Habitat selection and diet of the Neotropical otter (Lontra longicaudis) on the Osa Peninsula, Costa Rica, and range-wide monitoring recommendations

Chris Smith, Andy Whitworth, Elizabeth Brunner and Mateo Pomilia

Round River Conservation, Salt Lake City, UT, USA; Osa Conservation, Washington, DC, USA

ABSTRACT

The Neotropical otter (Lontra longicaudis) is listed as Near Threatened by the IUCN, which describes the standardization of field survey techniques and identification of key habitats as two research priorities. Basic ecological information such as habitat selection and diet is also lacking, especially in Central America. Using surveys for tracks and latrines from ten rivers on the Osa Peninsula of Costa Rica, we report results on habitat selection at the local and microhabitat scales, describe the general diet from 127 scats, and broadly discuss detection and general survey methods. We found that otters were positively associated with small-scale pastures surrounded by nearby forests at a local scale and/or negatively associated with densely forested areas. Otters further preferred deeper rivers at both local and microhabitat scales, while the availability of latrine substrates and sandbars was both important predictors of detection probability. We also deployed 12 camera traps to detect otters, and found they were much less efficient than sign surveys at determining occupancy, though our sample size is small. We conclude by proposing a methodology for standardized monitoring protocol using occupancy surveys which could be implemented across the Neotropical otter’s range.

Introduction

The Neotropical otter (Lontra longicaudis) is currently listed as Near Threatened by the International Union for Conservation of Nature (IUCN), and the lack of basic information kept the Neotropical otter listed as Data Deficient until 2015 [1]. The majority of research to date has been carried out in Brazil and Mexico, with a lack of information from Central America [2]. Thus, there remains a lack of basic ecological information such as diet and habitat use in this region [3–6].

The IUCN states that identifying key habitats is a conservation priority for Neotropical otters. Studying habitat quality is essential to understand which factors support viable populations, or where anthropogenic impacts might create unfavorable habitats. Habitat quality is ideally assessed by comparing population density, reproductive rates, and survival of individuals in different habitats [7,8], yet this is unfeasible for most studies of rare or elusive species.

Genetic studies of Neotropical otter show a significant overlap of home ranges, hypothesized to fall under the resource dispersion hypothesis, which suggests that when critical resources (especially food) are not a limiting factor, animals may share sections of their territory [9,10]. This likely indicates they do not defend classic territories and likely follow an ideal free distribution, in which density is an accurate indicator of habitat quality [8]. As few otter studies have estimated densities accurately [2], metrics correlated with density (e.g., occupancy), are most practically used to evaluate habitat quality.

Habitat selection can be determined using a variety of techniques, including density of signs (such as latrines or occupied shelters, e.g. [11,12]), presence-only data (such as species distribution models), presence-available data (such as resource selection functions of known and random locations), or presence-absence data (such as occupancy; e.g. [13]). Occupancy has the added benefit of incorporating detection probability, which is especially important when using a metric (such as latrines or scat density) where detection can vary with degradation rates, observer bias, or when suitable latrine sites are absent [14]. Traditionally, detection probability involves repeated “visits” to a specific site, generating repeated counts of the same location. Many otter studies have modified repeated temporal visits to a site for repeated spatial replications of a site. This assumes that a site (a river “segment”) has similar otter use along its entire length; it is therefore safe to assume that dividing the site into sub-sections of equal length (“sub-segments”) should mean each sub-section is also occupied, and can serve as a replicate for the larger site [2,4,15,16]. In this way, river “sub-segments” are spatial replicates for the larger river “segment”. These replicates then allow detection probability to be calculated, correcting imperfectly detected estimates of use, which are typically indexed by scats or latrines [16].
This method has been used across 3 species of otters and 4 recent publications [4,6,15,16]. Inferences that include detection probability are in theory more accurate [16], and able to be compared between studies and across extremely diverse environments.

The accuracy of using scats as an index of abundance is contentious, and much literature has been written on this debate (See Appendix A for more discussion). Studies have pointed out the relationship between number of latrines and otter density may be non-linear [17] and the effects of climate (degradation rates), presence of shelters (holts), shape of waterbodies, and more can influence scat deposition and accumulation rates [2]. There are few studies correlating actual densities to scat accumulation, and some find reasonable relationships, and others not [17–20]. Five-fold changes in scat abundance between winter and summer in the same location [20] seem to suggest the inefficacy of this method for comparing between study sites or years (though this study still found a rough correlation between otter and scat density). Perhaps as a result of this debate, many recent studies have used occupancy, i.e., the simple presence or absence of signs, to study habitat quality (e.g. [15,16]).

