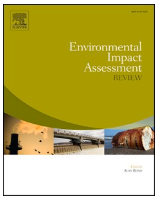
Environmental Impact Assessment Review 99 (2023) 107010

Contents lists available at ScienceDirect

Environmental Impact Assessment Review

journal homepage: www.elsevier.com/locate/eiar



The road towards wildlife friendlier infrastructure: Mitigation planning through landscape-level priority settings and species connectivity frameworks

Evi A.D. Paemelaere [a,b,*], Angela Mejía [a,b], Simón Quintero [a,b], Matthew Hallett [a,c,d,e], Fernando Li [a,e], Asaph Wilson [e,f,g], Howard Barnabas [e,f,h], Andrew Albert [e,f,i], Rhomayne Li [e,f], Leon Baird [e,f,g], Gerard Pereira [e,f,j], Jeremy Melville [e,f]

[a] *Centre for International Forestry Research (CIFOR), Bogor, Indonesia*
[b] *People & Wildlife Solutions, Lethem, Region 9, Guyana*
[c] *Department of Wildlife Ecology & Conservation, University of Florida, 110 Newins-Ziegler Hall, Gainesville, FL 32611, United States of America*
[d] *Conservation Department, Jacksonville Zoo & Gardens, 370 Zoo Pkwy, Jacksonville, FL 32218, United States of America*
[e] *Rupununi Wildlife Research Unit - Lethem, Region 9, Guyana*
[f] *Guyana Wildlife Conservation and Management Commission, Georgetown, Guyana*
[g] *South Rupununi Conservation Society - Wichabai Ranch, Region 9, Guyana*
[h] *Caiman House Research Station - Yupukari Village, Region 9, Guyana*
[i] *Kezeé EcoLodge - Karasabai Village, Region 9, Guyana*
[j] *Karanambu Trust - Karanambu Ranch, Guyana*

ARTICLE INFO

Keywords:
Barrier effect
Connectivity
Landscape planning
Underpasses
Wildlife crossing
Roadkill

ABSTRACT

The current global road network expansion scenario poses a conflict of interest between Sustainable Development Goals of human well-being and biosphere, which could be mitigated through strengthening of the Environmental Impact Assessment (EIA) process. Here, we propose the integration in EIAs of a method focusing on landscape-level connectivity for wildlife, based on easily accessible satellite imagery and basic species data that need not be site-specific. This method identifies key locations along the (proposed) road for wildlife connectivity based on expert-based wildlife connectivity models, and specifies the type of measures needed through a behavioral response framework. We tested our proposed method with field data on four species through a single-species occupancy model followed by Bayesian occupancy modeling. We show that the expert-based model resulted in a conservative identification of key locations for mitigation interventions. Furthermore, we highlight how already required traffic bridges and culverts can be incorporated as part of the mitigation strategy. Our method permits incorporation of proactive mitigation measures in the road design to reduce the impact of roads on wildlife and their habitat, helping to limit the need for expensive post-hoc solutions. We present this method through a case-study from Guyana, South America.

1. Introduction

An estimated 25 million km of roads will be added to the existing global network by 2050, 90% of which will be situated in developing nations (Dulac, 2013; Thacker et al., 2019). Tropical developing nations are home to the majority of biodiversity on Earth, and the expansion of road networks creates a conflict of interest between needs for human welfare and biodiversity preservation. Said otherwise, road network expansion is necessary for many of the United Nations' Sustainable Development Goals (SDGs) but could compromise the foundational SDGs focused on the biosphere (Thacker et al., 2019). Therefore, there is a need to balance the benefits of roads to rural communities with the negative impacts that road development is shown to have on wildlife and wildlife habitat (Benítez-López et al., 2010; Van Der Ree et al., 2015). Although Environmental Impact Assessments (EIAs) are meant to help safeguard wildlife from major impacts, processes are often limited by a lack of time, capacity, and resources in the agencies appointed to oversee and enforce them (Jaeger, 2015), and they often fail to consider

---

* Corresponding author at: CIFOR, Situ Gede, Bogor Barat, Bogor 16115, Indonesia.
E-mail address: PWSolutions.main@gmail.com (E.A.D. Paemelaere).

https://doi.org/10.1016/j.eiar.2022.107010
Received 13 November 2021; Received in revised form 4 December 2022; Accepted 5 December 2022
Available online 19 December 2022
0195-9255/© 2022 The Authors. Published by Elsevier Inc. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

