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Research Article

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Latrine site selection by African clawless otters, *Aonyx capensis*, and their behavior during latrine visitations

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Abstract

Latrine sites are used as areas for the deposition of scent-containing excretions and play important roles in intraspecific olfactory communication, territoriality, sexual attraction, and defense behaviors of many mammals. African clawless otters (*Aonyx capensis*) likely use latrine sites as primary areas for scent marking and scent communication but no studies to date have investigated their potential role or site selection. We assessed latrine site selection at 2 spatial scales (micro- and macroscale) and recorded behaviors via camera trap recordings. Thirty-eight latrine sites were identified and assessed at 2 locations in Mtunzini on the north coast of KwaZulu-Natal, South Africa (uMlalazi Nature Reserve and Zini Fish Farm) during the months of August to November 2021. Latrine sites were identified through several intensive surveys, while we characterized nonselected sites through a systematic sampling approach. Latrine and control sites were inventoried along a 52-m buffer around all water bodies in both study areas. At each site we measured a series of potential environmental predictors, including horizontal and vertical vegetation cover, surface slope, and averaged wind speeds for days classified as relatively wind-still and relatively windy. To assess the relative role of various environmental predictors, we used a binomial generalized linear model resource selection function to model both spatial scales of latrine site selection. The majority of latrine sites were located at the ecotone between 2 vegetation units or between a vegetation unit and a water source. At a macroscale, latrine sites were associated with areas containing little vegetative substrate cover and minimal canopy cover. The top-ranked models at the microscale also indicated that latrine sites were characterized as occurring in open areas with less canopy and horizontal cover and on flatter areas that are relatively protected against wind. The most common behaviors recorded at 3 latrine sites were the "jiggle dance" (42%) and sniffing (29%). We hypothesize that otters evaluate numerous environmental parameters to enhance the functionality of latrine sites. For example, sites with little vegetative cover may increase the conspicuousness of latrines to conspecifics, while areas exposed to less wind likely aid in the retention of scent. Ongoing research is characterizing the behaviors of otters around latrines and chemical signatures of latrine sites in an effort to facilitate interpretation of their social function to African clawless otters.

Key words: Mustelidae, olfactory communication, scent marking, small carnivore, territoriality.

Latrine sites are the accumulation of feces through the repeated use of a site by 1 or several individuals, and are believed to play an important role in intraspecific communication (Vitale et al. 2020). Many carnivores deposit their feces in specific dedicated latrine sites that are shared by several animals from a social group or by animals from neighboring territories (Buesching and Jordan 2022). Several species of social mammals deposit scent-containing excretion as a means of intraspecific olfactory communication (Torgerson 2014).

The spatial distribution of latrine sites can reflect their likely adaptive function. For instance, latrine sites placed peripherally within the home range of an animal are intuitively considered to have a territorial function (Vitale et al. 2020). Optimal spacing and distribution of latrines likely depend on the economic costs of maintaining 1 or several sites and the probability of intercepting territorial intruders (Gosling and Roberts 2001). Establishment of latrine sites along territorial boundaries act as both a visual and olfactory fence, indicating occupancy and competitive ability of the territory owner (Ziege et al. 2016). Core marking is done when latrine sites are established centrally within a home range such that an individual is able to "monopolize" and mark key resources (Roper et al. 1993; Dröscher and Kappeler 2014). Latrine sites located in core areas of home ranges facilitate information exchange, enhancing social bonds between members of a social group and maintaining dominance hierarchies (Roper et al. 1993). A further factor to consider is temporal variability in scent marking and latrine site use. Such changes may indicate short-term and seasonal changes in breeding behavior, environmental conditions, and possible long-term changes in population size and demography of a group (Roper et al. 1993; Rosell 2001). Habitat features including vegetation cover, ground elevation, water depth, and

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average wind speed are all features that might influence site selection.

The habitat characteristics of a site that are selected for a latrine can be used as potential indicators and clues to their role. For instance, habitat characteristics can influence several factors including scent dispersal and persistence, prey availability, protection from predators, and visual prominence to conspecifics (Depue and Ben-David 2010; Crowley et al. 2012; Raha and Hussain 2016).

Latrine sites facilitate information transfer and intraspecific communication—e.g. feces, urine, and/or scent gland secretions deposited convey information relating to resource use (Stewart et al. 2001) and habitat quality (Ben-David et al. 2005). Several other functions have been proposed regarding olfactory communication at latrine sites, including: information pertaining to the sex, diet, reproductive state, and movements of an individual (Gorman and Trowbridge 1989); territorial boundaries (Roper et al. 1993); defense of food resources (Piñeiro and Barja 2015); social recognition (Oldham and Black 2009); the social status of males (Rostain et al. 2004); mate attraction and selection (Allen et al. 2015); along with other intra- and interspecific communication functions. Overmarking—when 1 individual places their scent mark directly on top of the scent mark of another individual—is a common response in mammals when encountering scent marks (Brown and Macdonald 1985; Johnston et al. 1994; Jordan et al. 2011; Rodgers et al. 2015). Overmarking will typically occur within breeding pairs where males will scent mark over the scent of their mates, as described in the Neotropical otter (Michalski et al. 2021). Other examples of overmarking in breeding pairs include the Meerkat, *Suricata suricatta* (Jordan et al. 2007); Kirk's Dik-dik, *Madoqua kirkii* (Brotherton 1994); Grey Wolf, *Canis lupus* (Peters and Mech 1975); and the Wild Diademed Sifaka, *Propithecus diadema* (Miaretsoa et al. 2022).

Scent marking and latrine site use are employed by most mustelids, including otters (Ben-David et al. 2005; Buesching and Jordan 2019). Otter scent marking can occur in different ways, for instance, anal gland secretions can be added to feces prior to deposition or can be voided without feces (Kruuk 2006). Social mustelid species such as the European Badger (*Meles meles*) and Giant Otter (*Pteronura brasiliensis*) establish communal latrine sites—large areas for the deposition of excremental and secretion marking by all members of a group (Carter and Rosas 1997; Buesching and Macdonald 2001). Otters in particular tend to display rather elaborate marking behaviors that involve a scent-marking "dance"—for example Giant otters, Spotted-necked otters (*Hydrictis maculicollis*), and North American river otters (*Lontra canadensis*) have been recorded carrying out dance-like stepping postures, body rubbing, and intense sniffing at latrine sites (Mumm and Knörnschild 2018; Groenendijk 2019). Latrine use and behavior at latrine sites have not been extensively studied in African clawless otters (*Aonyx capensis*), but behaviors performed at latrines sites have been reported by Jordaan et al. (2017). Accordingly, before and during secretions a type of "jiggle dance" (where hind legs were stomped moved from side to side) was performed either by individuals or in groups. Jordaan et al. (2017) speculated on the social function of latrine sites in African Clawless Otter populations and suggested that they may play a role in demarcating territories between different social groups (clans) of otters.

We recorded the behaviors of African clawless otters at passively monitored latrine sites and further aimed to assess possible factors that influence the selection of latrine sites by this species at 2 ecological spatial scales. If latrine sites advertise territorial boundaries, we expected that they would have a higher probability of occurrence in areas with maximal exposure, prominent location, and increased wind exposure. Such locations would facilitate scent dispersal within the environment, such that other individuals or groups of otters are unlikely to miss them. Alternatively, latrine sites could be expected to have a higher probability of occurring in areas with more cover (vegetative or otherwise) and with less wind exposure if safety from aerial predators and/or scent retention are more important.

Materials and methods

Study area characterization

The study area was located in Northern KwaZulu-Natal, South Africa. One study area was located in the coastal town of Mtunzini (28°57′34.9″S, 31°45′00.4″E), while the second study area was located in Fairbreeze near the town of Gingindlovu (29°01′25.0″S, 31°34′47.3″E; Fig. 1).

