	Tungabhadra Otter Conservation Reserve

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-024-00492-x>.

Additional file 1: Figure S1. Hydro-environmental variables from high-resolution remote-sensed data and land uses as landscape scale covariates for modelling smooth-coated otter site use in Tungabhadra Otter Conservation Reserve. **Figure S2.** Pearson correlation matrix among local-scale and landscape-scale site covariates for modelling smooth-coated otter site use. **Figure S3.** The varimax rotation from Principal Component Analysis of high-resolution hydro-environmental variables along Tungabhadra Otter Conservation Reserve. **Figure S4.** High-resolution hydro-environmental variables in building a dendrogram and factor plot showing the nine clusters along 60 sampled sites from the Hierarchical Agglomerative Clustering method in Tungabhadra Otter Conservation Reserve.

Additional file 2: Table S1. Multi-scale covariates and their expected relationships for modelling the probability of smooth-coated otter site use and detection. **Table S2.** Local-scale and landscape-scale variables measured along the Tungabhadra Otter Conservation Reserve. **Table S3.** Model selection results for estimating detection probability (p) of smooth-coated otter with survey-specific covariates in Tungabhadra Otter Conservation Reserve. **Table S4.** Model selection results for determining the best local-scale (100–400 m) covariate for smooth-coated otter site use in Tungabhadra Otter Conservation Reserve. **Table S5.** Model selection results for determining the best landscape-scale (1 km²) covariate for smooth-coated otter site use in Tungabhadra Otter Conservation Reserve. **Table S6.** Results of model selection to identify the best multi-scale hydro-environmental and anthropogenic covariates influencing probability of smooth-coated otter site use in Tungabhadra Otter Conservation Reserve. **Table S7.** Contribution of hydro-environmental variables in building nine clusters from Hierarchical Agglomerative Clustering and the values correspond to the v -test and its significance (* P value < 0.05; *** P value < 0.001) calculated for each variable in each cluster. The average predicted probability of smooth-coated otter site use with standard error and 95% confidence intervals calculated from the top models for each cluster.

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Author contributions

AM collected the field data as part of his Master's dissertation; AM, RK, TR and RKP conceived the ideas and designed the methodology; AM and RK analysed the data and led the writing; RKP and MPM provided research permissions as Karnataka Forest Department officials, and provided logistic support and field staff to AM. All authors contributed critically to the drafts and provided comments for finalizing the paper for publication.

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Availability of data and materials

The data that support the findings of this study belong to the Sálím Ali Centre for Ornithology and Natural History and are available from the corresponding author upon reasonable request.

Declarations

Ethics approval and consent to participate

This study was conducted using otter evidence from spraints, latrine sites and camera-trap images of otters. No live animal was captured. All field surveys were performed under the scientific permit (UOK/WLS/2019) approved by the Bellary Territorial Forest Division, Karnataka Forest Department. This is an original research.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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