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Authors: Wallace, Robert, Ayala, Guido, Negroes, Nuno, O'Brien, Timothy, Viscarra, Maria, et al.

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Robert Wallace^{1,2} , Guido Ayala¹, Nuno Negroes³,
Timothy O'Brien², Maria Viscarra¹, Ariel Reinaga¹,
Robert Márquez^{4,5}, and Samantha Strindberg²

Abstract

In 2013, we conducted a baseline study on the presence, distribution and occupancy of medium- to large-sized mammals in Bolivia along the San Buenaventura-Ixiamas road that runs parallel to the Madidi National Park and Natural Area of Integrated Management boundary and cuts through the Tacana Indigenous Territory and a number of neighboring private properties. Establishing a 3 km buffer on each side of the road, we studied an 865 km² area divided into 1 km² cells and sampled a total of 356 of these cells. In each cell, we established one 300 m transect divided into 25 m sections and registered wildlife sign, mainly footprints, from eight wildlife species or species groups. The transects were placed either along streams (75% of cells) or within forest (25% of cells). Using single-season single-species occupancy models we estimated occupancy (ψ) for *Tapirus terrestris* ($\psi = 0.39$), *Pecari tajacu* ($\psi = 0.5$), *Mazama americana* ($\psi = 0.56$), *Dasyprocta* spp. ($\psi = 0.59$), *Cuniculus paca* ($\psi = 0.56$), *Leopardus* spp. ($\psi = 0.33$), and use for *Tayassu pecari* ($\psi = 0.17$) and *Panthera onca* ($\psi = 0.11$). Occupancy and use results verified community perceived wildlife corridors between Madidi and its area of influence. We identified additional corridors along many streams crossing the San Buenaventura-Ixiamas road. This connectivity is not only important for wildlife, but also from a food security perspective for the indigenous communities that depend on wildlife as an important source of protein. The results will be used to mitigate the impact of road improvements through the identification of priority areas for maintaining connectivity between Madidi and the surrounding landscape.

Keywords

Madidi, occupancy, roads, terrestrial vertebrates, jaguar

Globalization with its associated industrial and agricultural development is reaching the Amazon basin, causing rapidly increasing tropical deforestation and habitat degradation across the region. There is a pressing need to develop monitoring methodologies to assess how this development affects the environment and thereby design adequate mitigation strategies, and over the longer term assess whether these strategies are successfully mitigating negative impacts. Deforestation analyses are readily available at global (Hansen et al., 2013), regional (Red Amazónica de Información Socioambiental Georreferenciada [RAISG], 2015) and local scales (Forrest et al., 2008), and our understanding of what

¹Greater Madidi-Tambopata Landscape Conservation Program, Wildlife Conservation Society, San Miguel, La Paz, Bolivia

²Latin America and Caribbean Program, Wildlife Conservation Society, Bronx, New York, United States

³CESAM and Department of Biology, University of Aveiro, Campus de Santiago, Aveiro, Portugal

⁴Andean Bear Conservation Alliance, Cali, Colombia

⁵Department of Natural Resources, Cornell University, Ithaca, New York, United States

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Corresponding Author:

Robert Wallace, Wildlife Conservation Society, Greater Madidi-Tambopata Landscape Conservation Program, #340 Calle Gabino Villanueva, San Miguel, La Paz, Bolivia.
Email: rwallace@wcs.org



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drives deforestation in the Amazon has increased exponentially in the past 20 years (Karstensen et al., 2013; Ometto et al., 2011; RAISG, 2015). The most important drivers of deforestation in the Amazon are road construction and development, cattle ranching, and mechanized agriculture (Laurance et al., 2001). Road construction in the Amazon is expanding, and is often the precursor to the other deforestation drivers (Barber et al., 2014; Laurance et al., 2009).

Indigenous territories cover more than a quarter of the Amazon, often in close proximity to protected areas, and deforestation rates within Amazonian indigenous territories in the decade before 2013 were actually less than within protected areas (RAISG, 2015). For example, recent studies underlined how indigenous territorial management between 2005 and 2014 resulted in reduced deforestation along the San Buenaventura–Ixiamas road within the Tacana Indigenous Territory, in northern La Paz Department, Bolivia, where areas within 5 km of the road within the Tacana Indigenous Territory had deforestation levels 2.7 times less than areas outside the indigenous territory (Painter et al., 2013). Indigenous territorial management in the Tacana Indigenous Territory is therefore increasingly recognized as a regional benchmark for environmental stewardship. Indeed, in 2015, the Consejo Indígena del Pueblo Tacana (CIPTA) or the Tacana Indigenous Peoples Council received the Equator Prize (<http://equatorinitiative.org>) for innovative forest management in the Tacana Indigenous Territory.

The Tacana are evidently committed to sustainable natural resource management, reflected in a participative and bottom-up territorial vision including management and zoning plans (CIPTA & CIMTA, 2014) that prioritize ongoing community-based economic initiatives, several of which (cacao, spectacled caiman, ecotourism) have also been nationally and internationally recognized (<https://bolivia.wcs.org/en-us/ITM.aspx>). These efforts are based on local knowledge about natural resources including wildlife, for example, the award-winning spectacled caiman management initiative and associated monitoring efforts is a partnership between local people and biologists (Miranda-Chumacero et al., 2010). Thus, the overall partnership between CIPTA and the Wildlife Conservation Society (WCS; Painter et al., 2011) has implicitly recognized the fundamental values of local knowledge (Danielsen et al., 2009; Turvey et al., 2013) to all aspects of indigenous territorial management (<https://bolivia.wcs.org/en-us/ITM.aspx>).

These indigenous territorial management results are an important baseline in the face of a road improvement project (2011–2022) funded by the World Bank and the Bolivian government (<http://www.worldbank.org/projects/P122007/national-roads-airport-infrastructure-project>). The road improvements will asphalt the existing

dirt road, thereby widening the gap between forested habitat and increasing risk of collision mortalities due to greater vehicle speeds. In addition, reduced transport costs will provide harvest incentives for many of the forest's natural resources including wildlife, potentially leading to habitat degradation and increases in hunting offtake along the road.

Monitoring the changing status of wildlife following environmental changes is particularly challenging and resource intensive within large forested landscapes, where visibility is poor and direct wildlife observations scarce or dependent on expensive remote sensors. Occupancy methods use wildlife presence–absence data for studying and monitoring wildlife populations at local (Tobler et al., 2015), regional (Karanth, 2016; Kinnaird & O'Brien, 2012), national (Karanth et al., 2009), or even global scales (Beaudrot et al., 2016), and can be a cost-effective approach to wildlife monitoring. Occupancy data can be derived from a variety of sources, including camera traps (Tobler et al., 2015), observations and vocalizations (Hallam et al., 2016), spore and other wildlife sign (Gopalaswamy et al., 2012), interview data (Karanth, 2016; Zeller et al., 2011) or even media reports (Athreya et al., 2015).