Habitat variables and behavioral data were collected along the uMlalazi River (28°55′60″S, 31°48′0″E), located approximately 30 km southwest of Richards Bay in northern KwaZulu-Natal province, South Africa. The river drains into the Indian Ocean and is approximately 54 km long with a catchment area of 492 km^2. The study area associated with Mtunzini was further subdivided into a section within the uMlalazi River (28°57′14.7″S, 31°45′59.3″E) and a section within the Zini Fish Farm (28°57′13.7″S, 31°45′57.2″E).

The uMlalazi Nature Reserve (uMNR) covers an area of 1,028 hectares in extent and forms part of both the Maputaland–Pondoland–Albany Biodiversity Hotspot and the Maputaland Centre of Floristic Endemism (Van Wyk and Smith 2001; Zungu et al. 2018). The reserve is a natural area with low direct anthropic disturbance. Zini Fish Farm is 44.75 hectares in extent and comprises of 52 half-hectare earthen ponds. The primary product of the farm is saltwater tilapia (*Oreochromis mossambicus*). Zini Fish Farm is a transformed area with substantial anthropic disturbance. The uMNR and Zini Fish Farm are adjacent to one another, and although separated by a fence line, these 2 locations were treated as a single study area, based on their close proximity and the permeability of the fence line, specifically to otters.

In addition to this primary study area, camera traps were also established at Cottonlands Farm in Fairbreeze (29°02′16.5″S, 31°37′07.0″E), along the Nyezane River where the social behavior and communication of African clawless otters in and around latrine sites were recorded. Cottonlands Farm is located 20 km southwest of the uMNR and Zini Fish Farm and is characterized by similar climatic conditions. Sugar Cane (*Saccharum officinarum* L.) and macadamia nuts (*Macadamia integrifolia*) are farmed at Cottonlands Farm. The area surrounding camera traps along the river is characterized by grass and reed vegetation and rows of macadamia trees.

The uMNR and its surrounding areas contain major vegetation types such as Northern Coastal Forest, Swamp Forest, Mangrove Forest, Subtropical Estuarine Salt Marshes, Subtropical Dune Thicket, Subtropical Seashore Vegetation, and Subtropical Freshwater Wetlands (Mucina and Rutherford 2006). Study areas within the uMNR and Zini Fish Farm were stratified into several homogenous vegetation units based on both texture and color classes of aerial imagery (Google Earth Pro 7.3. 2021). Vegetation classifications and descriptions compiled by Zungu et al. (2018) were used as a guide for further refinement of the vegetation map in this study. At Cottonlands Farm, only latrine site behavioral

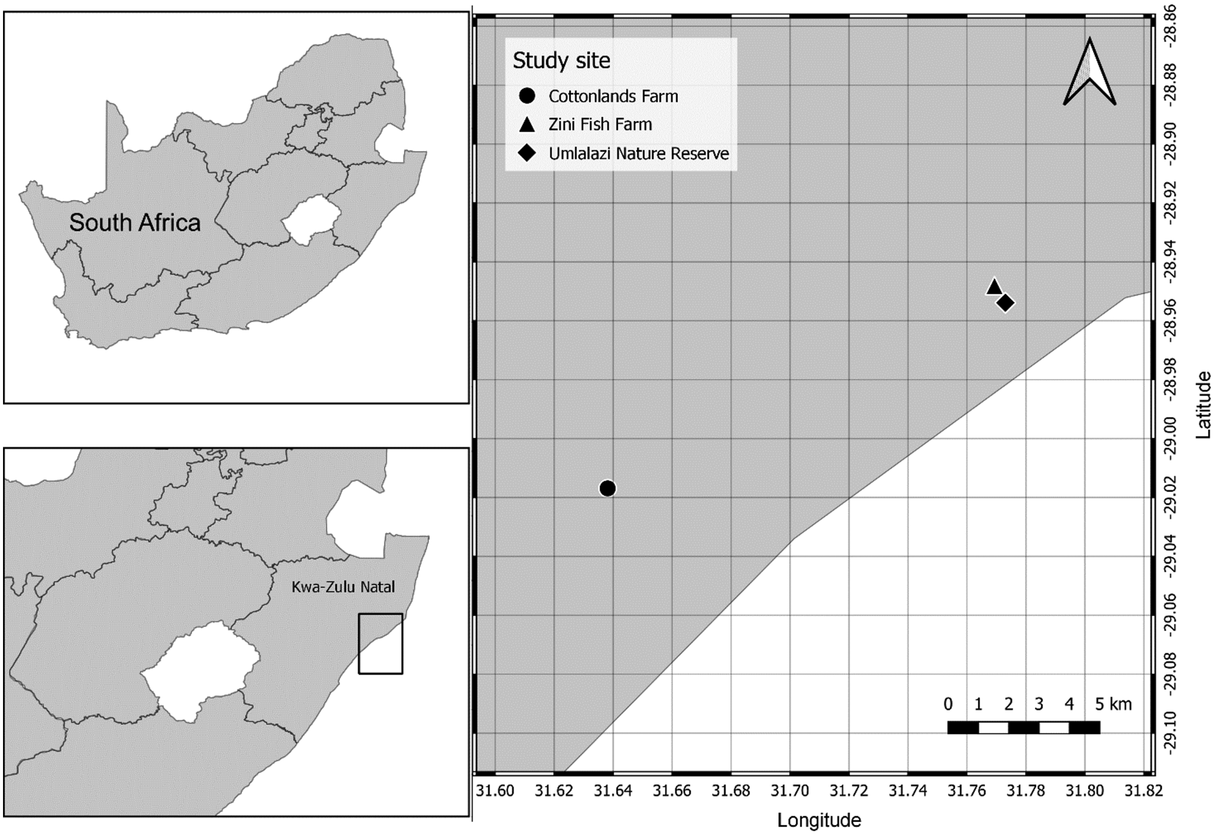

Fig. 1. Study area in northern KwaZulu-Natal province, South Africa. Cottonlands Farm and Zini Fish Farm are both transformed areas, uMlalazi Nature Reserve is a natural area.

data of African clawless otters were collected for analysis and no analyses of latrine site characteristics were undertaken.

Vegetation mapping of the study area was conducted such that each area was divided into its different plant communities at the association level and subassociation level. Mapping was done at a scale of 1:2,500 (as seen from an altitude of approximately 500 m above the surface) (Google Earth Pro 7.3. 2021). Detailed vegetation descriptions of each vegetation unit identified in both study areas are provided in Supplementary Data SD1.

The following vegetation types were identified and described within the uMNR: Vegetation unit 1, reed beds and hygrophilous grasslands; Vegetation unit 2, riverine woodlands and floodplain bush clumps; Vegetation unit 3, mudflats; Vegetation unit 4, mangrove forest; Vegetation unit 5; juncus beds; and Vegetation unit 6, dune forest.

In the Fish Farm, the following vegetation types were identified and described: Vegetation unit 1, reed beds and hygrophilous grasslands; Vegetation unit 2, riverine woodland; Vegetation unit 3, mudflats; and Vegetation unit 7, roads and paved surfaces.

Field data collection

Collection of data on latrine site selection took place at 2 spatial scales, namely a micro- (fine-scale analysis) and macroscale (course-scale analysis), such that the environmental features of African Clawless Otter latrine sites ("used") were contrasted with characteristics at control sites ("available vacant sites") within both study areas. The microscale analysis assessed habitat features in 1 × 1 m (1-m^2) grids, while the macroscale analysis assessed the habitat features in 5 × 5 m (25-m^2) grids around the center of each site.

Several intensive searches of the entire study area over a period of 1 month (1 to 30 August 2021, ±120 h) were conducted in uMNR and Zini Fish Farm, to ensure that the majority of latrine sites in the study areas were identified. Surveying for latrine sites in both study areas involved 4 people walking along the river in the uMNR and pond lines in the Fish Farm. The 4 people spaced themselves equidistantly over a distance of approximately 50 m to form a perpendicular transect line from the edge of the water and searched intensively along all accessible water edges. Locations of latrine sites in both study areas were mapped in relation to the Umlalazi River and drainage lines within the reserve and in relation to the ponds on the Fish Farm.