Johnson (1980) [21] hypothesized that animals select resources at different hierarchical scales, including home ranges across the landscape (henceforth “landscape-scale”), within a home-range (henceforth “local-scale”), and at finer scales (on the order of tens of meters; henceforth “micro-scale”). Few studies from Central America have examined Neotropical habitat use at multiple scales. At the landscape-scale in Guatemala, Quintana-Morales [5] found with presence-only data that otters used habitat more frequently at lower altitudes and in river systems with shallower inclines—thought to indicate areas where rivers were deeper and more abundant in their principal prey (cichlid fish). In northeastern Costa Rica, it has been suggested that otters use larger, less urbanized rivers, while at the local-scale selecting for areas with higher tree density [4]. This finding was similar to central Costa Rica, where occupancy was found to increase with forest cover and river width at the local-scale [6].

Camera trapping is a technique commonly used to study habitat-related questions and abundance of medium-sized carnivores (e.g. [22]), and has the advantage of knowing when a detection occurred, unlike scats and tracks which can accumulate over time or be washed away by heavy rains, making comparisons less accurate. Previous camera work with otters has been done with behaviors around shelters [23], and those placed at latrines have demonstrated higher detection rates than random placement on rivers [24]. Camera traps have been hypothesized to have low detection rates on otter species because temperatures of wet otter fur are too close to stream or ambient temperatures to trigger heat sensors [24,25]. No studies have compared detection rates between cameras and typical scat or track surveys.

Diet information can help provide answers for habitat-related patterns, is easy to collect from scat surveys, and for Neotropical otters in Central America is limited to two studies [3,6]. When combined with studies from southern Mexico [26,27], the literature suggests that otters locally should eat mostly fish and crustaceans, though regional variation occurs. The majority of reported crustaceans are freshwater shrimp (Caridea), which sometimes occur at higher frequencies than fish in otter scats [6,26,27], and can occur throughout a wide variety of stream habitats [28].

The objectives of this study were as follows: (1) to investigate regionally which habitats are of higher quality, (2) to determine if factors related to sign detection are necessary to accurately assess habitat quality, (3) to test whether camera traps are useful tools for studying otter populations, (4) to determine if otter diet on the Osa Peninsula is different from nearby regions. We hypothesized that (1) When scat and track detection variables were incorporated, otters would be associated with deeper rivers with more forest cover (where prey resources are likely more abundant) at both the local and micro-scale; (2) Remote cameras would prove more useful than scats or tracks in detecting otter presence; and (3) Otters would have a high proportion of crustacean in their scats, similar to other Central American studies. We conclude by providing recommendations for standardizing future studies, so comparisons can be made across the Neotropical otter’s range.

Methods

Study site

The Osa Peninsula of Costa Rica (8.405214N, –83.338032W) is a relatively intact biodiversity hotspot that was only sparsely settled until the 1930s when gold was discovered [29]. The peninsula consists of tropical lowland rainforest, where the mean annual temperature ranges between 24.5°C and 26.5°C, and rainfall ranges between 3000 and 7000 mm [30]. Although many areas outside of Corcovado National Park were deforested in the 1970s and 80s, by 1997 the Osa Peninsula had returned to 89% forest cover with comparatively low deforestation rates (0.83% per year; Sanchez-azofeifa et al. 2002). Currently, areas outside Corcovado National Park (which protects 425 km² of the Osa Peninsula) are used for ecotourism and ranching, with limited farming and urban land use [31].

We performed surveys along ten rivers located on the Osa Peninsula (Figure 1). Several of our study rivers were surrounded by pastures, of which roughly half had thin riparian strips. Qualitatively, pastures in our area had extensive vegetative cover on banks, lacked
large muddy areas nearby, and were directly accessible by livestock (although this was only observed during the dry season). Cattle grazing on the peninsula follows a rotation system with an average of 1–2 animals per ha (Personal comm., Raúl Sánchez, manager of Dos Rios Stables).

Rivers were chosen based on their accessibility from the road running from Puerto Jiménez to Carate and for variation in morphology, substrate, and land use history. For our surveys, rivers were accessed on foot (boats were not available). During the dry season, only a few of the dozens of rivers on the peninsula (outside Corcovado National Park) are too large to wade inside the channel; thus, although our selection of rivers was biased towards smaller rivers we could walk within, they represent what is generally available on the peninsula outside Corcovado National Park. Rivers were typically 4–9 m wide and 25–70 cm deep (up to 2 m). Surveys were stopped when rivers became extremely small (<25 cm deep). The Río Carate borders Corcovado National Park on the east, and it and Río Oro have been heavily mined for gold, with illegal mining continuing today [32].

**Data collection**

Each river was surveyed once throughout late June and early July 2017. Habitat data were collected at both random points (placed approximately every 150 m) and points with otter signs. Because of inaccuracy in the available spatial layers, we could not segment streams beforehand and therefore used a range finder to measure distances between points in the field.