From a management perspective occupancy models are especially attractive as they provide a quantitative measure of the degree to which a space is occupied by a given wildlife species, while controlling for imperfect detection (Hines, 2014; MacKenzie et al., 2006). In addition, covariates can be used to investigate environmental or human factors that might influence occupancy or detectability. From a management and monitoring perspective covariates can be divided into four categories: detection covariates that explain variation in detection probability; biological covariates that help explain how occupancy varies across space from the perspective of the species biology; anthropogenic covariates that attest to the influence of threats on a given species' occupancy; and finally management covariates that reflect the response of wildlife to specific management actions in a study area. Over time the change in occupancy values and the influence of different covariates can be assessed within an adaptive management framework (Nichols & Williams, 2013).

The overall objective of the current study was to determine quantitative occupancy values for several key mammal species, or occupancy derived use for wide-ranging species, along the road between San Buenaventura and Ixiamas (SBI). This broad objective had three sub-objectives:

- (i) To corroborate indigenous community identified wildlife corridors between Madidi National Park and Tacana Indigenous Territory;

- (ii) To further highlight the contribution of indigenous territorial management to biodiversity conservation in the region, and;
- (iii) To establish a comprehensive baseline with which to monitor wildlife into the future in the face of imminent and significant improvements to road infrastructure.

Methods

Study Site

We conducted this study along the 110 km road running between San Buenaventura and Ixiamas (SBI) within the Iturralde province of the La Paz Department of north-western Bolivia (Figure 1). The study area is within the Greater Madidi-Tambopata Landscape and the road itself runs along the eastern border of the Madidi national protected area (Madidi National Park and Natural

Area for Integrated Management) just outside the park itself. Immediately adjacent to the park and partially overlapping the Madidi protected area is the Tacana Indigenous Territory (Tacana Territorio Comunitaria de Origen), which the road bisects. At the time of study, the SBI road was still a dirt road originally constructed in the early 1980's (Wentzel, 1989). The SBI road, which runs along the bottom of the gently sloping portion of the last escarpment of the Andes, was scheduled for paving by the Bolivian government in 2015 and 2016 through funding from the World Bank. Preparations for the paving process began in 2016, but has been postponed since 2017 due to contract changes, political instability in Bolivia and the ongoing COVID-19 pandemic, and is not expected to recommence until at least 2021.

Annual precipitation in the region is between 1900 and 3200 mm and the annual mean temperature is 26°C (Ibisch et al., 2003). Climatic variability is significant, with a marked dry season between May and

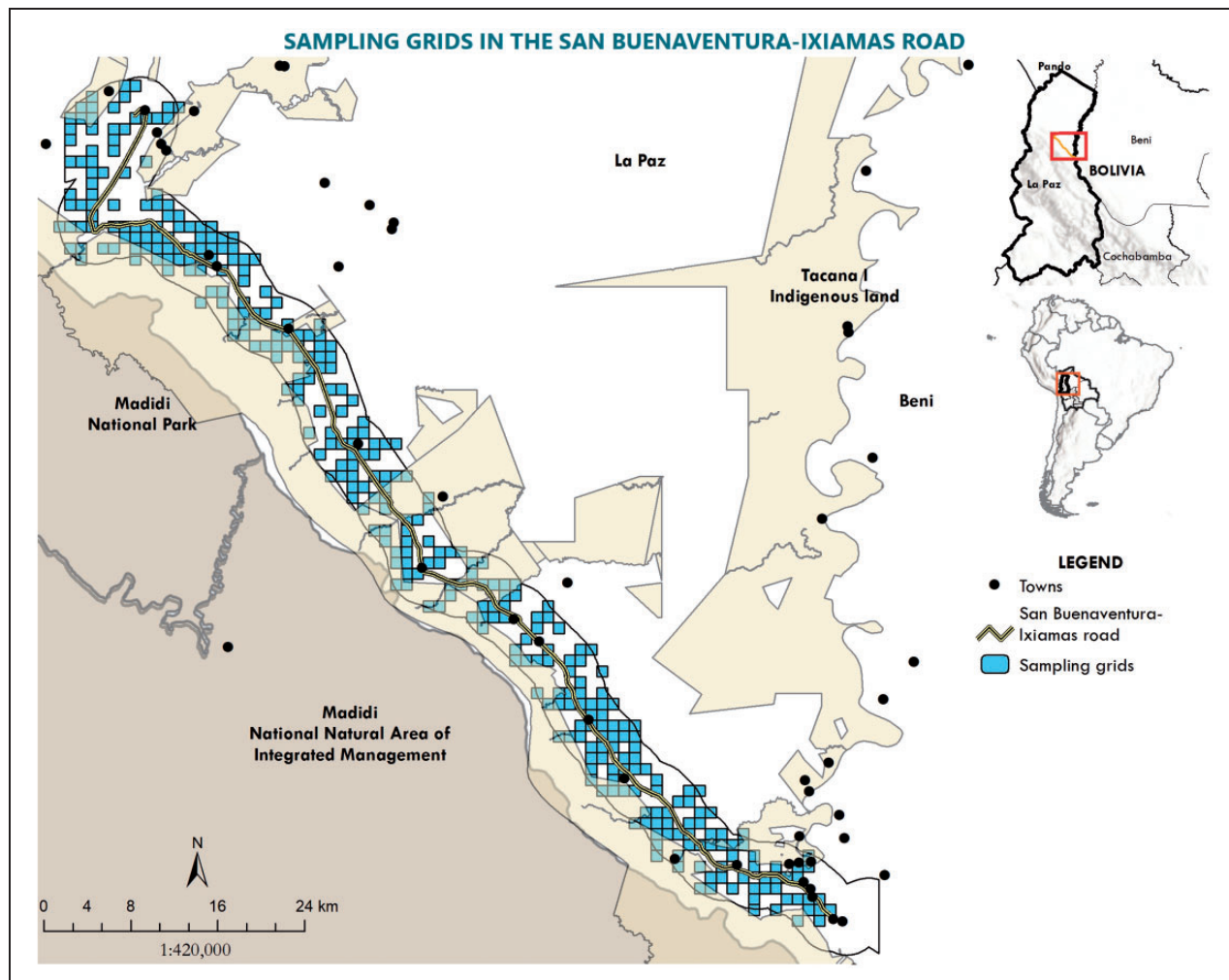


Figure 1. Study Area Along the SBI Road in Northern La Paz Department, Bolivia, Showing the Wildlife Occupancy/Use 1 km² Sampling Grid.

October (Fuentes, 2005). The study area was situated within the Sub-Andean Amazonian ecoregion (Ibisch et al., 2003). Details of the habitat types within this ecoregion are provided elsewhere (Fuentes, 2005). Tropical forests were riverine and adjacent humid terra firme forests characterized by relatively high canopies (30–40 m) and significant densities and diversity of palm species.