A latrine site was identified and included in the habitat selection analysis if it contained ≥1 scat (Barrett 2014). African Clawless Otter feces were identified based on its distinguished shape, size, and characteristic sweet and pungent fishy-like odor, as well as by the presence of crab carapace in the spraint (Rowe-Rowe 1992; Stuart and Stuart 2000). Global Positioning System (GPS) coordinates of latrine sites located within the study area were recorded using a handheld Garmin GPS providing an accuracy of approximately ≤5 m (Torgerson 2014).

The total study area was defined by the maximum distance from a water source that an otter latrine was recorded. Based on this, the study area was set to a 52-m buffer around all water bodies in the uMNR (the Umlalazi River, prominent pans, and drainage lines). The study area in the Fish Farm was limited to fenced property surrounding the ponds, ranging between 23 and 52 m from the edge of the water. Control sites were selected through a systematic approach within the 52-m buffer zone, independent of where latrine sites were located. This was done by dividing the study area into segments of homogeneous vegetation types and then allocating random sites within each segment where habitat features for each control (nonlatrine site) were recorded. The sampling area was stratified into homogeneous vegetation units based on the vegetation work done by Zungu et al. (2018). The number of control sites allocated to each homogeneous vegetation type was calculated pro rata based on percentage surface area covered by each unit within the study area.

A total of 100 control sites were randomly selected within the different stratified vegetation units in the uMNR and 20 control sites in the Zini Fish Farm (Table 1). In cases of overlap with a latrine site, control sites were reevaluated and another site selected nearby (the minimum distance that control sites were from any latrine sites was 15 m). Each control sampling plot at both the micro- and macroscale was critically evaluated according to the Zurich–Montpellier sampling method such that placement of the sampling plots fell within a representative homogeneous patch of the respective plant community (Werger 1974). Plot sampling was employed to assess both microsite and landscape scale features.

Otter behavior recording

Camera trapping with night vision capability was employed to document and record visitation patterns and behavior of African clawless otters at 3 latrine sites. Camera traps (Bushnell Trophy Cam HD Essential and PRIMOS ProofCam 3) were placed at latrine sites between September 2021 and September 2022. Cameras were positioned around 2 latrine sites on Zini Fish Farm, latrine A (28°57′02.8″S, 31°46′01.8″E) and latrine B (28°57′13.7″S, 31°45′57.2″E). The third monitored latrine was located at Cottonlands Farm (29°1′0.83″S, 31°38′17.30″E), where the camera was positioned close to a weir along the Nyezane River (latrine C). Cameras were visited on a weekly basis to evaluate equipment, collect and replace video storage cards, change batteries, and check for otter spoor.

Latrines A and B were located between 2 ponds on Zini Fish Farm and approximately 80 m apart from one another. Both of these latrines were located in relatively open areas, approximately 5 m from the ponds, with sparse covering and short- to medium-height grass and reed in the surrounding area. Latrine C was located approximately 10 m away from the Nyezane River, and was positioned on and around the man-made artificial concrete substrate of the weir, which is surrounded by thick and dense shrubby vegetation. African Clawless Otter activity was confirmed at these sites through the presence of spoor and otter feces. The camera traps were strategically positioned to capture the entirety of each latrine site. At the 3 latrine sites where behavior data were collected 1 camera trap was installed per latrine. The camera traps were active 24 h a day and programmed to record a 60-s video when triggered, followed by a 10-s delay before the next trigger event.

Microsite (fine-scale) selection

Sampling grids of 1 × 1 m, consisting of 10 × 10 cm cells, were used to characterize cover at each microsite. Features that were assessed at the microsite scale are listed in Table 2. Supratidal zone distance and distance from water were considered important features to measure given the semiaquatic lifestyle of otters (Verwoerd 1987; Estes 1991; Somers 2000; Somers and Nel 2003). Dominant plant species were considered to be prominent/dominant in a specific plant community based on their high cover values or abundance relative to that of other species in the community (Avolio et al. 2019). Descriptions of habitat variables that were assessed at latrine and control sites are defined below.

Vegetation characteristics

Vegetation cover was divided into herbaceous (low-growing plants, sedges, forbs, grasses, and reeds) and woody (shrubs and trees) layers, where the species and its average height within the grid were recorded. Herbaceous layer cover includes both living herbaceous plants as well as decaying leaf litter. This atypical approach of including both living and dead decaying vegetation was selected as otters are not likely to make

Table 1. The surface area size and percentages of the vegetation types of the uMlalazi Nature Reserve and Fish Farm and their respective number of control sites.

Vegetation types	Surface area (ha)	Surface area (%)	Number of control sites
uMlalazi Nature Reserve			
Grass and reed	8.49	9.93	10
Riverine woodland	15.17	17.75	18
Mudflat	4.71	5.51	6
Juncus beds	6.79	7.94	8
Mangrove forest	24.19	28.30	28
Dune forest	26.13	30.57	30
Total	85.48	100	100
Zini Fish Farm			
Grass and reed	12.84	63.06	12
Riverine woodland	2.52	12.38	3
Mudflat	1.96	9.63	2
Road	3.04	14.93	3
Total	20.36	100	20

Table 2. Variables used in the development of binomial count models for the selection of latrine sites by African clawless otters, based on microscale habitat characteristics.

Parameter	Description
Vegetation cover	Percentage total vegetation cover (herbaceous and woody layer)
Herbaceous cover	Percentage herbaceous cover
Woody cover	Percentage woody cover
Canopy cover	Percentage canopy cover
Horizontal cover	Horizontal cover (cm)
Slope	Bank slope (degrees)
Height above water	Height above water (cm)
Distance from water	Distance from water (m)
Supratidal zone distance	Distance from supratidal zone (m)
Windy days average wind speed	Average wind speed recorded on windy days (m/s)
Still days average wind speed	Average wind speed recorded on calm days (m/s)

distinction between living and dead vegetative material cover when selecting latrine sites (Gallant et al. 2009; Crowley et al. 2012). This approach was also followed to enable standardization in terms of structural cover between forest floors covered by decaying plant material versus other vegetation units covered by living herbaceous plants. Vegetation features and bare substrate (bare patches) of each 1 × 1 m quadrat (1-m^2 sampling plots) and its corresponding 5 × 5 m quadrat (25-m^2 sampling plots) were recorded through visual estimation. The foliar (aerial) cover of woody species (which measures the vertical projection of exposed leaf area) within each quadrat was recorded at a height of 1 m. Percentage foliar cover was measured by sequentially adding the percentage cover value for each plant species until a total was reached for each quadrat. Grass, forb, sedge, reed, shrub, and tree species were all identified to species level (where possible using practical field identification techniques) and recorded for each site. Bare patches (substrate type) were broadly divided into silt clay, sandy clay, sandy, gravel, and paved surfaces (man-made).

Horizontal and canopy cover

It is possible that horizontal and canopy cover could play a role in providing otters with cover and security from predators. Crocodiles, pythons, and aerial raptor predators occur in both study areas (Hocking et al. 1990; Alexander and Marais 2013). This vegetative cover could also potentially aid otters in avoiding exposure of their latrine sites to other species, e.g. the Water Mongoose (*Atilax paludinosus*) that may also utilize them for marking. Additionally, the habitat variables of canopy cover and horizontal cover could guard latrine site (scent-marking areas) from environmental changes, and vegetative cover could potentially play a role in retaining and protecting scents from elements prolonging its use for olfactory communication (Crowley et al. 2012).

In order to assess obstruction to olfactory cues around a latrine, horizontal closure and canopy cover of the area were assessed based on the horizontal and canopy cover around a latrine and control sites, following the procedures described by Joubert et al. (2014) and Toledo et al. (2008), which has been successfully implemented in predator behavioral analysis studies (Potash et al. 2019). Given that olfactory communication and scent dispersal are difficult variables to measure, horizontal vegetation cover was implemented as an approximate proxy for olfactory obstruction because it is believed to play a role in limiting or restricting the dispersal of scent around latrine sites. Horizontal closure (visual vegetative obstruction) was measured using a 2-m Robel pole with alternating 10-cm bands of red and white, each band subdivided into four 2.5-cm regions placed in the center quadrant of the latrine (Joubert et al. 2014). At each latrine and control site 4 observations were made of the pole from the 4 cardinal points. A 4-m-long string was attached to the pole at a 1-m height to provide the standard distance from the pole. Each recording noted the lowest visible segment of the Robel pole that was completely obscured by vegetation. The total visual obstruction measurements obtained at each observation point were recorded and divided by the total number of readings for that particular site, yielding the average horizontal obstruction (Potash et al. 2019). Canopy cover classes, as described by Goloran et al. (2020), used during visual estimations included: open (10% to 39% of the sky is obstructed by tree canopies); moderately closed (40% to 69% of the sky is obstructed by tree canopies); and closed (70% to 100% of the sky is obstructed by tree canopy cover).