River substrate varied greatly between rivers, potentially confounding our ability to observe tracks (in rocky locations) or scats (in areas without suitable latrine sites). We therefore created an index of the number of places latrine and tracks could potentially be found. To assess latrine substrate availability, we preliminarily measured the height and width of logs and rocks with scat (scats were infrequently located on sandbars; 20% of occasions). We then used these
measurements as a guideline for estimating the number of rocks and logs an otter could potentially use as a latrine site (cumulatively “latrine substrates”) within 50 m up or downstream of a point. All estimates were done by C. Smith for consistency, and trials checking all “latrine substrates” in several 150 m segments detected 100% of latrines. Only latrines with fresh scats (ones not fully flattened by rain) were considered in our analysis. To assess track detection probability, we counted all sandbars >3 m² within 50 m of a point and soft enough to hold tracks, as an index of the number of sites where tracks could be detected. All observed tracks were relatively fresh, due to heavy rains every few days during surveys. Track sites were considered independent if sandbars were not connected, usually constituting different bends in a river. A track site was simply considered occupied. Tracks were differentiated from Raccoon (Procyon sp.), Coati (Nassua narica), and Tayra (Eira barbara) by a combination of webbing, greater width (generally 6–8 cm), and lack of long claws [33,34].

The habitat variables measured during surveys included river slope (as an index for velocity, using a clinometer at 30–40 m), river wet width, deepest depth (sampled from a straight line across channel), canopy cover (at river’s center), and number of potential escape shelters within 10 m (defined with reference to [12]).

We split all surveyed rivers based on GPS tracks into 450 m “segments” (discarding any under 400 m); each “segment” was then further split into three 150 m “subsegments”. Sub-segments included 1–4 random habitat points, and to correct the uneven sampling of the full segment, we averaged all habitat data within a sub-segment, and then averaged the 3 sub-segment values together to represent the full segment. Any sub-segment lacking a point had the two nearest points’ values averaged. Overall, segments averaged ~3 random habitat points.

Using ArcGIS 10.4, we generated 10 m and 100 m linear buffers around each 450 m segment and using land cover published by Inogo Mapas [31], estimated the proportion of forest (Inogo codes 1 and 6), pasture (codes 705, 902), and emergent river vegetation (codes 3, 4, 9, 10, 705) around each river. Landcover was verified using recent ArcGIS imagery and ground truthing (class 705 was at times modified from pasture to emergent vegetation). Imagery was not accurate enough to include primary forest, tree plantations, or more detailed categories.

To evaluate the efficiency of using camera traps to detect otters, we set up 7 camera traps on latrines (two sites January to March 2017 and five sites from July to August) and 5 random locations. Bushnell Trophy HD Aggressor Cameras (.15 sec trigger speed) were placed <5 m from latrines, usually attached to a tree 1 m above the height of scats, and angled up or downstream to maximize the time otters occurred in the frame. Cameras captured photos 24 h per day and were set at a minimum of 400 m apart (Figure 1). No lures (baits/scents) were used.

To assess otter diet, C. Smith (again for standardization) quantified the presence/absence of fish, crustaceans, snails, and other items (lizard, mammal, bird, etc.) in each scat. Each scat within a latrine was considered a separate sample. Scats were also categorized as 1 (0-25%), 2 (26-50%), 3 (51-75%), or 4 (76-100%) for each food item (similar to Jenkins et al. 1979) [39]. This method is highly comparable to presence/absence results, and reflects actual dietary intake well [36,37]. Data from the Spring 2017 field season on two rivers (Ríos Piro and Cayunda) were used as well, and only rivers with ≥10 scats were included.

Analysis

Local-scale habitat analysis

Our study sites and sample size presented several unique issues. Rivers on the Osa Peninsula change rapidly morphologically and are often either completely rocky or muddy [30,38]. This means that the chance of detecting signs varies greatly and using “river” as an independent unit is biased due to rapid changes in substrate, width, and depth. Most 450 m segments in our sampling design abutted other segments, and a Mantel-test and variogram (package ncf) indicated that segments showed spatial autocorrelation beyond 450 m. Separating segments by 450 m would have reduced our sample size to ~25 and randomly sampling segments would have meant that many were still adjacent. As such, we dealt with issues of segments not being independent using random effects [39], necessitating a Bayesian framework because current R packages such as unmarked andPresence (which also support detection probability) do not support random effects.

The typical framework for evaluating Neotropical otter habitat quality is occupancy [14]. We therefore ran an initial occupancy model (see Appendix 2), but found results obscured due to enormous confidence intervals because few segments were unoccupied (12 of 53). We therefore ran the same model, using total number of scats per segment as the response variable (N-mixture models [40]), which yielded identical trends and effect sizes of variables, but with smaller confidence intervals. For clarity sake, we henceforth only reference this latter model.