Wildlife Corridor Identification

To identify the location of wildlife corridors between the Madidi national protected area and the Tacana Indigenous Territory we used unpublished data collected in 2001 through individual semi-structured interviews to document recent wildlife observations within 10 km of the road with the most recognized indigenous subsistence hunters ($n=26$) in six Tacana communities: Carmen Pecha, Machaua, Santa Fe, San Pedro, Santa Rosa and San Silvestre. This sampling buffer was the most relevant for local engagement, and the data were georeferenced by interviewees using satellite images with a 1 km^2 super imposed grid, and were collected within the context of the development of the first Life Plan, or integrated territorial development plan, for the Tacana indigenous people (CIPTA & WCS, 2002). Between 2000 and 2002, a combined CIPTA and WCS team made multiple visits to Tacana communities to conduct Participatory Rural Appraisals, provide feedback on the Life Plan development, as well regularly inform the Tacana on the progress of the ongoing land titling process.

Secondly, in 2002 individual semi-structured interviews were conducted with public transport drivers who regularly used the road ($n=15$), to document where they had witnessed jaguars (*Panthera onca*, Linnaeus 1758) or white-lipped peccaries (*Tayassu pecari*, Link 1795) crossing the SBI road.

Thirdly, we used wildlife corridors identified during 2005 supracommunal indigenous workshops on wildlife conservation within the Tacana Indigenous Territory. These corridors were first identified during sectorial workshops involving nine communities situated along the road, one for the Ixiamas sector of the Indigenous Territory (Carmen Pecha (3 people), Macahua (15 people), Santa Fe (1 person)), one for the Tumupasha sector (Santa Rosa de Maravilla (3 people), Tumupasha (11 people)), and one for the San Buenaventura sector (Bella Altura (1 person), Buena Vista (3 people), Capaina (2 people), Tres Hermanos (2 people)). At these Tacana leadership led workshops, community representatives selected by the communities in recognition of their wildlife knowledge, used participatory mapping methodologies to identify, discuss and agree upon wildlife corridors along the road. Teams of Tacana representatives and biologists then verified around half of these corridors in the field using transects and registering

footprints. Sectorial proposals were further reviewed and agreed upon in an overall territory-wide workshop that brought together 51 Tacana participants from the four sectors of the Tacana Indigenous Territory, including 10 of the 12 communities in the vicinity of the road and the Tacana leadership.

Finally, in late 2013 we updated these data using individual semi-structured interviews with 66 hunters across ten local Tacana indigenous communities along the San Buenaventura-Ixiamas road with the following sample sizes: Carmen Pecha (11 people), Buena Vista (9 people), Macahua (8 people), Santa Rosa (8 people), San Pedro (7 people), Bella Altura (6 people), Santa Fé (5 people), Tumupasa (5 people), San Silvestre (4 people) and Capaina (3 people). Again, using satellite images, Tacana interviewees for each community were asked to identify important movement corridors for wildlife in the context of hunting management and wildlife conservation in the indigenous territory.

Occupancy Study Design

A 3 km buffer of the 110 km SBI road was overlaid by a $1\text{ km} \times 1\text{ km}$ grid totaling 865 1-km^2 units (Figure 1). The 3 km buffer was chosen because at this distance the habitat dramatically changed on the southern side of the road due to the significant last escarpment of the Andes, the peak of which represents the limit of the Madidi national protected area. A random sampling design stratified by distance along the road and distance from the road was used to select 356 units for sampling, representing 41% of the potential sampling units. We decided on this large sample size because of the:

- (i) importance of a comprehensive and reliable wildlife baseline in the face of impending road infrastructure improvements;
- (ii) opportunity to evaluate optimal sampling intensity for wildlife occupancy studies, and;
- (iii) overall strategic importance of occupancy for the Wildlife Conservation Society as a “dashboard measure” for monitoring wildlife status at a landscape scale.

This sample design permits occupancy estimates for species with smaller home ranges such as lowland tapir (*Tapirus terrestris*, Linnaeus 1758), collared peccary (*Pecari tajacu*, Linnaeus 1758), red brocket deer (*Mazama americana*, Erxleben 1777), and paca (*Cuniculus paca*, Linnaeus 1766), as well as the *Leopardus* cat and agouti (*Dasyprocta*) species groups. The *Leopardus* species or small spotted cat group was made up of ocelots (*L. pardalis*, Linnaeus 1758), margay (*L. wiedii*, Schinz 1821) and possibly oncilla (*L. tigrinus*, Schreber 1775) whose footprints are not consistently

distinguishable in the field. Similarly, the *Dasyprocta* species group was made up of *D. variegata*, Thomas 1910, and *D. azarae*, Lichtenstein 1823. For the much more wide-ranging jaguar and white-lipped peccary our study design, and specifically the sample cell size, only allows occupancy methods to estimate the proportion of the study area used by the species, as opposed to the proportion of the study area occupied by the species. We selected these eight species/species groups as collectively they are representative of Amazonian terrestrial wildlife from both an ecological and socio-economic perspective, including carnivores, ungulates and large rodents, and the species that are the mainstay of subsistence hunting (Robinson & Redford, 1991).

Fieldwork was conducted between June and December 2013 with the majority of samples (75.6%) completed by three survey teams between October and November 2013. Each survey team was made up of one tropical forest biologist and one experienced local guide, thereby minimizing possible observer detection biases. A total of 189-person days were necessary to complete the 356-cell unit sample. Each sample unit was surveyed using transects of 300 m, divided into twelve 25 m segments, where presence (yes/no) of lowland tapir, white-lipped peccary, collared peccary, red brocket deer, paca, agoutis (*Dasyprocta* spp.), small spotted cats (*Leopardus* spp.), and jaguar, was registered by observing tracks and other sign (scat, direct observation) along a strip of 1 m width.

Due to a plethora of streams (100+) running off the final escarpments in the foothills of the Andes and crossing the perpendicular road running along the base of those escarpments, we decided to embrace the likelihood that detection probability would increase for many of the species by sampling for tracks along river banks or stream beds. As such, 78.4% of selected sample units ($n=279$) were distributed in cell units with at least 300 m of river or stream (referred to simply as river from this point onward), where the starting point for the 300 m transect was randomized subject to the condition that we could sample 300 m of river. The remaining 21.6% of sample units ($n=77$) were distributed in cells with no river presence. Two different sampling protocols were used for cells with or without rivers.