Topography and wind speed

Slope of a site was measured with a clinometer from the center of each site to the edge of water. Elevation above water was calculated by combining the clinometer estimate (i.e. the slope) with the diagonal distance (measured with a measuring tape) to the water edge. To infer whether otter latrine sites are located in strategic locations to facilitate wind dispersal of odor from latrine sites, wind speed readings (m/s) were recorded at each latrine and control site, measured with a handheld anemometer (Benetech Wind Meter Anemometer). Sampling was conducted under a range of conditions to quantify variability. Relative exposure of wind at sites was defined according to the Beaufort Wind Scale: "Still" days defined as being between calm (0 m/s) and light air movement (0.5 to 1.5 m/s); while "windy" days were defined as having a light breeze (2 to 3 m/s), gentle breeze (3.5 to 5 m/s), moderate breeze (5.5 to 8 m/s), or fresh breeze (8.5 to 10.5 m/s).

A total of 8 wind speed readings were recorded at each site over the course of 4 weeks from 13 November to the 16 of December 2021. Four readings were obtained at each of the sites on still days and 4 readings on windy days. Readings were taken in the early mornings and in the late afternoons. Each individual value recorded per site consisted of the average of 3 readings taken within a 5-min window. Wind readings were recorded directly above each latrine site, approximately 5 cm above the ground surface.

Macroscale (landscape)

The macroscale assessed each site by describing it according to ground vegetation cover, including average substrate cover, dominant tree and shrub species, dominant herbaceous species, their respective species cover percentages, and respective average heights; and canopy cover (Table 2).

Statistical analysis

Binomial generalized linear models (GLMs) were implemented in the R programming environment (R Core Team 2019) to explore the influences of predictor variables on latrine site selection. Ten variables were used to develop models for microscale selection (Johnson et al. 2006) of latrine sites, and 3 variables were used in the development of models for macroscale selection. The mean and standard deviations of predictor variables at both the micro- and macroscale are reported for each of the vegetation units. Covariation between predictor variables was assessed using pairs plots and covariates were removed prior to analyses. Herbaceous and woody layer vegetation cover at the microscale were the 2 predictor variables that were found to covary and which were subsequently removed.

All possible combinations of fixed variables were then compared to select the most parsimonious models using the "dredge" function in the MuMIn package (Barton 2020). Akaike's information criterion for small sample sizes (AICc) was used to identify the most parsimonious explanatory models of latrine selection by African clawless otters (Burnham and Anderson 2004). Both the delta-AIC (ΔAIC) and Akaike weights (w_i) were used to rank and compare models—the model that contains the lowest AICc score is considered the most parsimonious model. Model selection was determined based on maximum likelihood, second-order AIC (AICc) scores, corresponding AIC weights, and delta-AIC values ($\Delta AIC < 2$) to select the most parsimonious models (Burnham and Anderson 2002). *Z*-statistics were used to assess the importance of individual predictors contained in the most parsimonious models. Statistical significance was set at *P*

≤ 0.05. Mean values ± standard deviations are reported, unless otherwise stated.

Results

A total of 38 latrine sites were located across both sites, 25 latrines in the uMNR and 13 latrines in the Fish Farm. The latrine site search effort, ±120 h, was conducted 1 to 30 August 2021 and the latrine and control sites were assessed from September to November of the same year (Fig. 2).

Vegetation unit descriptions

Vegetation types were used as proxies for, and as indicators of the underlying ecosystems in which otters made latrine site choices (Fig. 2). Results of the vegetation unit descriptions for the 7 vegetation types defined and categorized in this study are detailed in Supplementary Data SD1. Representative photographs of each vegetation unit at both the microscale and macroscale are provided in Supplementary Data SD2. The vegetation unit descriptions are summarized for both the microscale and macroscale in Table 3.

African Clawless Otter latrine sites: characteristics and features identified

Distribution within Study area 1—uMNR

Across the 38 latrine sites, 19 were located at the ecotone between 2 vegetation units or at the ecotone between a vegetation unit and a water source, 10 in the medium tall closed reed beds and hygrophilous grasslands, 6 on hyper-saline mudflats, 2 in mangrove forest, and 1 in the medium tall *Juncus krausii* sedge beds. The ecotones between the mangrove forests and mudflats, between the mangrove forests and riverine forest bush clumps, and between the mudflats and *Phragmites australis–Juncus kraussii* medium tall closed sedge beds were the most common latrine site locations within the uMNR.

Distribution within Study area 2—Zini Fish Farm

Thirteen latrine sites were located in the Fish Farm. Here, 10 sites were located in the grass and reed vegetation type, while the remaining 3 were located at the ecotone between the road and grass and reed vegetation type.

Microscale (1-m² sampling plots)

Mean herbaceous cover recorded at latrine sites across both study areas was 25% ± 25%. The dominant herbaceous species recorded were the grasses *Stenotaphrum secundatum*, *Cynodon dactylon*, *Digitaria eriantha*, *Imperata cylindrica*; the forb *Euphorbia prostata*; the vine *Rhynchosia caribaea*; and an unidentified moss species. Mean herbaceous cover at control sites varied between vegetation types and ranged between 0% and 100%. At the microscale there were no woody species recorded at latrine sites. The common substrate types identified at latrine sites included sandy-silt clay, sandy soil, and gravel sands.

Canopy cover at the microscale was minimal (6% ± 14%), with most of the latrine sites located in open areas devoid of woody canopy cover. Canopy cover at control sites ranged between 0% and 100%. Horizontal cover at latrine sites was minimal with the mean height recorded being 4.6 ± 5.7 cm; with the control site horizontal cover ranging from 0 to 50.63 cm (41.4 ± 64.3 mm). Overall, most of the latrine sites were located in areas where the ground had a gentle slope and the mean slope recorded was 5° ± 3° (at control sites slope ranged between 1° and 12°). Mean distance that latrine sites were located from a water source was 13 ± 11 m (control sites ranged between 3 and 49 m). Mean