Initially, our 11 habitat variables included slope of river, number of shelters, river width and depth, and canopy cover, in addition to the proportion of pasture, forest, and emergent vegetation at a 10 m and 100 m buffer. Bayesian variable selection methods are difficult when variables are strongly collinear (such as in
our data [41]). We therefore selected which variables to include in the Bayesian analysis using an AICc approach, creating N-mixture models in program unmarked, including river as a fixed effect (to somewhat account for segment non-independence) in the state part of each model, along with each habitat covariate singly (similar methods as [15]). We also tested whether to include number of scat and track substrates as a detection covariate by creating the above model set with and without substrate variables included (totaling 22 models). We included all habitat variables in our Bayesian model that included >.01 AICc weight.

Model selection in a Bayesian framework can be difficult, and common methods such as DIC or QUAC do not work well with hierarchical models where parameter sizes are ambiguous, or where samples must be truly independent [42]. One method for assessing which of many variables is important is to put them all into a single model, which allows variables to be assessed as informative by whether their 95% credibility intervals (CRI) overlap 0; scaling their slopes also allows their effect size to be compared to other variables [43]. All selected covariates showed low collinearity (r <.50), except proportion forest and farm within 100 m (r = −.78); we therefore selected proportion farm, acknowledging the proportion of farm and forest cover were nearly inverses, and could not be teased apart ecologically (Note: a side analysis using proportion forest yielded identical results). Additionally, track and latrine substrates were found to be important and included as detection covariates.

In brief, our N-mixture Bayesian model included for each site i and observation j, a detection probability of:

\[
\text{Logit}(p_{ij}) = \alpha_0 + \alpha_1 * \text{latrinesubstrates}_j + \alpha_2 * \text{tracksubstrates}_j
\]

where \(\alpha_0\) is an intercept, and \(\alpha_1\) and \(\alpha_2\) are slopes for the three sub-segment-specific values for latrine or track substrates. The state part of our model was composed of:

\[
\log(\lambda_i) = \beta_0 [\text{river}_i] + \beta_1 * \text{Pasture}_i + \beta_2 * \text{Emergent}_i + \beta_3 * \text{Slope}_i + \beta_4 * \text{Depth}_i
\]

where \(\beta_0\) is a random intercept for each segment (implying the effect of habitat covariates is expected to be consistent across rivers) and \(\beta_1, \beta_2, \beta_3, \text{ and } \beta_4\) are segment-specific values for percent pasture within 100 m, percent emergent vegetation within 100 m, average slope, and average depth, respectively (See Appendix 3 for full R-script and model).

We used the package Rjags (4.6) in program R (3.4.1), using 2 million burn-ins of 3 chains, while saving 50,000 samples thinned 5 times, yielding 30,000 samples for the posterior distribution of each parameter. We assessed model convergence using Gelman-Rubin statistics (assuming those with values <1.2 generally indicate convergence) and inspecting traceplots for level chains [44]. We assumed variables with 95% credible intervals (function HPDinterval in package coda) indicated important variables, and those with higher scaled slopes had larger effect size than other habitat variables. We also assessed the goodness-of-fit of both models using Bayesian P-values [43].

**Micro-habitat analysis**

To compare how otters selected habitat at the micro-scale, we compared habitat data at each scat and track point (presence) with random points (available). We attempted to account for correlation within a river system of both habitat and detection variables by using River as a random effect, and using generalized linear mixed-effect models (GLMM) to compare the 5 local habitat variables (slope, depth, and width of river, number of shelters, and canopy cover). Competing models were compared in an AIC framework using package lme4 (1.1.13). Habitat covariates were scaled and variables with higher AICc weight and model-averaged 85% confidence intervals that did not overlap 0 were considered informative [45]; slopes were back-transformed to assess if their effects were biologically meaningful. We assessed over-dispersion and goodness-of-fit (\(R^2\) values) of models with random effects, using methods from Kery [43] and Nakagawa and Shielzeth ([46] package MuMim).

**Camera traps**

To test the feasibility of using remote cameras for otter surveys, we calculated the number of otter photos per camera day at latrines and random sites, and compared occupancy results from camera and sign surveys. All photos were captured on separate days and were therefore considered independent events.

**Diet**

To analyze general diet and to compare between rivers, we used the six rivers that had >10 scats. Only five of 127 scats were found with materials other than crustacean or fish, and we therefore limited our analyses to these two categories. Using presence/absence data, we also used generalized linear models to test for differences between rivers, using a binomial distribution. 95% confidence intervals for the ordinal data on proportion crustacean in scats for each river are presented.