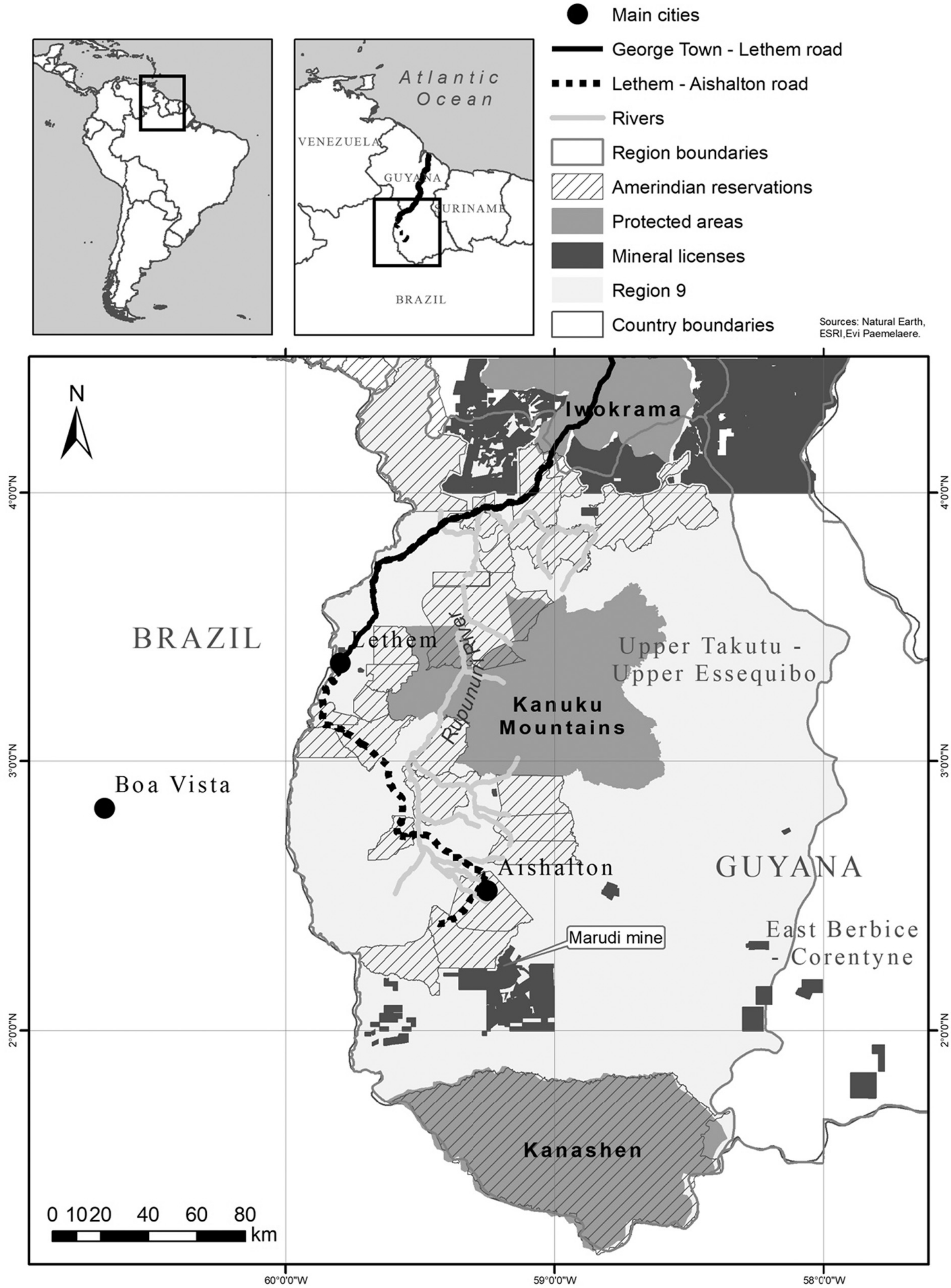


Fig. 1. *Map of the study site.* All roads are unpaved, but the Georgetown Lethem Road is awaiting an upgrade to connect Manaus (Brazil) with a deep-water port in Georgetown, capital of Guyana.

landscape-level connectivity, which lies at the base of nature conservation.

During the construction and operational phase, roads have both direct and indirect impacts on wildlife that can be divided into four categories: habitat degradation, resource inaccessibility, population isolation, and traffic mortality (Coffin, 2007; Jaeger et al., 2005; Laurance et al., 2009; Trombulak and Frissell, 2010). The development of road infrastructure drives indirect impacts, such as 'fish bone' development with habitat degradation from branching secondary roads that reach as far as 100 km away from the main road (Barber et al., 2010; Linkie et al., 2004; Pfaff et al., 2007; Veríssimo et al., 2002), and increased harvest pressure from hunting, fishing and wildlife trade (Bennett et al., 2002; Chaves et al., 2017; Espinosa et al., 2014; Laurance et al., 2009; Peres, 2000; Wilkie et al., 2000), which should be managed through regulatory frameworks. Direct impacts, on the other hand, include habitat removal, followed by air and water pollution from car fumes, vehicle fluids and dust, as well as noise and light pollution extending into the surrounding habitat through edge effects (e.g., Brodie et al., 2014; Eigenbrod et al., 2009; Laurance et al., 2011). Furthermore, roads directly impact wildlife through reduced access to essential resources, such as food, nesting sites or mates, forming a barrier to wildlife that cannot cross the road due to physical or biological barriers (e.g., Holderegger and Di Giulio, 2010; Jaeger et al., 2005; McGregor et al., 2008), or because attempts to cross result in frequent roadkill relative to the species' population size (Grilo et al., 2012; Jackson and Fahrig, 2011). The latter direct effects can largely be managed through smart, wildlife friendly road construction.

Carcasses from wildlife-vehicle collisions are a highly visible effect from roads on biodiversity, and roadkill can be a major issue for some species (Ascensão et al., 2013; Jackson and Fahrig, 2011; Jaeger and Fahrig, 2004). Nevertheless, it is not the only concern for wildlife, nor is it the best indicator of impact (Ascensão et al., 2019; Zimmermann Teixeira et al., 2017). In fact, the likelihood of a species to be killed on the road depends on its ecology and behavior (Jacobson et al., 2016a, 2016b). "Non-responder" animals are easy targets for roadkill on roads with high traffic volume or speed because they enter the road surface but fail to react to oncoming traffic. "Pausers" face a similar fate because they stop in the face of danger, but with high traffic volume their pausing will occur at the road edge and the barrier effect comes into play. "Speeders", which run away from danger, can cross, but this also becomes more difficult with increasing traffic volume or speed. "Avoiders" are those that do not try to cross or that may not even approach the road, and no roadkill will occur, but in this case the road forms an absolute barrier leading to population fragmentation. Although not specifically mentioned, avoiders could also include those not able to cross the road surface due to specific habitat needs, such as canopy connectivity for arboreal species that cannot descend to the road surface. This behavioral framework applies to terrestrial, aerial, arboreal and semi-aquatic species. These less visible and more complex impacts from roads on wildlife are often ignored, even though they are highly biologically or ecologically important (Holderegger and Di Giulio, 2010; Shepard et al., 2008).