In the first instance, for sampling units with river, 2-person survey teams started transects adjacent to the river or on the riverbed for rivers not flowing in the dry season. In the second instance, for units without rivers, the 2-person survey teams started from the center of the unit, randomly selecting a direction and starting a 300 m straight line transect with twelve 25 m segments registering species presence in each segment. To enhance species identification and maximize detection probabilities, whenever an animal trail bisected the transect, field teams were allowed to follow the animal trail for a

maximum distance of 15 m before returning to and continuing on the transect. In this way species presence was recorded in each of the twelve 25 m segments within the 300 m transect.

For all units, the field teams also recorded detection probability covariates in the field for each 25 m segment of each 300 m transect. These included substrate type (fine sand, sand, clay, humid clay, mud, rock, soil, fine soil, humid soil, grass and leaves), type of sample unit (stream or non-stream), and the number of days since rain (range 1–6 days), as determined by known rainfall during the previous week, or unknown in cases where the period extended beyond 6 days.

We selected ten occupancy covariates that were calculated for all 865 cells in the study area using a GIS database. For this single-season occupancy study, we considered two broad classes of occupancy covariates. The first class included variables that might explain the largely unknown natural history of the different study species: Distance to Stream-Rivers, Average Slope, Habitat Heterogeneity, Percentage Primary Forest Cover and Percentage Secondary Forest. The second class were those that might reflect anthropogenic influences on wildlife distribution: Distance to Large Towns, Distance to Villages, Distance to SBI Road, Distance to Secondary Roads, and Percentage Bare Ground. The percentage bare ground covariate is a proxy for the degree of human-based landscape conversion in a cell, as bare ground in the study area is related to deforestation associated with roads, human settlements, and recent, intensive agricultural activity.

To calculate the distance variables, we firstly determined the location of the center of each sample cell across the study area and then calculated the shortest straight-line distances from the center of the cell, using ArcGIS ET GeoWizards and the “Point Distance” tool (ET GeoWizard, ET Spatial Techniques Company, 266 Degas Street, Faerie Glen 0043, South Africa). The distances were calculated using the UTM Zone 19 South projection.

Data Analyses

For data analyses we combined the 25 m transect segments into three longer segments of 100 m. Exploratory analyses revealed that using the 100 m segment data, single-season occupancy null models for each species or species group outperformed both spatial correlation occupancy models (Hines et al., 2010), and single-season occupancy models with trap affinity for each 100 m section included as a detection covariate. Therefore, from a detection perspective, we considered the three 100 m segments as spatially independent for all species. Occupancy and covariable data are provided as Supplemental Material (SM 1).

For each species or species group we first calculated naïve occupancy as the proportion of cells with animal sign present. Using the PRESENCE software (Hines, 2014) we then estimated occupancy with a single species-single season occupancy model (MacKenzie et al., 2006). From the pool of detection and occupancy covariates we built specific hypotheses for each target species and reduced our set of general models to include only models with species-specific covariates. For each species-specific general model, we ran a goodness of fit test (Mackenzie & Bailey, 2004), based on 1,000 bootstrap iterations in PRESENCE, to assess whether or not there was over-dispersion in the data. The model adequately fits the data if the resulting estimated overdispersion parameter $\hat{c}=1$ and there is more variation in the occupancy data than expected by the model if $\hat{c} > 1$ (Mackenzie & Bailey, 2004). When \hat{c} values exceeded 1 we accounted for overdispersion in subsequent selection of the best models for each species. We excluded models that displayed numerical issues related to parameter estimation. Remaining models were ranked by Akaike's Information Criterion (AIC) value or by quasi-AIC (QAIC) that accounts for overdispersion \hat{c} (Burnham & Anderson, 2002). The model with the lowest AIC or QAIC value was selected as the best model, unless QAIC values were tied in which case competing models were averaged to produce occupancy values.

Finally, we compared the best occupancy models for each species with the wildlife corridors identified by local people. To visually compare occupancy results between the six species or species groups with significant covariables, we prepared maps grouping occupancy values for each species into four categories using the "natural breaks" methodology which categorizes into a predetermined number of categories considering minimum and maximum values. To further evaluate our occupancy models, we produced occupancy error maps using four categories of standard error which are provided as Supplemental Material (SM 2).

For the map to compare with wildlife corridors identified by local people we selected the most significant natural break category (occupancy values closest to 1) for four of the species or species groups for which occupancy extrapolation was possible using relevant covariable, and for whom wildlife corridors are most relevant due to their ranging requirements: *Tayassu pecari*, *Tapirus terrestris*, *Pecari tajacu*, *Leopardus* spp. Using this criterion, we indicated which cells were relevant for between 1 and 3 of these target species.

Results

Interviews

In 2001 interview distribution records ($n=217$) for target species from indigenous hunters included jaguar

($n=61$), collared peccary ($n=46$), red brocket deer ($n=37$) and lowland tapir ($n=73$) were generated within 10 km of the SBI road (Figure 2).

In 2002 eight of fifteen public transport drivers had observed white-lipped peccaries and/or jaguars exclusively between the Cuñana and Tequeje rivers along the SBI road (Figure 2). Four drivers had not seen white-lipped peccaries for 10 years, 2 had seen them between four months and four years previously, and two had observed them in the previous 3 months. For jaguar, four drivers had not seen them for 10 years, 3 between 7 months and one year previously, and one in the last six months.

In 2005 community representative interviews identified 28 wildlife corridors along the SBI road (Figure 2). These corridors are concentrated in four portions of the study area: a) around the Tacana communities in the immediate vicinity of San Buenaventura, b) around the Tacana cultural capital, Tumupasa about half way along the road to Ixiamas, c) along the majority of the road between Tumupasa and Ixiamas, and d) around the Tacana communities in the immediate vicinity of Ixiamas. Most of these corridors run from the Madidi National Park to the Tacana Indigenous Territory. There is a noticeable absence of community identified corridors along the road in the ca.50 km between San Buenaventura and Tumupasa.

Finally, in 2013 interviews with 66 hunters in ten Tacana communities along the SBI road identified nine wildlife corridors. In summary, some observations of white-lipped peccaries occurred around the Tacana communities near San Buenaventura, as well as a large concentration around Tumupasa, some observations around the Tacana communities near Ixiamas, and another concentration between the Cuñana and Tequeje rivers situated between Tumupasa and Ixiamas.

Occupancy

In total, we registered 4,140 footprint records and 78 other sign records. For three medium- to large-sized mammals (*T. terrestris*, *P. tajacu*, *M. americana*) and two mammal species groups (*Leopardus* spp. & *Dasyprocta* spp.), PRESENCE provided robust single season occupancy models with covariates that generally outperformed the null single season models (Tables 1 and 2). Only for *Cuniculus paca* did the null model outperform models with covariates. Occupancy estimates for these species and species groups using the best performing models ranged between 0.31 and 0.59 (Table 2).