**Results**

We surveyed a total of 26 km along 10 different rivers (average 2.5 km/river; range 1.3–3.5 km) from June to July 2017, for a total of 53 450 m segments. All rivers except Rio Carate were occupied by Neotropical otters. A total of 53 latrine sites and 20 otter track sites
were found and surveyed, and a total of 199 random points were surveyed. Among latrine sites, most were placed on logs (37%) or rocks (43%), with only 20% on sandbars. The naïve occupancy rate was 60%, with an average of 1.4 signs per 450 m segment. Detection probability holding covariates at mean observed values for the N-mixture model was 21% (95% CRI: 1-62%). The large 95% CRI of overall signs per segment and detection probability suggest these metrics alone should be interpreted with some caution (whereas CRI of habitat covariates were much more reasonable).

Local-scale habitat use

The N-mixture model had a Bayesian P-value of .28 while the occupancy model was .31, suggesting a reasonably good fit for both (not close to 0 or 1). The N-mixture model for local-scale otter habitat selection had only one habitat variable with 95% credibility intervals that did not overlap 0: Percent Pasture (Table 1, recalling that Percent Forest is also collinear with this variable). River depth was also 92% certain to have a positive effect, and the mean scaled slope indicated

Table 1. Results from the Bayesian N-Mixture Model, using number of sign per segment as the response variable, and from Occupancy modeling of repeated river sub-segments. Variables were considered informative if the upper and lower 95% credibility intervals (CRI) did not overlap 0, and slopes were scaled to make their magnitudes comparable. Latrine and track substrates were treated as detection covariates.

| Parameters               | N-Mixture Model | Occupancy       |
|--------------------------|-----------------|-----------------|
|                          | Lower 95% CRI   | Upper 95% CRI   | Mean Scaled Slope | Lower 95% CRI | Upper 95% CRI | Mean Scaled Slope |
| Farm 100 m**             | 0.013           | .824            | 0.4             | −11.23        | 18.47         | 3.65             |
| Forest 100 m**           | −.826           | .027            | −0.415          | −21.63        | 6.82          | −6.66            |
| Emergent 100 m           | −.613           | .407            | −0.087          | −11.05        | 21.68         | 6.15             |
| Slope                    | −.279           | .164            | −0.063          | −19.04        | 9.23          | −4.69            |
| Depth                    | −.048           | .493            | 0.24            | −9.75         | 21.83         | 5.56             |
| Latrine Substrates       | .035            | .205            | 0.378           | 0.457         | 0.725         | 1.14             |
| Track Substrates         | −.066           | .418            | 0.227           | −0.138        | 0.7256        | 0.302            |

*Note these variables are collinear, and otters may select for one or both.

Figure 2. Effects of the proportion of pastures within a 100 m buffer and average river depth on number of signs detected along 450 m segments. The black line represents the mean and gray represents the 95% credibility intervals of posterior distributions.
it had roughly half the impact of pasture. Although the average effect size (across all rivers) of these two variables had wide 95% CRI’s, the mean trends appear biologically relevant, with changes in >10 signs/segment over the range of observed proportion of pasture and depth (Figure 2).

Number of latrines and likely sandbars (with 80% certainty) within 100 m appeared to influence detection probability dramatically (7-55% and 17-53%, respectively) over the range of observed substrates (Figure 3). The large 95% confidence intervals on track substrates are likely due to the small sample size of occupied track sites (n = 20). Latrines (n = 64) were generally placed 42 cm above water (95% CI: 36–49 cm, range: 4–105 cm), on logs >16 cm wide and rocks >45 cm diameter.

**Micro-habitat selection**

The micro-habitat selection analysis suggested that otters were only selecting for deeper areas of rivers (Table 2), with a back-transformed slope indicating an increase in 1 track or scat site per 2 cm depth. The models were slightly under-dispersed (0.90), and had an $R^2$ value of 0.068 including fixed and random effects and 0.015 for fixed effects only.

**Camera traps**

Our seven camera traps on active latrines totaled 144 camera days. A single camera caught all six photos (~1 event/25 camera days) of at least 3 different lone individuals visiting at least a day apart, with five of six detected near dawn or dusk (Figure 4). Relative sizes of individuals could be differentiated because all three visited the same location (i.e. the latrine) within photos and all were caught broadside on the same-fixed camera, making otter sizes comparable between photos. The five cameras randomly placed on

![Figure 3.](image)

Figure 3. Effects of the number of latrine substrates (large rocks or logs) and sandbars ($\geq 3$ m$^2$) within 100 m of a point, on detection probability within 150 m sub-segments of river. The black line represents the mean and gray represents the 95% credibility intervals of posterior distributions.
rivers had one otter “event” over 80 camera days. Of these sites, all six 450 m segments were occupied via sign within a month of the camera being set.