Although a variety of mitigation strategies to address impacts of roads on wildlife have been applied, approaches have typically been post-hoc solutions, such as wildlife overpasses, or non-solutions, such as road signs (Ruediger and Jacobson, 2013; Rytwinski et al., 2016). Post-hoc solutions are not always evaluated for effectiveness and drastic interventions, such as overpasses, may not always be cost-effective (Sijtsma et al., 2020). An efficient proactive approach that starts at the road design phase would be optimal, as it allows for the integration of wildlife connectivity with engineering needs, reducing costs of mitigation measures, increasing the likelihood of their implementation, and helping to prevent negative impacts from the start (Mcguire et al., 2021; Ruediger and Jacobson, 2013). Such an approach, however, is often hampered by lack of data on wildlife to determine where such interventions must be considered and what factors of construction must be considered at each location to be optimal for safe crossings of target species.

Factors that should be considered to mitigate road impacts on wildlife at the planning stage are road alignment, road width, roadside vegetation, and the design and location of traffic bridges and culverts, which could function as wildlife underpasses (Bager and Fontoura, 2013; Glista et al., 2009; Grilo et al., 2008, 2010; Jacobson et al., 2016a, 2016b; Serronha et al., 2013). To ensure safe passage of animals, Kintsch et al. (2015) developed a framework for wildlife crossing structures – over- and underpasses – that considers the size of the animal, but also whether the animals are habitat generalists, or specialists that would require specific elements, such as water, touching canopy over road surfaces, or vegetation cover on the ground. This framework can be applied to optimize structures required for road engineering or to wildlife-specific passages. The frameworks by Jacobson et al., 2016a, 2016b and Kintsch et al. (2015) help to determine which species to consider, what type of impact can be expected, and what is required for mitigating it. However, they do not provide road planners with a simple method on where to locate safe underpasses.

To determine priority sites for road impact mitigation measures, a variety of methods have been applied. Generally, road impacts are evaluated post-hoc, and based on roadkill (e.g., Cramer et al., 2014; Ford et al., 2011; Russo et al., 2020; Spanowicz et al., 2020), which is not necessarily reflective of wildlife crossing needs and ignores the barrier effect (Cerqueira et al., 2021; Jacobson et al., 2016a; Kintsch et al., 2015; Zimmermann Teixeira et al., 2017). Others have used wildlife movement data or live crossing sites (Colchero et al., 2011; Cushman and Lewis, 2010; Roesch, 2010), which can be very useful in identifying priority sites, but may be misleading if movements were recorded post road development (S. Jacobson, Personal communication). Collecting movement data is also resource intensive and rarely possible for multiple species during environmental impact assessments. Therefore, these methods are less useful at the planning stage to help develop preventative measures.

Modeling has gained ground in identifying priority sites for mitigation strategies, although there still remains a heavy focus on the occurrence of roadkill (e.g., Fabrizio et al., 2019; Grilo et al., 2011; Kang et al., 2016; Polak et al., 2014). Models are either based on habitat suitability or least cost movement (Vanthomme et al., 2015). Although the latter has been deemed more suitable for prioritizing mitigation sites (Cerqueira et al., 2021; Fabrizio et al., 2019; Vanthomme et al., 2015), least cost movement models assume that the animals have perfect knowledge of the landscape (McClure et al., 2016). Models based on circuit theory may provide a more realistic approach, and have been found to predict wildlife movements better overall compared to least-cost models (McRae and Beier, 2007; Unnithan Kumar and Cushman, 2022). Predictive modeling has been recommended in road impact studies, particularly in cases where data are scarce or lacking altogether (Pinto et al., 2020). Moreover, inclusion of landscape-level, quantitative connectivity analyses in environmental impact assessments is scarce but urgently needed (Torres et al., 2022). Connectivity is often considered too late in the development process (Patterson et al., 2022). A recent example shows the application of circuit theory models in an impact assessment in a highly developed area (Kor et al., 2022).

Here, we present a feasible and holistic approach for prioritizing locations for mitigation based on a combination of the existing road response framework by Jacobson et al., 2016a, 2016b, the crossing guilds from Kintsch et al. (2015) and an expert-based resistance model. The road response helps to understand the willingness of animals to cross a road, determining whether mitigation strategies need to address roadkill risk, or barrier effects, or both for target species. Crossing guilds determine requirements of animal crossing structures to be functional for the target species, which are particularly useful a-priori in the planning phase of traffic bridges and culverts but can also be applied to retrofit such structures for increased functionality as underpasses (Smith et al., 2008), or to assess the need for species-specific solutions, such as

Table 1
Attributes (bold) and list of categories used in the resistance to movement layer creation. Attributes and categories were selected based on our focal species and their habitat needs as derived from the literature and author expertise.