Single season occupancy estimates ($\psi = 0.39 \pm 0.05$, $p = 0.45 \pm 0.04$) for the lowland tapir (Figure 3(a)) had reasonable confidence limits (0.3–0.5) and identified two occupancy covariates (Table 2), and one detection covariate. Detection probability increased when the sample



Species	Naïve	Single season-single species null occupancy			
		psi	St. Err	LCL	UCL
<i>Panthera onca</i>	0.09	0.11	0.02	0.08	0.16
<i>Leopardus</i> spp.	0.18	0.34	0.06	0.23	0.48
<i>Tapirus terrestris</i>	0.33	0.38	0.03	0.32	0.45
<i>Payassu pecari</i>	0.1	0.11	0.02	0.08	0.16
<i>Pecari tajacu</i>	0.45	0.5	0.03	0.44	0.56
<i>Mazama americana</i>	0.52	0.56	0.03	0.50	0.62
<i>Cuniculus paca</i>	0.52	0.56	0.03	0.50	0.62
<i>Dasyprocta</i> spp.	0.53	0.59	0.03	0.53	0.65

transect was conducted along a stream. The strongest occupancy covariate was a negative relationship with the Percentage of Bare Ground in a given sample cell (Online Appendix 1a). A positive relationship was present for Distance from Main Road (Online Appendix 1b).

For collared peccaries (Figure 3(b)), single season occupancy estimates ($\psi = 0.5 \pm 0.05$, $p = 0.53 \pm 0.03$) had reasonable confidence limits (0.4–0.61), no detection covariates, and three occupancy covariates (Table 2). The strongest relationship was again a negative one with the Percentage of Bare Ground in a given sample cell (Online Appendix 1c). A weaker negative relationship also existed with Slope (Online Appendix 1d), and a positive relationship existed with Distance to Large Towns (Online Appendix 1e).

In the case of red brocket deer (Figure 3(c)), single season occupancy estimates ($\psi = 0.56 \pm 0.04$, $p = 0.59 \pm$

Table 2. Highest Ranked Occupancy Models With Detection Probability Covariates and Occupancy Covariates With Their Estimated Beta Values and Standard Errors (St. Err) for Six Wildlife Species and Two Species Groups Along the SBI Road.

Species	Preferred occupancy models								Detection probability covariates			Occupancy covariates		
	\hat{c}	AIC wgt	psi	St. Err	LCL	UCL	p	St.Err	Covariate	Value	St. Err	Covariate	Value	St. Err
<i>Panthera onca</i>	2.77	1	0.11	0.02	0.08	0.16	0.39	0.07						
<i>Leopardus spp.</i>	0.98	0.89	0.33	0.07	0.21	0.48	0.24	0.05	Time Last Rain	-0.2	0.08	Distance to River-Stream	-1.11	0.37
												Habitat Heterogeneity	0.64	0.2
<i>Tapirus terrestris</i>	3.96	0.62	0.39	0.05	0.3	0.5	0.45	0.04	Stream?	0.97	0.36	% Bare Ground	-6.19	1.69
												Distance to Main Road	0.46	0.16
<i>Tayassu pecari</i>	1.95	0.35	0.17	0.07	0.1	0.25	0.3	0.18	Time Last Rain	0.49	0.12	% Forest	3.05	0.99
		0.22							Time Last Rain	0.49	0.12	Habitat Heterogeneity	-0.64	0.2
		0.18							Time Last Rain	0.45	0.12	Distance to Village	0.55	0.17
<i>Pecari tajacu</i>	1.87	0.77	0.5	0.05	0.4	0.61	0.53	0.03				% Bare Ground	-5.21	1.12
												Slope	-0.46	0.14
												Distance to Large Town	0.41	0.13
<i>Mazama americana</i>	5.06	0.68	0.56	0.04	0.49	0.63	0.59	0.02				% Bare Ground	-4.03	0.94
<i>Cuniculus paca</i>	4.88	1	0.56	0.03	0.5	0.62	0.57	0.02						
<i>Dasyprocta spp.*</i>	6.38	0.52	0.59	0.05	0.5	0.68	0.53	0.03				% Secondary Forest	3.39	0.85
		0.32										Habitat Heterogeneity	0.56	0.13

Shown are the overdispersion parameter \hat{c} , each model's AIC or QAIC value and the estimated probability of occupancy (psi) together with its standard error and lower (LCL) and upper (UCL) confidence limits, and detection probability (p) and its standard error.

*Occupancy value derived from competing model average.

0.02) had reasonable confidence limits (0.49–0.63) with no detection covariates and one occupancy covariate (Table 2), a negative relationship with Percentage of Bare Ground in a given cell (Online Appendix 1f).

For the paca, single season occupancy estimates ($\psi = 0.56 \pm 0.03$, $p = 0.57 \pm 0.02$) had excellent confidence limits (0.5–0.62) with no detection or occupancy covariates (Table 2).

For the agouti species group, single season occupancy estimates averaged from two competing models ($\psi = 0.59 \pm 0.05$, $p = 0.53 \pm 0.03$; Figure 3(d)), each with a different occupancy covariate, had reasonable confidence limits (0.5–0.68; Table 2). The two covariates in the competing models represented positive relationships, primarily with Percentage of Secondary Forest (Online Appendix 1g), and less so for Habitat Heterogeneity in a given cell.

For small spotted cats (Figure 3(e)), single season occupancy estimates ($\psi = 0.33 \pm 0.07$, $p = 0.24 \pm 0.05$) also had reasonable confidence limits (0.21–0.48), with one detection covariate and two occupancy covariates (Table 2). Detection probability was influenced by the time since the last rain –with probabilities higher just after rain. The strongest occupancy covariate was a negative relationship with Distance to Stream-River (Online Appendix 1h) and a weaker positive relationship with Habitat Heterogeneity (Online Appendix 1i).

For the two wide-ranging target species PRESENCE provided robust occupancy models. The use estimates for jaguar ($\psi = 0.11 \pm 0.02$, $p = 0.39 \pm 0.07$) and white-lipped peccaries ($\psi = 0.17 \pm 0.07$, $p = 0.3 \pm 0.06$) were

low (Table 2). However, the single season occupancy model for jaguar had no detection or occupancy covariates. For white-lipped peccary (Figure 3(f)) detection probability was influenced by time since last rain, with probability increasing with time since rain. Three competing models, each with one occupancy covariable in addition to the detection covariate were averaged. The three covariates were: Percentage of Forest (Online Appendix 1j) which was positively related to white-lipped peccary use in a given cell; Habitat Heterogeneity which was negatively related to white-lipped peccary use, and; Distance to Village which was positively related to white-lipped peccary use in a given cell.