**Diet**

The presence/absence diet data suggested that 70% of otter scats contained fish and 91% contained crustaceans (Table 3). Nearly all observed crustaceans in scats (and seen in rivers) were freshwater shrimp (Caridea). The 95% confidence intervals for the binomial GLM testing the proportion of fish in otter scats suggested

| Model          | K | AICc | Δ AICc | AICc Wt | Cum. Wt | LL    |
|----------------|---|------|--------|---------|---------|-------|
| Depth          | 3 | 272.17 | 0.98   | 0.98    | −133.03 |
| Slope          | 3 | 282.19 | 10.01  | 0.01    | 0.99    | −138.04 |
| Width          | 3 | 282.54 | 10.37  | 0.01    | 0.99    | −138.22 |
| Shelters       | 3 | 282.62 | 10.45  | 0.01    | 1       | −138.26 |
| Canopy cover   | 3 | 283.17 | 11.00  | 0       | 1       | −138.53 |

**Table 3.** Scat composition data from 6 rivers on the Osa Peninsula. Average Crustacean Score represents average percent of each scat that was crustacean (1 = 0–25%, 2 = 26–50%, 3 = 51–75%, 4 = 76–100%); as all scats were only composed of fish or crustacean, Fish scores are inverses of Crustacean.

| River          | Number of Scats | Proportion of Scats with Fish Present | Proportion of Scats with Crustacean Present | Average Crustacean Score ± 95% CI | Average Fish Score ± 95% CI |
|----------------|-----------------|--------------------------------------|------------------------------------------|----------------------------------|------------------------------|
| Piro           | 14              | 0.00                                 | 1.00                                     | 4 ± 0                            | 0.00 ± 0                     |
| Platanares     | 11              | 0.18                                 | 0.82                                     | 3.45 ± 0.72                      | 0.55 ± 0.72                  |
| Cayunda        | 28              | 0.61                                 | 0.93                                     | 3.18 ± 0.36                      | 0.82 ± 0.36                  |
| Corozal        | 10              | 0.90                                 | 1.00                                     | 2.60 ± 0.78                      | 1.40 ± 0.78                  |
| Agua Buena South | 34            | 0.97                                 | 0.91                                     | 1.94 ± 0.36                      | 2.06 ± 0.36                  |
| Cienegra       | 30              | 0.93                                 | 0.87                                     | 1.80 ± 0.33                      | 2.20 ± 0.33                  |
| Total          | 127             | 0.70                                 | 0.91                                     | 1.25 ± 0.22                      | 1.41 ± 0.22                  |

**Figure 4.** Camera trap images of two different otters, showing different body size and tail length relative to body.

**Figure 5.** Mean and 95% confidence intervals of 6 rivers, with scats divided into 4 ordinal categories of proportion crustacean: 1 (0–25%), 2 (26–50%), 3 (51–75%), and 4 (76–100%).
that one river had significantly more fish (Ciénega), and three significantly less (Piro, Cayunda, Platanares). As the proportion of fish in a scat was the near-inverse of its crustacean composition, ordinal data on crustaceans showed these same differences between rivers (Figure 5).

Discussion
Neotropical otters on the Osa Peninsula surprisingly appear to select for pasture and/or against dense forest within 100 m of rivers, and more intuitively select for deeper river segments on a local and microhabitat scale. These results were only accurate when taking into account the number of suitable rocks or logs for latrines and sandbars for detecting tracks. Track and scat signs also appeared to have a much higher detection probability than camera traps, where only 2 of 12 cameras detected otters on river segments that otherwise all contained fresh sign. Finally, diet analyses suggested a high amount of both fish (70%) and crustacean (90%) in scats, which is similar to other regional studies and probably does not help to explain the unusual habitat patterns we observed.

Our most surprising finding is that Neotropical otters are associated with river segments with a higher proportion of pasture within 100 m and/or areas with a lower proportion of forest cover. Otters likely do not use pasture or forest within 100 m of streams regularly, and these variables are likely proxies for a variable that directly influences otters. Pasture had low correlations \((r < .25)\) with all our measured morphological variables, including river slope, depth and width, but may be associated with unmeasured variables. Pastures were generally situated on wide, flat areas underlaid by alluvial plains [38]; thus it is possible that otters are directly responding to changes in landscape morphology (e.g., sediment loads, larger fish or freshwater shrimp), which is positively correlated with pastures. Previous research at the local scale has found the opposite effect, with otter use increasing with higher tree density (northeast Costa Rica \([4]\)) and forest cover (central Costa Rica \([6]\)). Recent deforestation maps of Costa Rica suggest that these other study sites were located in areas that at a landscape scale appear more fragmented and covered by early-succession forests \([47]\). Our results may support an intermediate-disturbance hypothesis proposed for other mammal generalists, including mustelids, which argues that opportunistic species can do well in disturbed areas up to a threshold \([48]\). If moderate human disturbance deters animals such as jaguar \((Panthera onca)\) or puma \((Puma concolor)\), which are likely the otter’s main predators in our study system (large crocodiles are absent in these smaller rivers), otters may select for these areas to reduce their risk of predation.