Attribute	Categories
Forest cover	**0–10%; 10–20%; 20–40%;40–60%;60–100%**
Distance to forest	**0–0.25 km; 0.25–0.50 km; 0.51–1.0 km; 1.01–1.5 km; 1.51–2.0 km; 2.01–4.0 km; > 4 km**
Distance to permanent water bodies	**0–0.25 km; 0.25–0.50 km; 0.51–1.0 km; 1.01–2.0 km; > 2.0 km**
Distance to villages	**0–0.25 km; 0.25–0.50 km; 0.51–1.0 km; 1.01–1.5 km; 1.51–2.0 km; 2.01–4.0 km; 4.01–8.0 km; 8.01–16.0 km; >16 km**
Distance to roads	**0–0.25 km; 0.25–0.50 km; 0.51–1.0 km; 1.01–1.5 km; 1.51–2.0 km; 2.01–4.0 km; 4.01–8.0 km; 8.01–16.0 km; >16 km**
Slope	**0–20; 20–30; 30–50; > 50**

wildlife overpasses or underpasses with the sole purpose of a wildlife crossing. Finally, the model guides the decision on where to focus such interventions. This approach can inform best practices in a-priori wildlife friendly road construction, which can be incorporated as an integral part of policies on Environmental Impact Assessments (EIA) and on road planning in general. We exemplify the approach through a case study from Guyana.

2. Methods

2.1. Study area

Guyana is situated in northern South America and maintains 80% of its natural habitat. Currently, a 4000 km road network exists, of which 90% remains unpaved, and the majority of roads connect mining and logging areas in the interior to the capital city, Georgetown (Taddia et al., 2005). Guyana's major interior road runs 538 km, traversing the country from Georgetown to the border town of Lethem and onto Boa Vista and Manaus in Brazil. Except for the first 100 km from Georgetown to the town of Linden, this Georgetown-Lethem Road (hereafter GTLR) is unpaved. However, the process to upgrade the entire road and its bridges has already begun. About 30% of this road traverses the largest administrative region in the country: Region 9, the Upper Takutu-Upper Essequibo region, the focal area of this study.

Generally referred to as 'the Rupununi' (Fig. 1), Region 9 covers 3,336,095 ha and is home to several threatened species and key habitats, such as protected areas, Important Bird Areas, and Indigenous titled lands with nearly 24,000 inhabitants (Guyana Bureau of Statistics, 2016). The landscape includes a mosaic of savannas and wetlands, gallery forests, lowland primary forest, and forested mountains up to an elevation of 1070 m. During the major rainy season, from May to September, much of the savannah and riparian forests flood, connecting the Region's Essequibo and Rupununi Rivers to the Amazon watershed.

The Rupununi Region has two mayor roads: 1. the Lethem-Surama Road, along the GTLR starting at the border of the Iwokrama reserve, and 2. the Lethem-Aishalton Road, which connects the GTLR with the Indigenous village Aishalton and a major mining area - Marudi - in the Deep South of the Region (Fig. 1). All roads in the region are currently constructed of a mix of laterite and sand that requires annual maintenance following the rainy season.

2.2. Species prioritization

In a desktop analysis, we compiled a list of vertebrates occurring in the habitat bordering the GTLR (Hollowell and Reynolds, 2005). The project considered terrestrial, arboreal, and semi-aquatic species, as well as representative bird species. These species were initially prioritized based on IUCN conservation status, CITES category, and existing stakeholder-based species prioritization for Region 9 published in gray literature (Conservation International, 2002; Fredericks et al., 2016; Pierre and Paemelaere, 2018). Species with international conservation concern (IUCN, CITES) were considered because they are the species most likely to be negatively affected by the road through secondary impacts from increased access, such as hunting for meat or trade, rendering them potentially very sensitive to road impacts overall. Local prioritization, on the other hand, considered the importance of species in terms of protein sources, source of income from wildlife trade, tourism and cultural practices. From this prioritized list, a selection of species was considered for detailed analysis based on a species crossing guild classification to cover different structural needs.

2.3. Species crossing guilds

To predict the type of impact the roads would have on the priority species (mortality or barrier effect), we applied Jacobson et al. (2016b) crossing guilds model. The model predicts how a species will respond to the road with changing traffic volume and speed based on basic ecological knowledge of the species. We also incorporated an evaluation of obligate habitat features for the priority species, including cover obligates (requiring vegetation cover to cross), openness obligates (requiring open line of sight to cross), and semi-aquatic obligates, as well as medium and large generalists, who require only that structures are adequately sized to permit passage based on the animal's size (Kintsch et al., 2015). Evaluations were based on species habitat use combined with data from crossing structure research (Gonzales-Gallina et al., 2018). The resulting classification grouped species based on their mitigation strategy needs and is available as supplementary information (Supplementary information Table S1). This information was used in this case study to evaluate the potential of existing traffic bridges and culverts to function as underpasses at the identified priority sites.

2.4. Landscape analysis I: expert-based model

To define locations where mitigation measures would be necessary, we defined the most likely areas where priority species might be approaching and potentially crossing the road with a landscape connectivity analysis for Region 9 that predicted wildlife movement probabilities. This connectivity analysis was conducted in the software CIRCUITSCAPE 4.0, using core areas and a resistance-to-movement matrix (RM) . We considered the following habitat attributes: forest cover, distance to forest, water, villages and roads, and slope (Table 1). For these attributes, we selected satellite images with <20% clouds from the United States Geological Survey (USGS) and classified landcover into forest and savanna, at a resolution of 10 m per pixel. Details on how each layer was generated and the sources used are available as supplementary information (Supplementary information Table S2).

As core areas in the landscape connectivity model, we used forested patches larger than 2050 ha, which were considered to be important forest remnants (Magioli et al., 2013; Shah and Mcrae, 2008). Our analysis also included species inhabiting savanna. Nevertheless, we did not use savanna as core areas for these species for two reasons: 1. savanna or open habitat is not distinguishable from deforested land in satellite images, and deforested land does not hold the same ecological values for these species as natural savanna; 2. these species use forest patches and forest edges as essential elements in their habitat.