Discussion

Interviews and Corridors

The various interview techniques and selected interviewees provided valuable information on the location of wildlife corridors along the SBI Road, which in several cases were identified by all of the four methods over a period of 12 years. This underlines that interviews with wildlife knowledgeable local people can provide very useful conservation planning information. However, since most interviewees (89.9%) were members of indigenous Tacana communities along the road, wildlife observations and identified corridors were concentrated in areas in the immediate vicinity (within 10 km) of those Tacana villages and towns, corresponding with community hunting areas identified in Participatory Rural

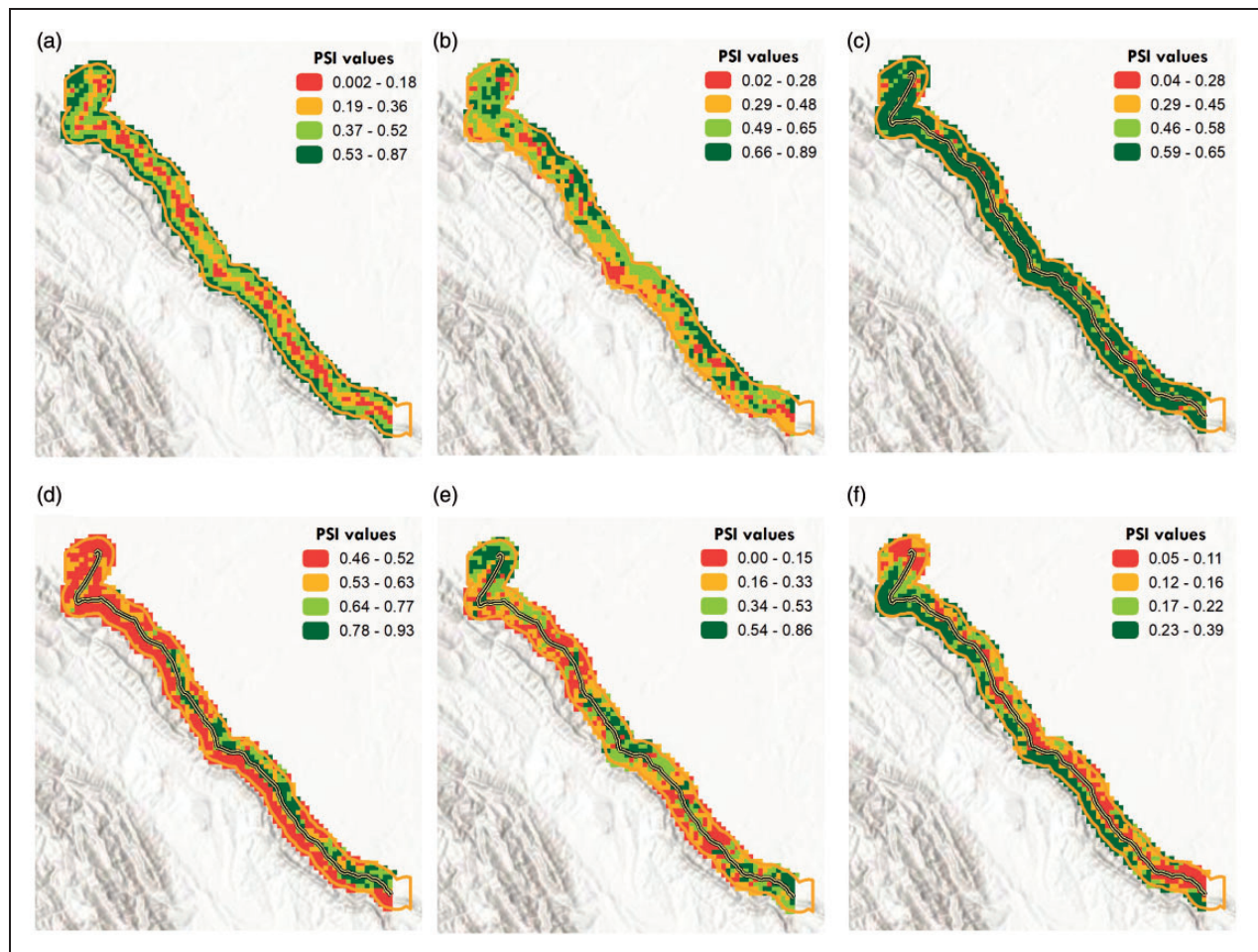


Figure 3. Wildlife occupancy along the SBI road using standardized categories based on minimum and maximum occupancy values for (a) lowland tapir (*Tapirus terrestris*), (b) collared peccary (*Pecari tajacu*), (c) red brocket deer (*Mazama americana*), (d) agouti (*Dasyprocta* spp.), and (e) small spotted cats (*Leopardus* spp.), and minimum and maximum occupancy derived use values for (f) white-lipped peccary (*Tayassu pecari*).

Appraisals for each community (CIPTA & WCS, 2002). This is highlighted by the fact that very few corridors were identified in a 35 km stretch between San Buenaventura and Tumupasa, where no Tacana villages occur (Figure 2).

Occupancy and Use

Exploratory analyses revealed that combining the original 25 m segment data into three 100 m segments or spatial replicates eliminated the spatial autocorrelation problem for most of the study species. Future studies should explore spatial correlation further in order to make appropriate study design recommendations for Amazonian forest medium and large-sized mammals. In any case, in this study, once the data was combined into 100 m segments, the single season-single species occupancy models outperformed the spatial correlation

models (Hines et al., 2010) based on the original 25 m segments.

To improve occupancy detection probabilities for Neotropical large carnivores (*Panthera onca*, *Puma concolor*, Linnaeus 1771, and *Tremarctos ornatus*, Gervais 1855), as well as further improving the precision of occupancy estimates for wildlife in general, we recommend three 600 m transects for sign-based surveys (Isasi-Catalá et al., 2019; Márquez et al., 2017), effectively increasing sampling in the cell by a factor of six as compared to this study.

Our study design provided robust occupancy results for most target species, including wildlife with low population densities, such as lowland tapir, that are often threatened in landscapes with significant human activity (Medici et al., 2007; Taber et al., 2009). Although occupancy results describing jaguar ($\psi = 0.11$) and white-lipped peccary ($\psi = 0.17$) use along the road are below

the recommended range for occupancy studies ($\psi = 0.2$ – 0.8 ; MacKenzie et al., 2006), the estimates also have small standard errors and good detection probabilities, and so may facilitate longer term monitoring efforts. The percentage of cells sampled in this study was relatively high (39.77%), underlining the need to increase sampling effort in each selected sample cell, either through increase sample trails and/or repeated samples over time, in order to increase detection probabilities.

Our results provide insights on important covariates to consider for conservation planning for species with low estimated use values. For white-lipped peccaries, detection probability increased as time passed since rain. White-lipped peccary herds are large, up to 200 animals (Taber et al., 2009), and a herd's tracks are resilient and only truly eliminated with significant rain. Thus, for this species time since rain is equivalent to the total time sampled. White-lipped peccaries used cells with a high percentage of forest as would be expected by this forest specialist (Taber et al., 2009).