Range-wide, two studies using species distribution models to predict otter distribution have found otters to be negatively correlated with human settlements \([49]\) and human densities, although higher human densities are not completely unsuitable for otters \([50]\). At the local scale, shelter use (a metric of habitat use) has also been found to be similar between pristine and intensely disturbed areas \([12]\). Knowing if and where a disturbance threshold (i.e., where densities start to decline) lies seems important for this region. For now, we suggest a conservative interpretation of our findings: pastured habitats at their current stocking rates, with nearby tracts of fragmented forest, are more attractive to Neotropical otters than rivers surrounded by dense contiguous forests.

Also, worthy of note was the complete absence of otter signs in Río Carate, which borders Corcovado National Park and had the highest levels of surrounding primary forest. This river has been heavily mined and mining continues to this day \([32]\). The substrate of this river and Río Oro (also mined historically) were significantly different from other rivers we observed, with high loads of sand-sized sediment, even in narrow fast-flowing sections where it had been days since rain fell. These two rivers also occur near a transition to coarser soil material \([30]\). Further research should examine whether this mining is responsible for the increased sediment load and whether this is linked to low otter use and/or prey items disappearing. Additionally, poisoning of freshwater shrimp (discussed below) may be frequent in these areas as food for gold miners, further contributing to the otters’ absence.

Otters were associated with deeper rivers at the 450 m (local) scale. Other studies have found this to be true at the micro-scale (e.g. \([51]\)) thought we are unaware of this being observed at larger scales within home ranges. Our rivers varied from 10 to 200 cm in depth, and it may be that within our study, the small to medium size rivers in the dry season cause otters to actively select for deeper segments, hypothesized by many to have more prey (e.g. \([5]\)). At the landscape scale, Plata \([4]\) found otters selected for higher-order (larger) rivers and Quintana-Morales \([5]\) found otters selected for areas with lower slope and flow, both which may be correlated with deeper areas.

Including an index of available latrine and track substrates as detection covariates in our model appeared to be important in correcting raw data from surveys. Within our study, detection probability varied much more for latrines than for tracks. Perhaps intuitively, this indicates that tracks and latrines have different detection probabilities. This has consequences when comparing occupancy rates between two studies that do not include detection probability, if one uses mostly tracks and another scats as their primary detection method. Several habitat selection studies correcting for detection probability have also held capture probability constant \([4,6]\), which is likely
not an issue in systems where river substrate is relatively similar throughout the study area. However, studies such as ours that incorporate many river systems that differ in substrate and sediment deposition should consider this approach for valid comparisons of detection probabilities between rivers.

We found that otters select micro-habitats with deeper pools, but not areas that are wider, steeper, more shaded, or had more escape cover (shelters). Here, we believe a word of caution is necessary when interpreting results on this small of scale. Other mammals routinely select specific features for defecating/marking, unrelated to actual habitat quality; canines are known to preferentially mark trail intersections, felines urinate on prominent objects, and raccoons often place latrines behind large trees [52]. Deeper pools intuitively hold more prey and escape cover for otters; however, we feel it is important to test (e.g., with camera traps) that otters do not simply prefer to scat or mark next to deep pools before concluding they prefer them as habitat.

Although our sample size of camera trap days is small, we believe our results are still useful for informing future monitoring efforts. The fact that cameras detected otters on two of 12 segments, all of which were known to have scats or tracks, suggests un-baited camera traps are less efficient than simple sign surveys at establishing otter presence. Even when placed on known latrines, only one of six cameras detected otters. This also points to otters either avoiding latrines after cameras were placed or cameras missing otters travelling by. Cameras placed on shelters had frequent otter re-use in other studies, suggesting cameras do not deter otters [23]. Like Lerone et al. [25], we believe cameras are likely missing otters that pass by, likely because wet otters do not trigger cameras because their temperature is similar to background river temperatures, or because they pass by underwater. This is further supported by the fact that the randomly placed camera that captured an otter was set in a very narrow and shallow section of stream (<10 cm deep), which required otters to move by above water. Similar to Wagnon and Serfass [24], we believe setting cameras on latrines or in shallow sections where otters are forced to transit above-water may yield highest rates of detection for studies deciding to use camera traps. Another alternative are cameras placed over scent lures or baits. No studies on camera traps to date have tested baits or scent lures other than latrines for Neotropical otters [2], which for some carnivores drastically improves detection probabilities (e.g. [53]).