The RM represents the relative level of resistance that each of the landscape categories of the habitat attributes has on the species' movement. This was based on expert opinion, considering data from the literature and author expertise (Clevenger et al., 2002). Authors of this paper agreed on a score between 1 and 99 for each of the landscape categories, where 1 was given to the most suitable areas showing no resistance ('ideal habitat'), and 99 to those unsuitable areas that impose nearly complete resistance to the species' movement. Additionally, the authors assigned a weight to each of the variables, representing how

Table 2
Crossing guilds and their structural needs to be willing to cross an under-or overpass based on Kintsch et al. (2015). Multiple guilds may have to use a single crossing structure, and single structures can be fitted to meet requirements of multiple guilds.

Level	Require	Structural Requirements					
		Description crossing structure	Height[1,*]	Width[2,*]	Vegetation inside	Vegetation at entrance	Bottom surface/ water
General	Medium	Underpass with sufficient height for animal size;	>1.5 m	Stream + dry	NA	NA	Dry
	Large	overpass	>3.0 m		NA	NA	Dry
Specialist	Canopy	Ropes or cables over the road; overpasses with natural vegetation; touching canopies (least cost); viaducts with natural vegetation underneath	NA	Minimal	(Natural)	NA	NA
	Aerial	Very high underpasses (viaducts); *posts or fences that guide fauna high enough over traffic.*	>6 m	NA	NA	NA	NA
	Other	Crossing structures adopted to specific needs	To be evaluated on a per case basis				
Obligates	Openness	Large open underpasses with clear line of sight (nothing blocking entrances); dry, natural surfaces; overpass	>3.0 m	Stream + dry	NA	Limited to permit open line of sight	Dry, natural
	Cover	Natural vegetation at entrances, and inside larger; dry natural surface; overpass with vegetation cover	<1.5 m >1.5 m	Stream + dry	NA Natural; cover (logs, rocks, vegetation)	Natural	Dry, natural
	Semi-aquatic	Water flow through underpass or near entrances; overpass with water on or near structure	$>$ Body size	Stream	NA	NA	Ideally water flow or nearby water source

[1] Height may vary based on species in the area, but is assumed to be the height of the target species with an additional margin for easy passage.

[2] The width of the underpassage is really the length of the bridge or the diameter of the culvert. Many terrestrial species will require that there is a dry area along the stream (stream + dry), to be evaluated at the time of typical maximum level water height.

[*] The length of the passage (road width) should also be considered. A general rule is: the shorter (<10 m) the more species will be able to use the structure. For avoiders (Jacobson et al., 2016a, 2016b), length must be minimized, and natural habitat must be abundant on both sides of the road. Fencing may have to be considered after construction for other behavioral response groups, particularly if roadkill becomes a problem.

important they are for facilitating or restricting movement across the landscape. For example, a higher weighted value was given to the distance to water bodies attribute for semi-aquatic species than for terrestrial ones; regardless of the resistance value for each of the categories. The scores and the weighted values used in the RM matrix for each species are available in supplementary information Table S3.

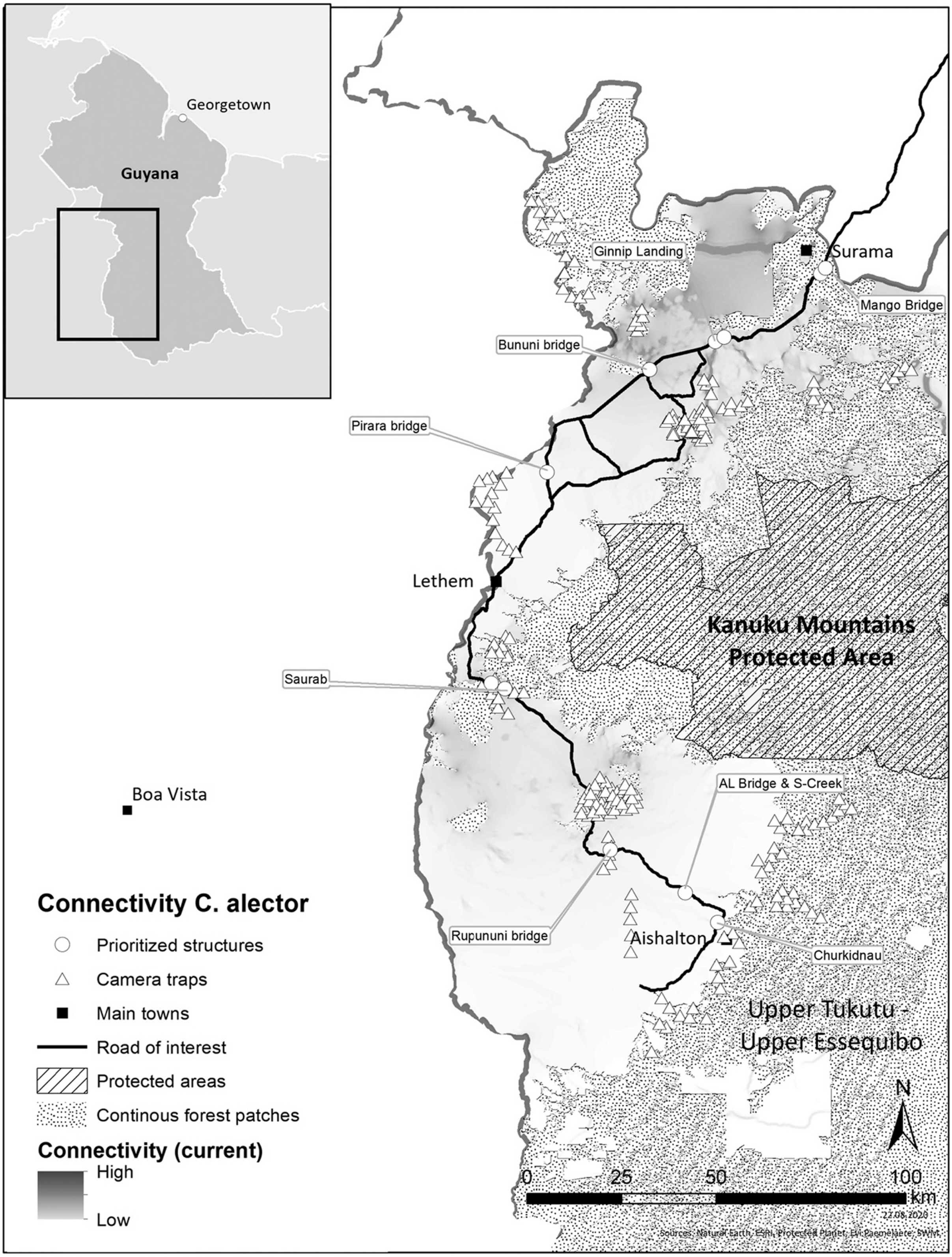
2.5. Landscape analysis II: expert-based model's validation