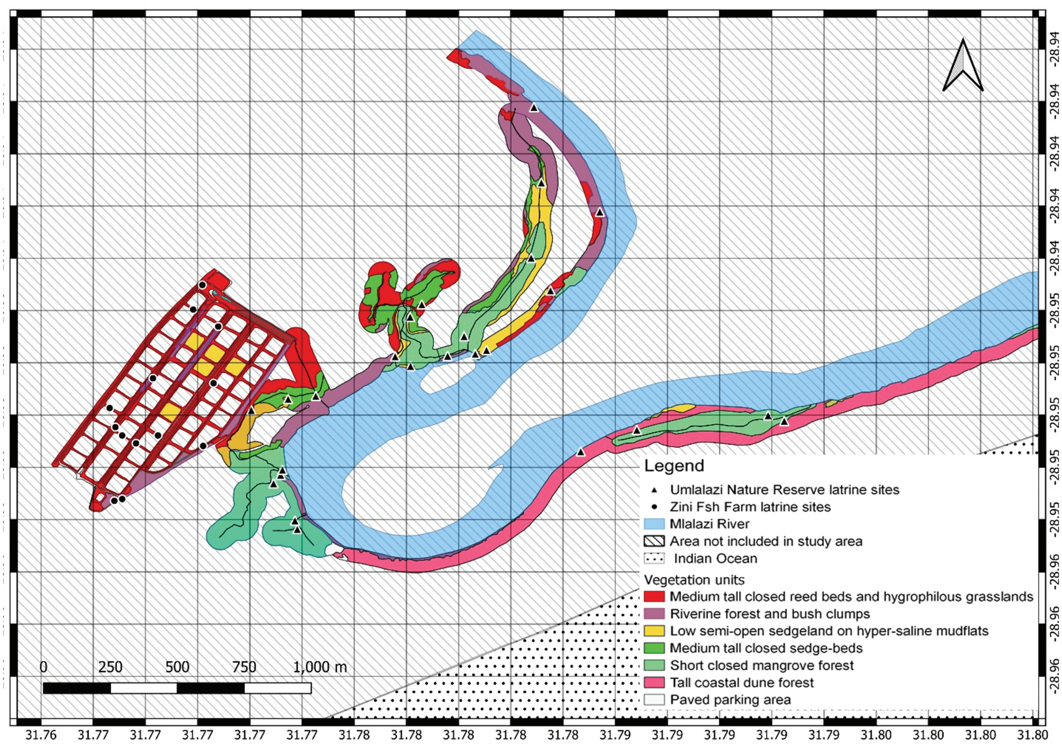

Fig. 2. Vegetation units and latrine site location in the 2 study areas of the Umlalazi Nature Reserve and Zini Fish Farm, on the north coast of KwaZulu-Natal, South Africa.

Table 3. Summarized findings of the predictor variables at both the micro- and macroscale of the 7 vegetation units and latrine sites of African clawless otters.

Predictor variables	Vegetation unit—Microscale							African Clawless Otter latrine sites
	1	2	3	4	5	6	7	
	Reed beds and hygrophilous grasslands	Riverine woodlands and floodplain bush clumps	Mudflats	Mangrove forest	Juncus beds	Dune forest	Roads and paved surfaces	
Herbaceous cover (%)	94 ± 6.18	91 ± 7	34 ± 35	27 ± 12	59 ± 10.54	79 ± 21	21 ± 15	25 ± 25
Woody cover (%)	2.5 ± 0.7	3 ± 3	-	77 ± 6	-	2 ± 3	-	-
Canopy cover (%)	0.4 ± 2	93 ± 9	2 ± 2	88 ± 19	-	90 ± 13	-	6 ± 14
Horizontal cover (mm)	190 ± 140	180 ± 10	29 ± 24	9 ± 2	370 ± 70	5 ± 3	10 ± 20	41.4 ± 64.3
Slope (degrees)	4 ± 2	5 ± 2	1.5 ± 1	3 ± 1	3.5 ± 2	7 ± 5	3 ± 5	5 ± 3
Elevation above water (mm)	2,030 ± 2,570	1,220 ± 71.9	490 ± 360	890 ± 570	90 ± 77	279 ± 219	600 ± 480	900 ± 80
Distance from water (m)	13.2 ± 10.58	19 ± 12	20 ± 12	17 ± 7	15 ± 8	22 ± 10	10 ± 5	13 ± 11
Supratidal zone distance (m)	15 ± 10	17 ± 12	0 ± 0	4 ± 7	8 ± 7	17 ± 9	-	3 ± 6
Windy days average wind speed (m/s)	1.99 ± 0.45	1.53 ± 0.04	2.19 ± 0.32	1.6 ± 0.29	0.74 ± 0.24	1.1 ± 0.35	2.39 ± 0.46	1.82 ± 0.43
Still days average wind speed (m/s)	0.08 ± 0.05	0.06 ± 0.05	0.12 ± 0.05	0.08 ± 0.05	0.08 ± 0.05	0.06 ± 0.04	0.09 ± 0.02	0.1 ± 0.05

Predictor variables	Vegetation unit—Macroscale							African Clawless Otter latrine sites
	1	2	3	4	5	6	7	
	Reed beds and hygrophilous grasslands	Riverine woodlands and floodplain bush clumps	Mudflats	Mangrove forest	Juncus beds	Dune forest	Roads and paved surfaces	
Vegetation cover (%)	92 ± 6	65 ± 41	44 ± 64	9 ± 9	84 ± 6	83 ± 16	11 ± 7	40 ± 28
Canopy cover (%)	2 ± 4	91 ± 19	1 ± 1.7	93 ± 8	-	92 ± 9	-	17 ± 23
Substrate cover (%)	8 ± 20	35 ± 13	56 ± 35	90 ± 17	16 ± 6	16 ± 26	88 ± 32	60 ± 17

distance from the supratidal zone was 3.36 ± 6.09 m. Average elevation above water was 900 ± 80 mm; control sites ranged between 27 and 909 mm. Mean wind speed recorded on windy days at latrine sites was 1.82 ± 0.43 m/s, while on still days it was 0.1 ± 0.05 m/s. Mean wind readings recorded at control sites on windy days was 1.65 ± 0.37 m/s, and on still days was 0.08 ± 0.04 m/s.

Macroscale (25-m² sampling plots)

Mean vegetation cover at the macroscale was 40% ± 28% (and ranged between 0% and 100% at control sites), with mean herb layer height measuring at 271 ± 323 mm. Dominant species at the herbaceous level include the grasses *S. secundatum*, *C. dactylon*, *D. eriantha*, and *Sporobalus africanus*; the reeds *P. australis*; the sedge *J. kraussii*; the herbs *Indigofera spicata*, *E. prostata*, *Conyza albida*, *R. caribaea*; the succulent plant *Salicornia pachystachya*; and an unidentified moss species. Bare patch substrate cover at the macroscale was relatively extensive at latrine sites with the mean ground cover estimated at 60% ± 17% (ranged between 0% and 100% at control sites). Latrine sites on the Fish Farm did not contain any woody species at the macroscale; thus, the canopy cover estimate is averaged from the latrine sites in the uMNR. Mean canopy cover recorded at the macroscale was 17% ± 23%, with mean tree height recorded as 2.78 m ± 2.49. Canopy cover at control sites ranged between 0% and 100%.

Model outputs

Microscale

The 4 top-ranked models at the microscale all retained canopy cover, horizontal cover, slope, vegetation cover, and moderate and minimal wind exposure (Table 3). The top-ranked models at the microscale indicated that latrine sites were characterized as occurring in open areas with less canopy and horizontal cover on elevated areas that had lower wind speeds (Fig. 3). The interaction of wind exposure and bank slope proved to be an important feature in latrine site selection. Accordingly, sites located on steeper slopes were more likely to be used as latrines when wind exposure was also higher—this association being the opposite in flatter areas (Fig. 3).

Latrines were characterized as occurring on sloping terrain in areas that were either exposed to wind or more sheltered from the wind. The structure of the 4 most parsimonious models at the microscale are presented in Table 4 and the respective binomial GLM AIC scores for the microscale habitat predicators are