Recent use of the first baited remote underwater video (BRUVs) setup for Neotropical Otters yielded 1 detection within 72 hours of footage, which is a much higher detection rate than our cameras placed on latrines (1 detection per 256 hours), suggesting baited cameras may be more efficient [54]. However, maintaining baits or lures for camera traps in areas with widely fluctuating water levels and other bait-consuming fauna presents challenges that still need addressing. Although likely not as efficient as sign surveys at this time for Neotropical otters, cameras are also key to investigating important questions such as daily activity patterns [23] or group sizes.

Though our sample size of 127 scats is small for most diet studies, we believe it is sufficient to answer our broad question of what food categories are generally important for neotropical otters within our local region of Costa Rica. Diet analysis from our study suggests that our region is similar to many other areas of southern Mexico and central America, where crustaceans comprise a primary food item, mostly in the form of freshwater shrimp [3,6,26,27,55]. Our results between different rivers are preliminary because of our small sample sizes. However, they do suggest that different rivers within a small geographic area may support very different proportions of fish and freshwater shrimp within an otter’s diet. Though we did not measure availability, other studies have suggested otters are opportunistic and characterized by plastic diets even at a local scale, where they may change their diet in relation to what is available [56]. This may suggest these rivers hold very different prey populations within a small area. Range-wide, crustacean-based diets are correlated with fast-flowing environments (often upper streams where extreme changes in water levels make it hard for fish to survive), rivers closer to the coast, and mangroves [56]. However, all of these factors are relatively similar within our study site (i.e., all rivers are located a similar distance from the coast with similar climate), suggesting that smaller-scale stream morphology or other local factors are likely causing otter diet to change between rivers. Also worth noting is the yearly salt-water migration of freshwater shrimp in our region make to reproduce [28]. Structures such as dams and waterfalls impede re-establishment of these migratory populations, and events such as poisoning rivers to harvest shrimp (frequent in our study area; several personal communications) could extirpate otters’ food sources from these areas permanently.

**Conclusion and monitoring recommendations**

Although our study is local, suggesting that Neotropical otters in our region select deeper rivers with some human disturbance and consume a large proportion of crustaceans in their diet, we believe the study-design and analysis methods have much larger implications for Neotropical otters across their range. The near-threatened status of the Neotropical otter, in addition to its status as a top carnivore in these aquatic ecosystems [2], strongly supports the need for effective population monitoring and habitat use studies. We believe the robust methodology which is becoming
commonly employed for other otter species (e.g. [4,15,16]) is currently the most feasible method for addressing these key priorities. The IUCN’s Conservation Actions for this Near Threatened species includes the standardization of field survey techniques to map the species’ range, the identification of key habitats, and the protection of areas where large populations remain [1]. To date, however, there has been no real standardization of field survey techniques, and we know of no quantitative studies of Neotropical otter populations over multiple years [2]. In contrast, the giant otter (Pteronura brasiliensis) Specialist Group has had a standardized protocol used by researchers for population and range-wide surveys using presence-absence data for years [57]. Their boat-driven survey and use of individually identifiable chin patches is not feasible for Neotropical otters that often live in higher elevation streams (where boats cannot pass) and which lack these markings [56,57]. This suggests a different technique is needed for population monitoring. A complete monitoring protocol is beyond the scope of this paper and requires consensus from the larger body of researchers; however, we feel suggestions for the basic framework of a larger protocol will greatly aid in Neotropical otter conservation. Most studies incorporating detection probability should be able to use package “unmarked” or others in R for analyses; only when segments are not independent (ideally separated by 5–10 km) and additional random effects are necessary, is the more complicated Bayesian model more appropriate (as no current packages in R using GLMM’s support both detection probability and random effects).

After briefly reviewing the population monitoring techniques commonly used and available for Neotropical otter researchers (Appendix 1), we put forth the following five recommendations for range-wide population monitoring:

1. The use of sign-based occupancy surveys incorporating detection probability.
2. The use of two standardized segment lengths so that occupancy rates can be compared between studies.
3. For landscape-scale studies, we suggest 4200 m segments (ideally spaced >1 home range, or ~5-10 km apart for independence) and for local-scale studies, 600 m segments (based on a review of literature, otter home-range size, and detection probabilities).
4. The sampling of >60 segments to avoid overly large confidence intervals of covariates.
5. Modeling or standardizing other variables that effect detection probability, including fresh vs old scat, wet vs dry season, or availability of track or latrine substrates.

Disclosure Statement

No potential conflict of interest was reported by the authors.

ORCID

Chris Smith http://orcid.org/0000-0003-2626-3426

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