Expert-based RM is a subjective method, and while it has been shown to be reliable, ideally it should be validated by data when available (Zeller et al., 2012). To do so, we modeled the habitat use of four focal species using single-species, single-season occupancy models (MacKenzie et al., 2002), based on data from Hallett et al. (2019) and additional unpublished observation data obtained from camera-traps deployed at 205 sites across the region between 2011 and 2019. The purpose of these models was to determine the preferred habitat types of certain species at the study site and to identify the variables that influence such preference, thus validating the selection of variables in the RM. The focal species included in the model validation were those priority species for which sufficient field data were available: the black curassow (*Crax alector*), lowland paca (*Cuniculus paca*), giant anteater (*Myrmecophaga tridactyla*) and jaguar (*Panthera onca*). Species detection histories were restricted to 120 days to meet the closure assumption, and occupancy probability being understood as probability of use (MacKenzie et al., 2004, 2006; MacKenzie and Royle, 2005).

For each of the species, we used sampling effort as the detection covariate the, defined as the number of days that the camera trap was active; and ran occupancy models for all corresponding combinations of habitat covariates. The habitat covariates used were: slope (SLO), proportion of forest cover (GFC75), distance to nearest forest patch (DFor), distance to nearest water source (DWat), distance to nearest village (DVill), and distance to nearest road (DRoad). Next, we identified the important habitat-use covariate(s) for each species, based on the Akaike Information Criterion (AIC) and the estimated summed model weight values. This was done using the R packages “unmarked” (Fiske and Chandler, 2011), “AICcmodavg” (Mazerolle, 2017), and “MuMIn” version 1.43.6 (Bartoń, 2019). The code is available in Supplementary information – R-code. Afterwards, we built and ran Bayesian occupancy models for each species considering only the important covariates identified in the previous phase, using the JAGS (Plummer, 2003) and JagsUI packages (Kellner, 2018) in R 3.6.2 (R Core Team, 2017). We considered a covariate to have an effect on either detection or habitat use probability, if the 95% Bayesian credible interval (CRI) of the posterior untransformed coefficient excludes zero. Finally, we constructed a habitat use predictive map for each species based on the effect coefficients estimated in the previous step, using ArcGIS version 10.4 (https://www.arcgis.com/). If the priority sites identified by the connectivity model were situated within the habitat predictive model and if the variables detected to influence habitat selection were the same or similar to the ones used in the connectivity models, we considered the occupancy model to be supporting the expert-based RM.

2.6. Evaluation of traffic bridges as underpasses at key crossing sites

We evaluated all traffic bridges along the Surama-Lethem and Lethem-Aishalton roads, which included 19 and 20 bridges, respectively. Both roads also counted numerous pipe and box culverts, of which 79 were located and evaluated. The evaluation was based on the crossing guild frameworks (Jacobson et al., 2016a, 2016b; Kintsch et al., 2015) and considered the following characteristics: structure dimensions, sufficient height to permit up to the largest species (e.g. jaguar, tapir, giant anteater, deer), sufficient width to permit free water flow and dry area alongside the water body for most of the year where applicable, natural vegetation up to the bridge edges and ideally continuing underneath, presence of water, an open field of vision from one end to the other, and limited human activity under or near the bridge, particularly during dusk, dawn and night time. Next, we selected structures that were situated in key crossing areas as identified by the connectivity model to evaluate which bridges could serve as underpasses for priority species and those species with similar characteristics. A summary of structure requirements for each of the crossing guilds by Kintsch et al. (2015) is provided in Table 2.



22.08.2020

Sources: Natural Earth, ESRI, Protected Planet, Evi Paemelaere, SWM

Fig. 2. a Connectivity map for the black curassow (*Crax alector*) in the study area.
b Connectivity map for the lowland paca (*Cuniculus paca*) in the study area.
c Connectivity map for the giant anteater (*Myrmecophaga tridactyla*) in the study area.
d Connectivity map for the jaguar (*Panthera onca*) in the study area.