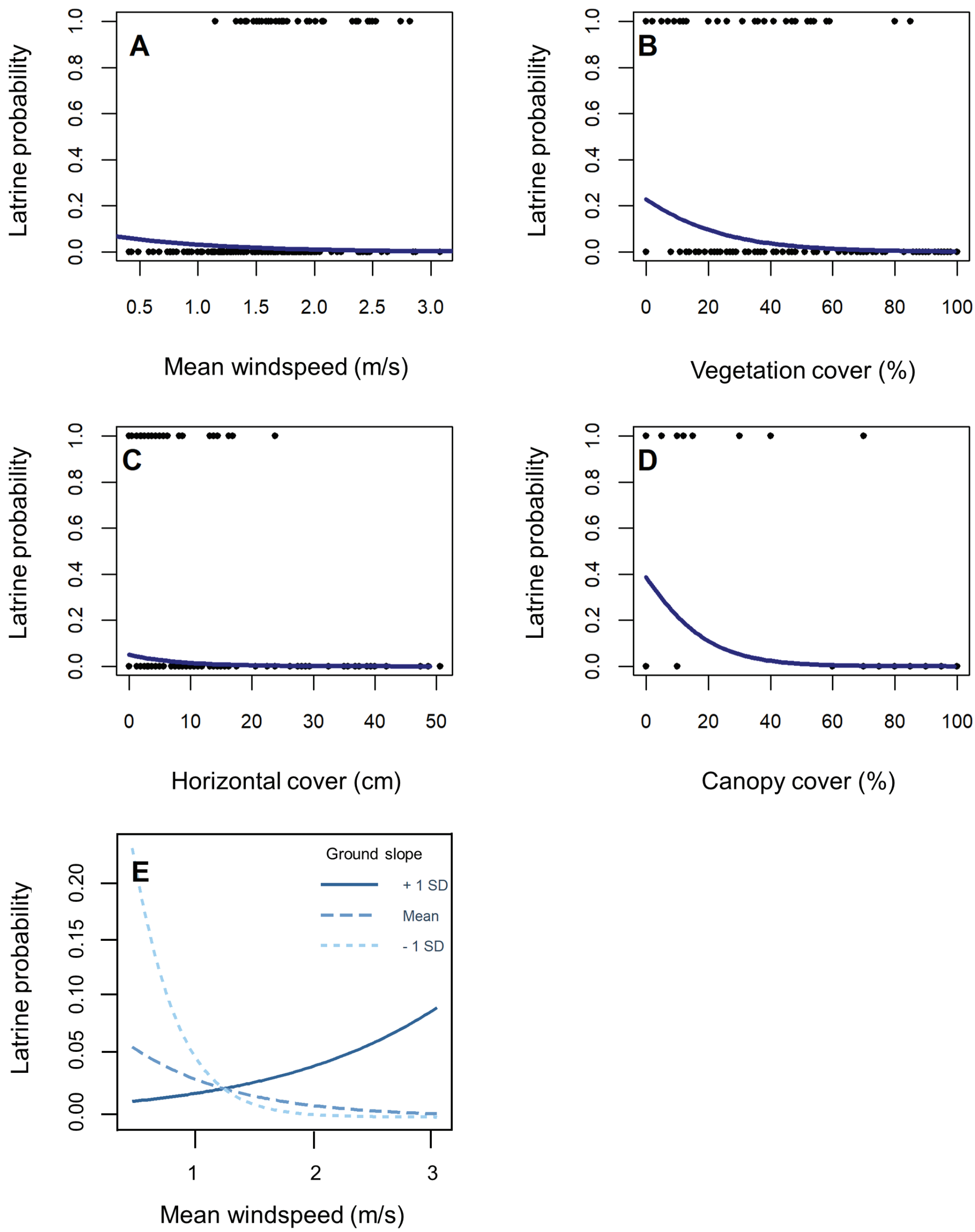

Fig. 3. Predicted probability of latrine site selection in relation to the 4 predictors retained in all the top 4 models at the microscale that retained the same effect direction across all models. The predicted probability of latrine site in relation to wind speed average (A); horizontal cover (B); vegetation cover (C); and canopy cover (D). The interaction plot depicting the relationship between the predictor of slope and mean wind speed on windy days is also depicted (E).

presented in Table 5. Model output of the remaining top models (models 2 to 4) is supplied in Supplementary Data SD3. Similarly, latrine site selection at the macroscale was associated with areas containing little vegetative cover and minimal canopy cover.

Macroscale

The top-ranked model at the macroscale retained the variables canopy cover and substrate cover (Table 6). Latrine site selection at the macroscale indicated that substrate cover was positively related to the presence of latrine sites, while canopy cover had a negative association with latrine site selection by otters (Fig. 4).

The structure of the 3 most parsimonious models at the macroscale are presented in Table 6 and a summary of the top-ranked model provided in Table 7.

Behavior video analysis

The camera traps recorded 16 videos of African clawless otters visiting latrine sites. No group scent marking of otter groups were recorded and all individuals visiting the latrine sites were alone. In addition to African Clawless Otter detections 11 other naturally occurring mammal species were recorded by camera traps

Table 4. Summary of the top 4 candidate models (binary generalized linear model) predicting latrine site based on microscale habitat data collected in the uMlalazi Nature Reserve and Fish Farm in Mtunzini, South Africa. AICc = second-order Akaike Information Criterion; w_i = Akaike weight.

Model	Rank	AICc	ΔAICc	*wi*
Canopy cover ± horizontal cover ± slope ± still average ± vegetation cover ± windy average ± slope * still average ± slope * windy average	1	71.2	0.00	0.151
Canopy cover ± horizontal cover ± slope ± still average ± vegetation cover ± windy average ± slope * windy average	2	72.1	0.99	0.092
Canopy cover ± height above water ± horizontal cover ± slope ± still average ± vegetation cover ± windy average ± slope * still average ± slope * windy average	3	72.8	1.65	0.066
Canopy cover ± horizontal cover ± slope ± still average ± vegetation cover ± windy average ± slope * still average	4	73.0	1.82	0.061

Table 5. Summary outputs of the top-ranked model assessing the selection of latrine sites based on microscale habitat data collected. ChiSq = Chi-squared; df = degrees of freedom.

Parameters	Estimate	Std. error	ChiSq	df and residual df	*P*-value
Intercept	8.776	3.355	-	-	0.008
Canopy cover	−0.081	0.023	40.870	1,160	<0.001
Horizontal cover	−0.127	0.058	5.698	1,159	0.017
Slope	−1.119	0.773	13.784	1,158	<0.001
Still average	−0.349	15.533	7.595	1,157	0.005
Vegetation cover	−0.051	0.014	20.735	1,156	<0.001
Windy average	−3.799	1.340	6.257	1,155	0.012
Slope: windy average	0.571	0.362	4.060	1,154	0.043
Slope: still average	5.473	3.448	3.235	1,153	0.072

during the study period in both study areas: Water Mongoose (*Atilax paludinosus paludinosus*), Large-spotted Genet (*Genetta tigrina*); Side-striped Jackal (*Lupulella adusta*); Brown Greater Galago (*Otolemur crassicaudatus*); Greater Cane Rat (*Thryonomys swinderianus*); Acacia Rat (*Thallomys paedulcus*); Vervet Monkey (*Chlorocebus pygerythrus*); Red Forest Duiker (*Cephalophus natalensis*); Bushbuck (*Tragelaphus scriptus*); Burchell's Zebra (*Equus quagga antiquorum*); and Bushpig (*Potamochoerus larvatus koiropotamus*).

The time otters were present in the 60-s videos ranged from 6 to 37 s. A total of 8 videos were recorded at latrine A and 4 videos each were recorded at latrine B and C. At latrine A, 7 of the 8 videos were recorded consecutively, separated by time intervals between 20 to 30 min, on 2 November 2021. The final video at latrine A was captured on 8 November 2021. At latrine B, the first 2 videos were captured on consecutive days, 13 and 14 October 2021, while the other 2 videos were recorded on 24 October 2021 and 2 November 2021. At latrine C, 2 videos were recorded on 7 November 2021 and the other 2 videos were recorded on 4 and 11 November 2021. A characterization and description of all behaviors observed at latrine sites are shown in Table 8.

During visits, otters were recorded displaying scent marking, sniffing, standing, stomping, body rubbing, defecation, urination,

Table 6. Summary of the candidate models predicting latrine site selection by African clawless otters based on macroscale data collected in the uMlalazi Nature Reserve and Fish Farm in Mtunzini, South Africa. AIC = Akaike Information Criterion; w_i = Akaike weight.

Model	Rank	AICc	ΔAICc	*wi*
Canopy cover ± substrate cover	1	130.1	0.00	0.421
Herbaceous cover ± canopy cover	2	130.3	0.20	0.381
Canopy cover ± herbaceous cover ± substrate cover	3	131.7	1.51	0.198

and the "jiggle dance" (first identified and described by Jordaan et al. 2017; Fig. 5; Supplementary Data SD4).