For our target species occupancy methods were extremely effective, with acceptable occupancy values and generally narrow 95% confidence limits, suggesting that monitoring efforts with this sampling design, or indeed an increased sampling intensity within each sample cell, would provide informative results in the future. Taken together, the results for the target wildlife species or species groups reveal a number of commonalities in terms of relevant detection and occupancy covariates for the study area, as well as some expected differences.

The only detection covariate relevant for lowland tapir was whether sampling was conducted along a stream or not. As the largest and heaviest animal in the Amazon, tapir footprints are some of the most detectable and resilient tracks, and tapirs are known to prefer habitat near water sources (Emmons & Feer, 1997). Time since last rain was important for the spotted cats, but in the opposite direction to white-lipped peccary: as time since rain increased detection probability decreased due to the relative fragility of small to medium sized carnivore tracks.

Overall the strongest occupancy covariate for lowland tapir, collared peccary, and red brocket deer was the proxy measure for degree of intensive human activity present in a sample cell (Percentage Bare Ground). This result reflects the recognized vulnerability of this suite of species to hunting in the Neotropics (Robinson & Redford, 1991), and underlines the usefulness of this proxy covariate for explaining wildlife occupancy patterns in the study area.

Weaker relationships also existed for two of the other anthropogenic covariates for two of the species most vulnerable to hunting: Distance to Large Town (collared peccary), and Distance to Main Road (lowland tapir).

The larger towns in the study area included San Buenaventura (3,416 people in 2012 census), Rurrenabaque (13,446 people in 2012 census) and Ixiamas (3,952 people in 2012 census; INE, 2012). It is therefore unsurprising that occupancy values were markedly reduced near these towns, where hunting, forest degradation, and habitat destruction over the last decade of human population growth (Population Growth 2001–2012: Ixiamas 123%, Rurrenabaque 59%, San Buenaventura 51%) have impacted wildlife. Collared peccaries are one of the least cryptic species in the study and so over time their presence has been eradicated in areas near the large towns in the study area. The main road affords access for hunting, legal and illegal logging, as well as public transport.

Occupancy or use was higher for spotted cats closer to streams and rivers reflecting their preference for proximity to water (Martins Wolff et al., 2019). Meanwhile, agoutis were more frequent in cells with secondary forest. Agoutis are also known to flourish in fragmented and secondary forests (Jorge, 2008). Habitat heterogeneity in a given cell increased agouti and spotted cat occupancy.

In general, occupancy values from this study were broadly comparable with previous studies. In the case of lowland tapirs, occupancy along the SBI road ($\psi = 0.39$) was lower than that observed for *T. bairdii* in Los Chimalapas, Mexico ($\psi = 0.81$; Pérez-Irinea & Santos-Moreno, 2016), and *T. terrestris* in two national protected areas in the Colombian Guiana Shield ($\psi = 0.56$ – 0.68 Tuparro National Natural Park and Puinawai National Natural Reserve; Gómez et al., 2016). In the Brazilian Atlantic forest lowland tapir occupancy was highest in protected areas (0.83) and comparable with the SBI Road study in intermediate (0.5) and poorly (0.4) protected portion of the forest (Cruz et al., 2014). In neighboring southern Peru, occupancy values for lowland tapir were 0.85 in relatively undisturbed floodplain and *terra firme* forests (Tobler et al., 2015).

Previous occupancy studies for brocket deer (*Mazama* spp.) have been typically high, between 0.82–1 (Gómez et al., 2016; Licona et al., 2011; Pérez-Irinea & Santos-Moreno, 2016). In a study in the Atlantic forest in Brazil brocket deer occupancy was highest at sites with a high large tree density and in areas greater than 500 m from water (Ferreguetti et al., 2015). In southeastern Mexico, brocket deer occupancy increased as distance increased from the nearest human population, mirroring results along the SBI Road, given that in this study the Percentage of Bare Ground covariable is a proxy for level of human influence. In nearby southern Peru, occupancy levels were 0.67 in floodplain forest and 0.71 in *terra firme* forest (Tobler et al., 2015).

Similarly, published occupancy values for collared peccaries were high in two protected areas in the

Colombian Guiana Shield (0.89–0.93; Gómez et al., 2016), as well as the Tambopata National Reserve in southern Peru (0.93; Licona et al., 2011), and 0.68 to 0.7 in a broader study across Madre de Dios (Tobler et al., 2015). Occupancy values in an unprotected area of southeastern Mexico (0.59; Pérez-Irinea & Santos-Moreno, 2016) and in and around a protected area in the Brazilian Cerrado (0.5; Paolino et al., 2016) were comparable with results reported here ($\psi = 0.5$).

White-lipped peccary occupancy derived use along the SBI road ($\psi = 0.17$) was considerably lower than the aforementioned study sites in Colombia (0.44–0.51; Gómez et al., 2016) and Mexico (0.32; Pérez-Irinea & Santos-Moreno, 2016), and Madre de Dios in southern Peru ($\psi = 0.64$ –0.93; Tobler et al., 2015), emphasizing the value of identified corridors to retain connectivity between the neighboring Madidi National Park and the surrounding lowlands.

A previous study for agoutis (*Dasyprocta azarae*) in the Brazilian Pantanal showed a seasonal variation in occupancy between 0.39–0.83 (Cid et al., 2013), with significantly lower values observed in the dry season. Our results from the Bolivian dry season are intermediate ($\psi = 0.59$), suggesting a flourishing population of agouti within the study site. Indeed, they are approaching levels reported for relatively protected sites in southern Peru (0.66–0.73; Tobler et al., 2015). In contrast, in and around a protected area in the Brazilian Cerrado, as well as in southern Peru, *Leopardus* occupancy was higher ($\psi = 0.66$; Paolino et al., 2016; $\psi = 0.65$ –0.85; Tobler et al., 2015) than along the SBI Road ($\psi = 0.33$).