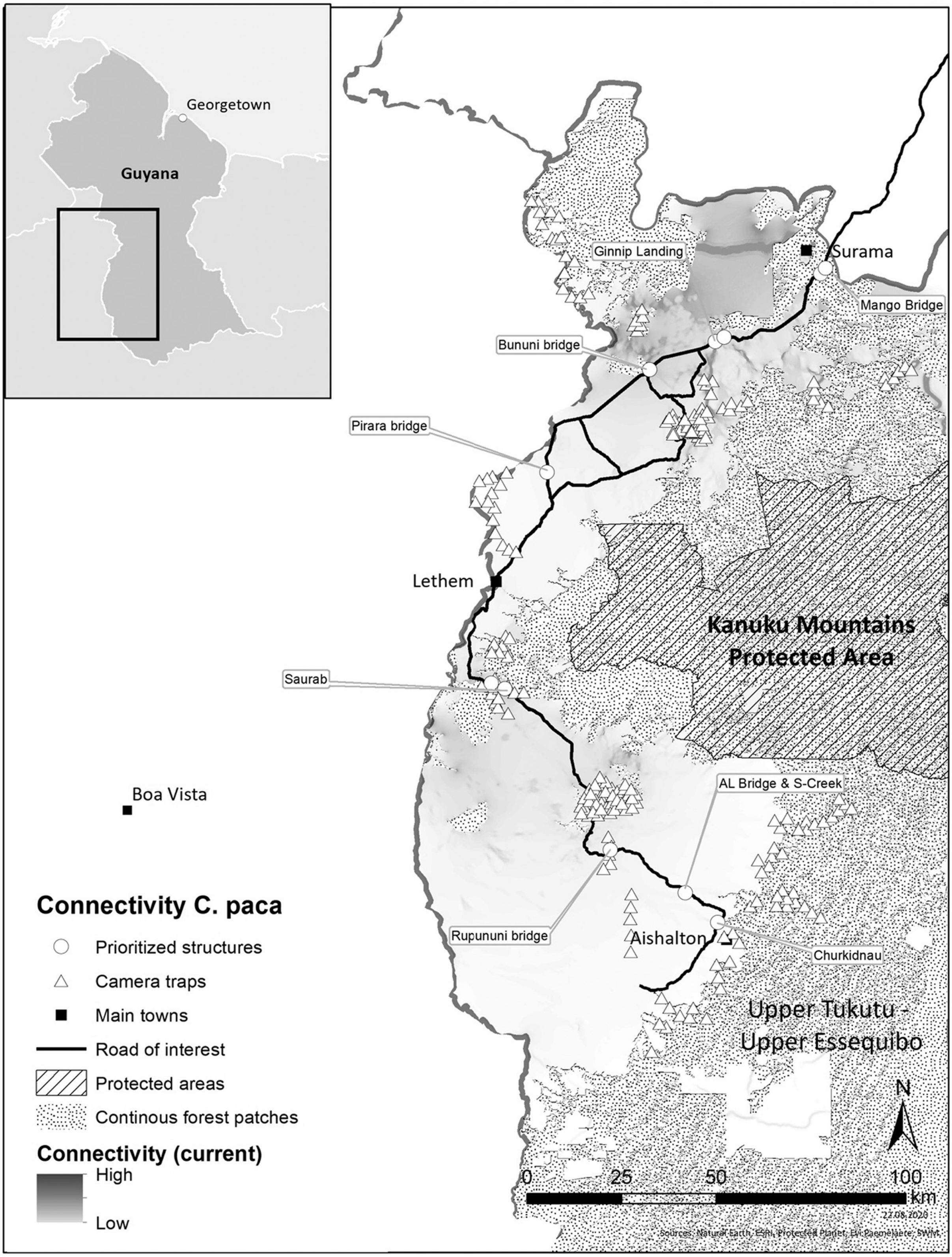


Fig. 2. (*continued*).