The first 2 video records of otters at latrine A (13 October and 2 November 2021) recorded both otters running with their heads elevated. The first video recorded at latrine A (13 October 2021) captured a short snippet of an otter running through the latrine site with its head and tail elevated. In addition, the first known recording of otters overmarking at a latrine site was captured at latrine A. The last video at latrine site A (8 November 2021) recorded an otter intensely sniffing the area for a period of 18 s. All other videos in latrine A were on 2 November 2021 from 08:00 to 24:00. In each of these videos, otters were recorded performing the "jiggle dance" and intensely scent marking through anal gland secretions on the low-level ground-cover vegetation of the latrine site. When performing the "jiggle dance" the otters would pivot their forelimbs from side to side, while their hind legs would be thrust from 1 side of their body to the other. The otters would scent mark in this manner while rotating their body 180° to complete a semicircle. In some cases, an otter would complete the "jiggle dance" pivoting their forelimbs while stomping and moving their hind legs from side to side. It is unclear whether or not these were separate individuals or the same individual scent marking the latrine site over the course of the night.

At latrine B only 1 of the 4 recordings was of an otter defecating. This was also the only recording of an otter during daylight hours (09:24 h on 14 October 2021), showing it first urinating for 4 s while the defecation took approximately 8 s—during this process the otter completed a 360° rotation dispersing the urine and feces on the ground-cover vegetation. This otter was wet, indicating that it had potentially just come out of the pond after a hunting expedition. All recordings at latrine C showed otters scent marking through the "jiggle dance," in the early hours of the morning between the hours of 03:00 h and 05:00 h (between 2 and 11 November 2021). In 3 out of the 4 recordings taken in this locality the otters were observed intensely sniffing (for about 6 to 13 s) before they commenced the "jiggle" dance. Once the otters had completed the "jiggle dance," they would immediately leave the latrine site from the same area they had entered. The otters in this locality were also recorded as typically sprainting on the cement blocks and concrete weir along the Nyezane River.

Discussion

Latrine site selection

African Clawless Otter latrine site selection was expected to be driven by 1 of 3 factors (or a combination thereof): (1) to facilitate the dispersal of scent; (2) to facilitate the retention of scent; and/or (3) to avoid predation. Latrine sites were well-distributed throughout the study area and the majority of the latrine sites located in the uMNR were located at the ecotone between 2 vegetation units or at the ecotone between a vegetation unit and a water source. Many animal species use ecotones—breaks in natural vegetation and road-verge transitions—as territory boundaries (Gosling 1974; Underhill 2003). Therefore, it seems reasonable that the selection of ecotones as latrine sites by otters may also play a role in securing territorial boundaries. Further selection for latrine sites in areas with minimal vegetative, canopy, and horizontal cover, and areas with moderate wind exposure could potentially aid in making the latrine sites more conspicuous to conspecifics and other species in the area, supporting the territorial marking hypothesis.

Canopy and horizontal vegetation cover were hypothesized to play an important role in latrine site selection, as they off a form of protection against predation. The fact that this showed a negative association with the presence of latrine sites could indicate that otters in this area do not face major predation threats that would require their latrines to be concealed. At the same time, the generally close proximity of latrine sites to water sources (a mean distance of 13 ± 11 m) may provide otters with quick access to the parts of the river, water channels, and ponds to limit their detectability. Despite this close proximity, we found no support for a significant relationship between latrine site selection and distance to water. Similar findings were found in the Hog Badger (*Arctonyx collaris*), where latrine site selection was negatively correlated to high-density food resources (Zhou et al. 2015). Latrine site selection in our study was positively associated with bare ground cover such that spraint was typically deposited on sandy-silt clay, sandy soil, and gravel sand substrates. Sandy substrates were identified as an important feature for Neotropical Otter olfactory communication (Michalski et al. 2021). While Neotropical river otters have been recorded making burrows in areas devoid of vegetation (Pardini and Trajano 1999), our study did not locate any otter burrows in close proximity to latrine sites.

We suggest that latrine sites are selected in "open" areas devoid of vegetation to increase the likelihood of conspecifics or other species coming across the site. Otters in our study are seemingly not reliant on a substantial amount of scent dispersal by wind but we found some support for selection of conditions that would favor wind-assisted scent dispersal (e.g. the selection of windier areas where slope gradients are steeper). The study area of Mtunzini is in a subtropical climate that is relatively warm, with

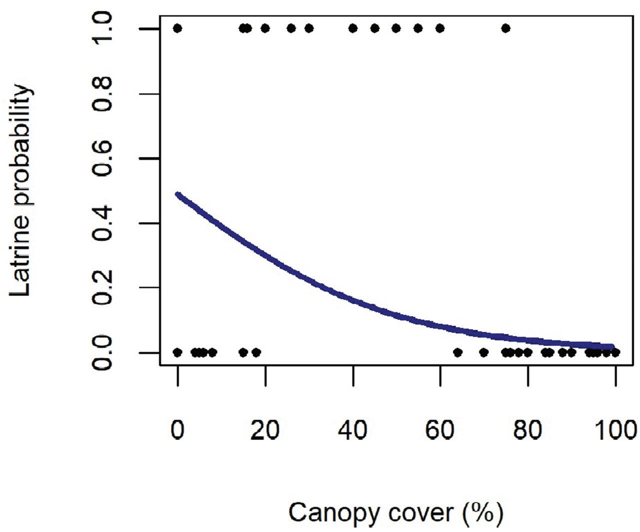

Fig. 4. Predicted probability of latrine site selection in relation to canopy cover at macroscale.

Table 7. Summary outputs of the top-ranked model for the selection of latrine sites based on macroscale habitat data collected. ChiSq = Chi-squared test; df = degrees of freedom.

Parameters	Estimate	Std. error	ChiSq	df	P-value
Canopy cover	−0.040	0.007	42.885	1,160	<0.001
Substrate cover	0.033	0.008	24.885	1,159	0.375

Table 8. Characterization and description of all the African Clawless Otter (*Aonyx capensis*) behaviors observed at latrine sites.

Behavior	Definition
Standing	Stationary, no walking or running movement
Walking head down	Walking with head down, pointed at ground
Walking head up	Walking with head up, parallel to or not pointed at ground
Head raise up and down	Stationary or moving with head moving intermittently up and down
Running head down	Running with head down, pointed at ground
Running head up	Running with head up, parallel to or not pointed at ground
Sniffing	Nose to ground, head movement back and forth, either while the animal is stationary or walking
Jiggle dance	Anterior stomped and posterior legs would move from side to side
Urination	Urine is voided
Defecate/sprainting	Elimination of fecal matter and/or anal gland secretions

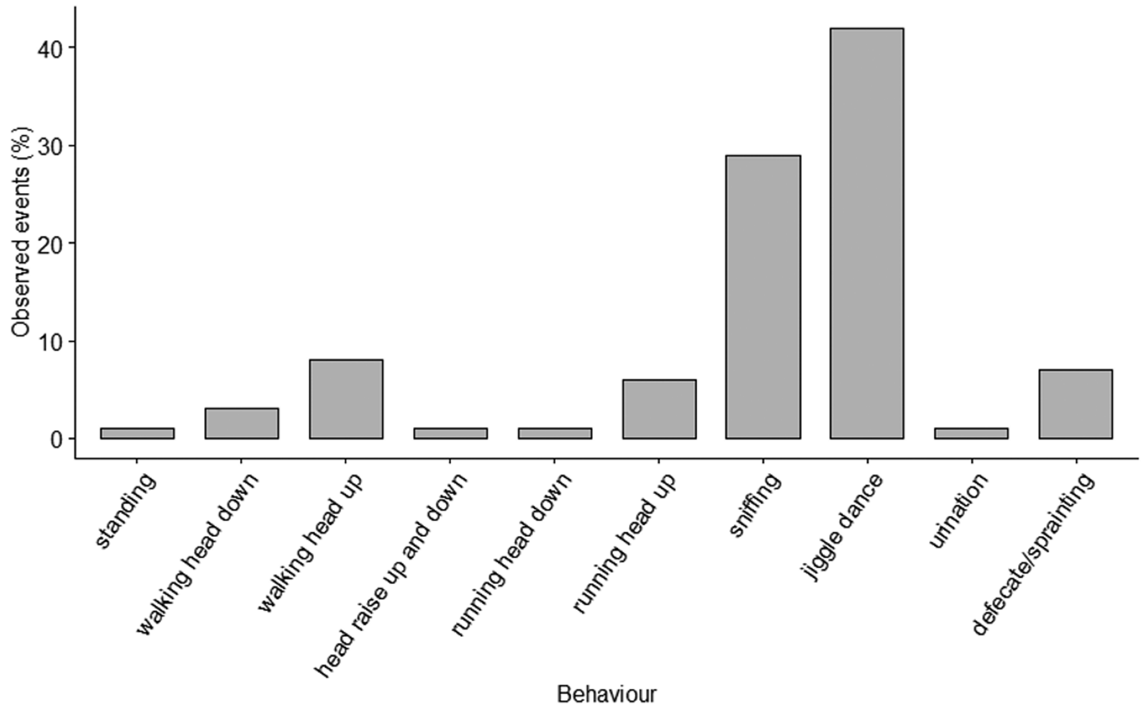

Fig. 5. Percentages of the various behaviors of African Clawless Otter recorded at 3 latrine sites within Zini Fish Farm and along the Nyezane River in Northern KwaZulu-Natal from September 2021 to September 2022. Cases where otters were not in sight were excluded.