Finally, whilst our occupancy derived jaguar detection probabilities are comparable with previous studies (Arroyo-Arce et al., 2014; Petracca et al., 2014; Tobler et al., 2015; Zeller et al., 2011), the actual occupancy values were rather lower, reflecting the impacts of the

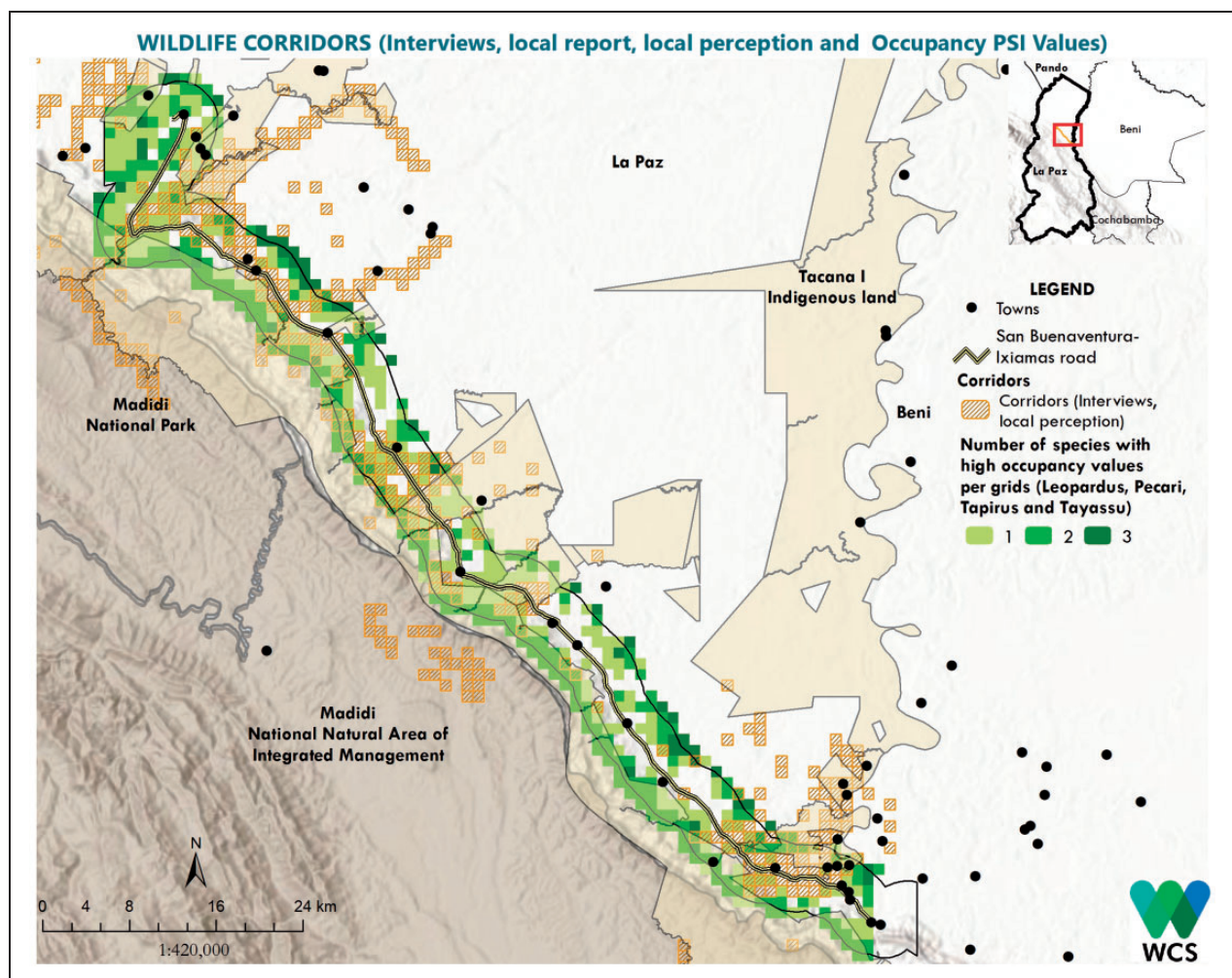


Figure 4. Comparison of Community Identified Corridors With Occupancy-Based Corridors Along the SBI Road Using Four Mammal Species or Species Groups (*Pecari tajacu*, *Tapirus terrestris*, *Tayassu pecari*, *Leopardus* spp.).

road, especially given that within the neighboring Madidi National Park jaguar populations are relatively high (Silver et al., 2004; Wallace et al., 2003).

Wildlife population data from the Tuichi and Hondo valleys of the immediately adjacent Madidi protected area is demonstrating population recovery between 2001 and 2014 for several study species, including lowland tapir (Wallace et al., 2012). This recovery since the creation of the park emphasizes the importance of Madidi as a source population for many wildlife species harvested by traditional indigenous hunters in the Tacana Indigenous Territory. Thus, the maintenance of priority wildlife corridors is not just a crucial step for the conservation of many charismatic and threatened species in the landscape, but is also crucial from a cultural and food security perspective, particularly for the Tacana people of northern La Paz who like many Amazonian indigenous people are heavily dependent on wildlife as a protein source (Townsend et al., 2020). Promoting the conservation of corridors will also ensure better watershed protection, since many of the identified corridors are associated with the rivers and streams running off the lower foothills of the Andes.

Interviews with local people underlined the importance of the following corridors along the road (Figure 2):

1. between the Jiruma and Zapata rivers near San Buenaventura,
2. between the Mamuque and Sayuba rivers near Tumupasa,
3. between the Enadere and Enadeve rivers, again near Tumupasa,
4. and especially, between the Cuñaca and Tequeje rivers between Tumupasa and Ixiamas.

Amalgamated occupancy results for four large mammal species provide support for these four corridors, but also identified an additional fifth priority corridor along the road (Figure 4), between the Mayge and Moa rivers between San Buenaventura and Ixiamas. We recommend that these five corridors are prioritized for mitigation efforts that minimize corridor disruption during the road improvement project. Further studies could employ camera traps to examine and monitor the frequency of wildlife use along the road (O'Brien & Kinnaird, 2013; O'Brien, 2016).

Implications for Conservation

Our combined methods of community interviews with local hunters and other local expert informants for wildlife and sign-based occupancy surveys proved an extremely cost-effective approach to identifying, and then independently verifying and locating further

priority wildlife corridors. Camera trapping within identified corridors would provide information on frequency of wildlife use for each corridor. We recognize that our occupancy study would be further improved by increasing sampling effort within a given sampling cell, and future wildlife monitoring along the road would benefit from this recommendation. Nevertheless, the results reported here represent a solid baseline with which to monitor wildlife within this road improvement project.

After a significantly delayed start, the initial construction contract was abandoned in early 2017, and only now, mid-2020, is the current interim government looking to renew the contract. We are currently engaged with the World Bank and the environmental consultancy firm contracted to re-evaluate the indirect impact assessment and have helped recommend a series of mitigation efforts to retain the identified wildlife corridors.

The potential of occupancy modelling for wildlife monitoring is significant, given that usually it competes favorably with other methods in terms of cost-effectiveness, and especially from a spatial perspective an area of this size can be surveyed relatively rapidly. In this paper, we have presented results from single-season occupancy models that provide an understanding of how wildlife responds spatially to the natural world, as well as anthropogenic threats. As data accumulate, multi-season occupancy models can be used for monitoring over time and providing input into adaptive management (Nichols & Williams, 2013), which will allow refining and monitoring of the most important covariates for each species, and assessment of the effectiveness of specific conservation actions.

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ORCID iD

Robert Wallace  <https://orcid.org/0000-0001-7411-6338>

Supplemental Material

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