very little daily or seasonal temperature fluctuations. This lack of extreme fluctuations, along with rainfall in both the summer and winter seasons, results in vegetation types and vegetation structures remaining relatively stable throughout the year. The findings of this research study may be relevant to African Clawless Otter populations inhabiting areas where predators, prey, and habitat types are somewhat similar to the environmental and ecological features of this study area. While specific micro- and macroscale habitat features may vary between different localities, the importance of bare ground, and minimal horizontal and canopy cover at both spatial scales have likely arisen as a result of selective pressures common to many coastal African Clawless Otter populations.

The importance of lakeshore topography on the distribution patterns of latrine sites have been documented in North American river otters (e.g. Newman and Griffin 1994). More recently, shoreline topography and terrestrial convexity were reported to be important habitat features predicting the presence of North American River Otter latrine sites at a coarse scale (Albeke et al. 2010). Detailed assessments of shoreline and overall study area topography were beyond the scope of this study and could be investigated in future research. For instance, future research could investigate the importance of additional microscale variables such as the sizes and structural complexity of habitat features (e.g. tree logs and boulders) and the influence of man-made structures (e.g. docks) to latrine site selection.

It is only through knowledge on habitat selection and scale-specific processes that effective conservation and management strategies can be implemented for otter populations (Mason and Macdonald 1986; Douglas 2003) and understanding latrine site selection may provide insights into the mechanisms that drive the distribution and activity of otters (Crowley et al. 2012). Our study illustrated that environmental variables have an influence on the selection and distribution of latrine sites by African clawless otters at both the micro- and macroscale and this multiscale approach allowed for a more detailed description and understanding of African Clawless Otter latrine site selection.

Scent marking behavior

Anal gland secretions have been well-documented in otters (Ruiz-Olmo and Gosálbez 1997; Rostain et al. 2004; Ben-David et al. 2005; Leuchtenberger and Mourão 2009; Green et al. 2015; Jo and Won 2020); however, the manner in which the African Clawless Otter scent mark is not well-documented. African Clawless Otter scent marking behavior previously identified as the “jiggle dance” by Jordaan et al. (2017) was recorded at all 3 of the latrine sites. All of the otter videos captured at latrine A and B in the Fish Farm, or at latrine C located at the farm in Fairbreeze recorded otters traveling and scent marking alone. The most common behaviors recorded at latrine sites were sniffing (29%) and the jiggle dance (42%), supporting the hypothesis that latrine sites are primarily used for olfactory communication. Gaits where otters would elevate their heads at either the run (6%) or walk (8%) accounted for a higher percentage of recorded behavior than gaits where their heads would be positioned downwards at the walk (3%) or run (1%).

Stomping behavior has been described in *L. canadensis* (Green et al. 2015; Rifenberg 2020; Barocas et al. 2021); however, this behavior has only been associated with defecation and urination. The stomping behavior which forms part of the “jiggle dance” has been documented and described in African clawless otters (Somers 1997), and has recently been associated with both anal gland secretions and defecation (Jordaan et al. 2017). Observations recorded in this study confirm the findings by Jordaan et al. (2017), where foot stomping behavior and ‘jiggle dance’ are associated with anal gland secretions and defecation. A common behavior recorded in otters at latrine sites is body rubbing, documented in the Giant Otter (*P. brasiliensis*; Leuchtenberger and Mourão 2009), the Neotropical Otter (*Lontra longicaudus*; Michalski et al., 2021), the North American River Otter (*L. canadensis*; Green et al. 2015), the Spotted-necked Otter (Reed-Smith et al. 2014), and the African Clawless Otter (Estes 1991; Jordaan et al. 2017). Body rubbing is hypothesized to play a role in scent marking (Leuchtenberger and Mourão 2009; Green et al. 2015). Michalski et al. (2021) recorded novel body rubbing behaviors in the Neotropical Otter, where males would rub their belly and genitalia on sandy substrates along river margins. The observation of African Clawless Otter body rubbing by Rowe-Rowe (1978) was believed to play a role in drying. However, recent evidence of otters displaying both solitary and social body rubbing—which resulted in a pungent odor different to that emitted from spraint—suggests that body rubbing behaviors function in scent marking (Jordaan et al. 2017). Jordaan et al. (2017) speculate that the function of body rubbing and the "jiggle" dance are linked to inter-clan territorial marking. That body rubbing behavior was not recorded at any of the latrine sites in this study could indicate that body rubbing and the "jiggle" dance serve different functions conveying different messages to conspecifics.

The scent marking and overmarking behaviors reported here could potentially play a variety of roles from encoding information relating to resource availability, mate attraction, territorial marking, and maintenance (Gosling and McKay 1990; Rostain et al. 2004; Buesching and Jordan 2019). The Eurasian Otter (*Lutra lutra*) is believed to scent mark in or to locate key food resources (Remonti et al. 2011), while Kruuk (1992) speculates that Eurasian otters scent mark to signal resource use, enabling foraging efficiency to be increased. Observations reported here, where the African clawless otters visited latrine sites and scent marked individually, possibly indicate that scent marking could function in intra-clan communication or territorial marking. Intra-clan communication also serves an important function in encoding and conveying social dominance, health, and reproductive status (Hutchings and White 2000; Arakawa et al. 2008). Observations reported here of otter scent marking do not preclude the alternative functions of scent marking where information is encoded relating to health, reproductive status (Arakawa et al. 2008; Buesching and Jordan 2022), sex, age, dominance (Vaglio et al. 2016), social status, and resource availability (Rostain et al. 2004).

Latrine sites are an important feature in otter ecology and provide an opportunity to relate latrine characteristics and habitat features to patterns of otter activity. Future research studies would benefit from assessing the location of latrine sites in relation to home ranges (and whether there are overlaps with female home ranges), territorial boundaries, as well as frequency and seasonal changes in latrine site use.

Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Detailed descriptions setting forth the distribution of each vegetation unit identified within the uMlalazi Nature Reserve and Zini Fish Farm. The description of each predictor variable is also discussed for each vegetation unit at both the microscale and macroscale.

Supplementary Data SD2.—Representative photographs at both the micro- and macroscale of each of the 7 vegetation units identified in uMlalazi Nature Reserve and Zini Fish Farm.

Supplementary Data SD3.—The binomial generalized linear model's AIC scores for the microscale habitat predicators for the remaining top models (models 2 to 4).

Supplementary Data SD4.—Camera trap screenshots of the various behaviors observed and described in the ethogram of African clawless otters recorded in the uMlalazi Nature Reserve and Fish Farm in Mtunzini, South Africa.

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Author contributions

SGN contributed to design of the study, reviewed literature, collected and analyzed the data, applied statistical analyses, and wrote the manuscript; THCM contributed to the design and development of the study and reviewed and edited the manuscript; TM contributed to the design and development of the study, secured funding for the research, and reviewed and edited the manuscript.

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Conflict of interest

None declared.

Data Availability

Data and code are available upon reasonable request to the corresponding author.

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