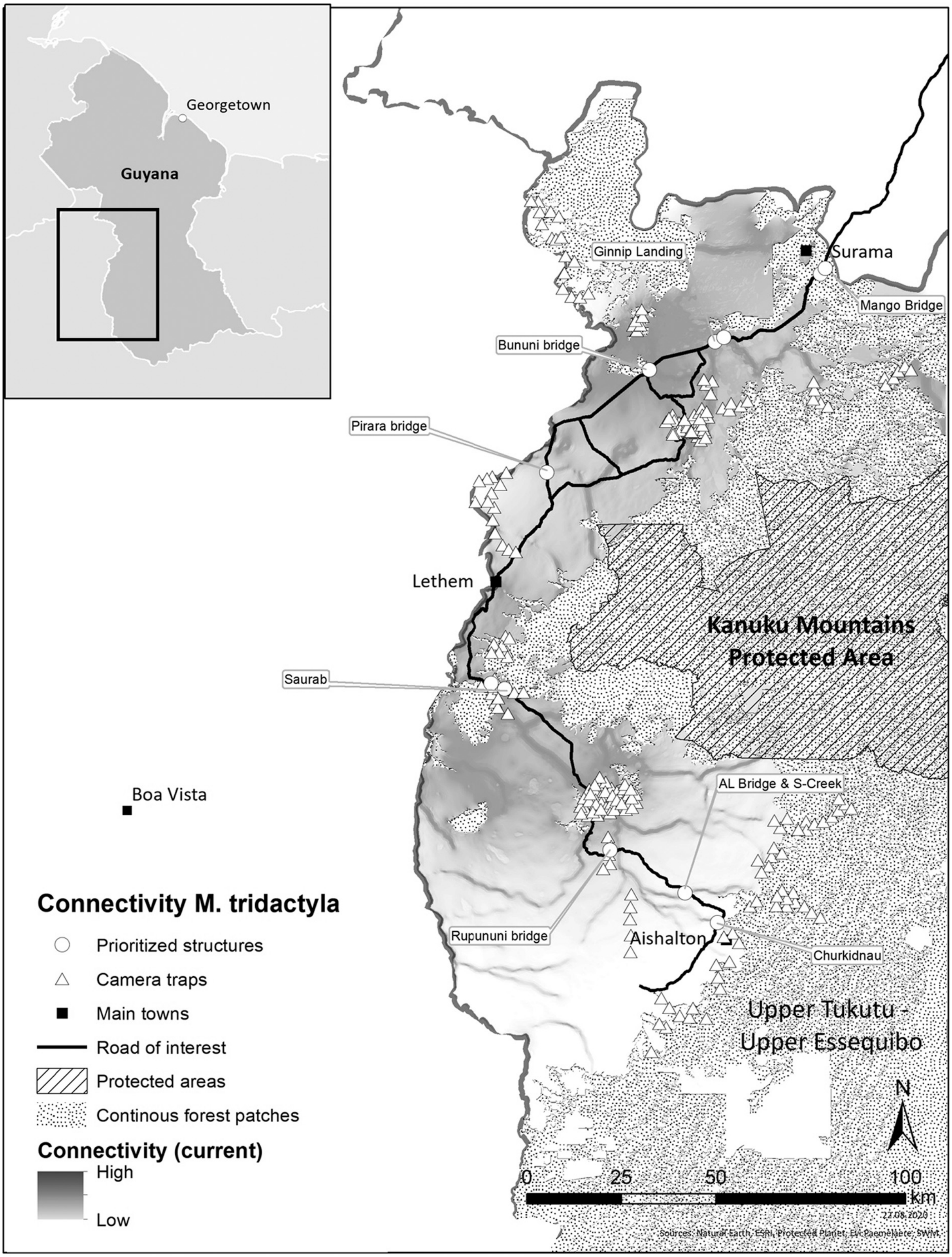


Fig. 2. (*continued*).

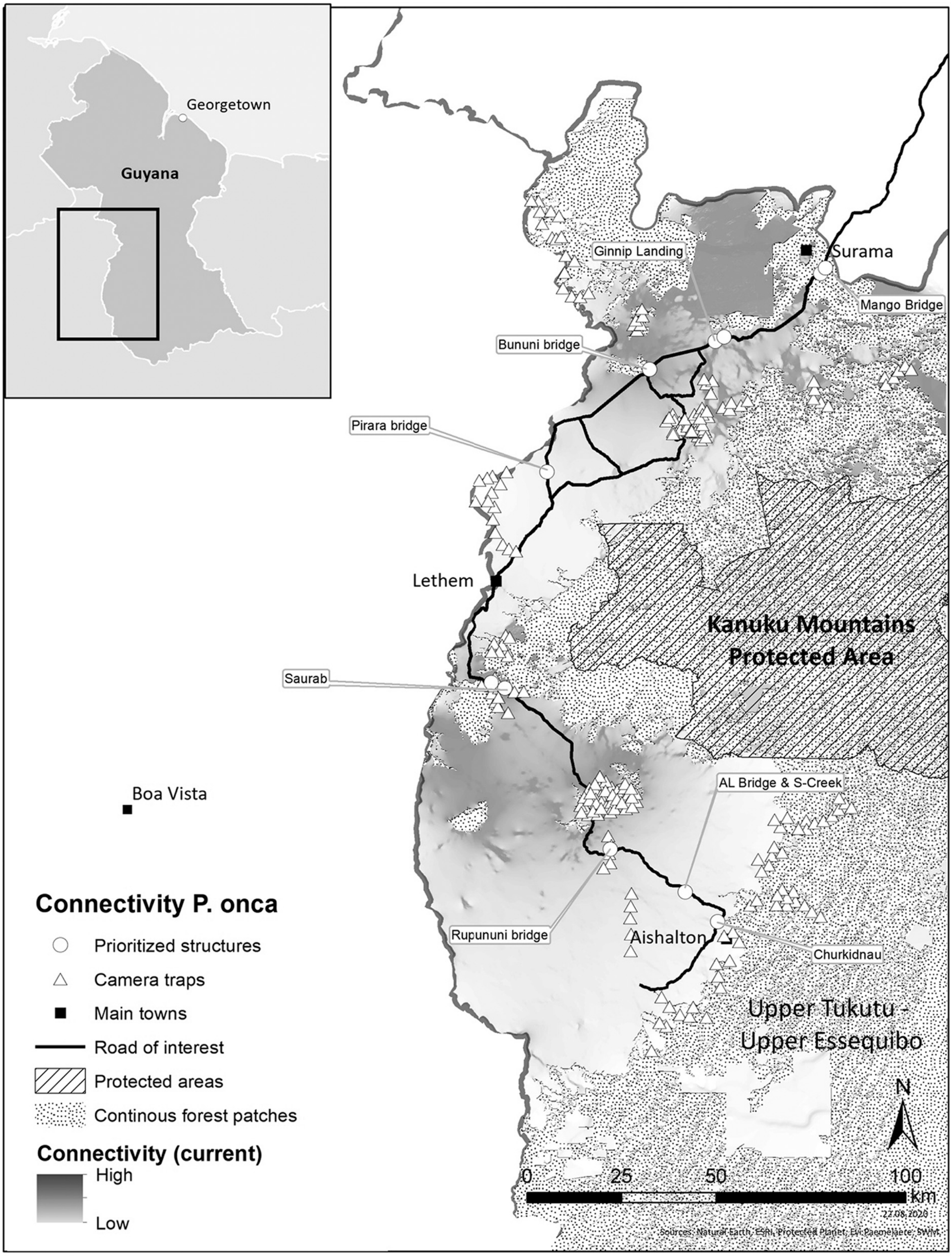


Fig. 2. (*continued*).

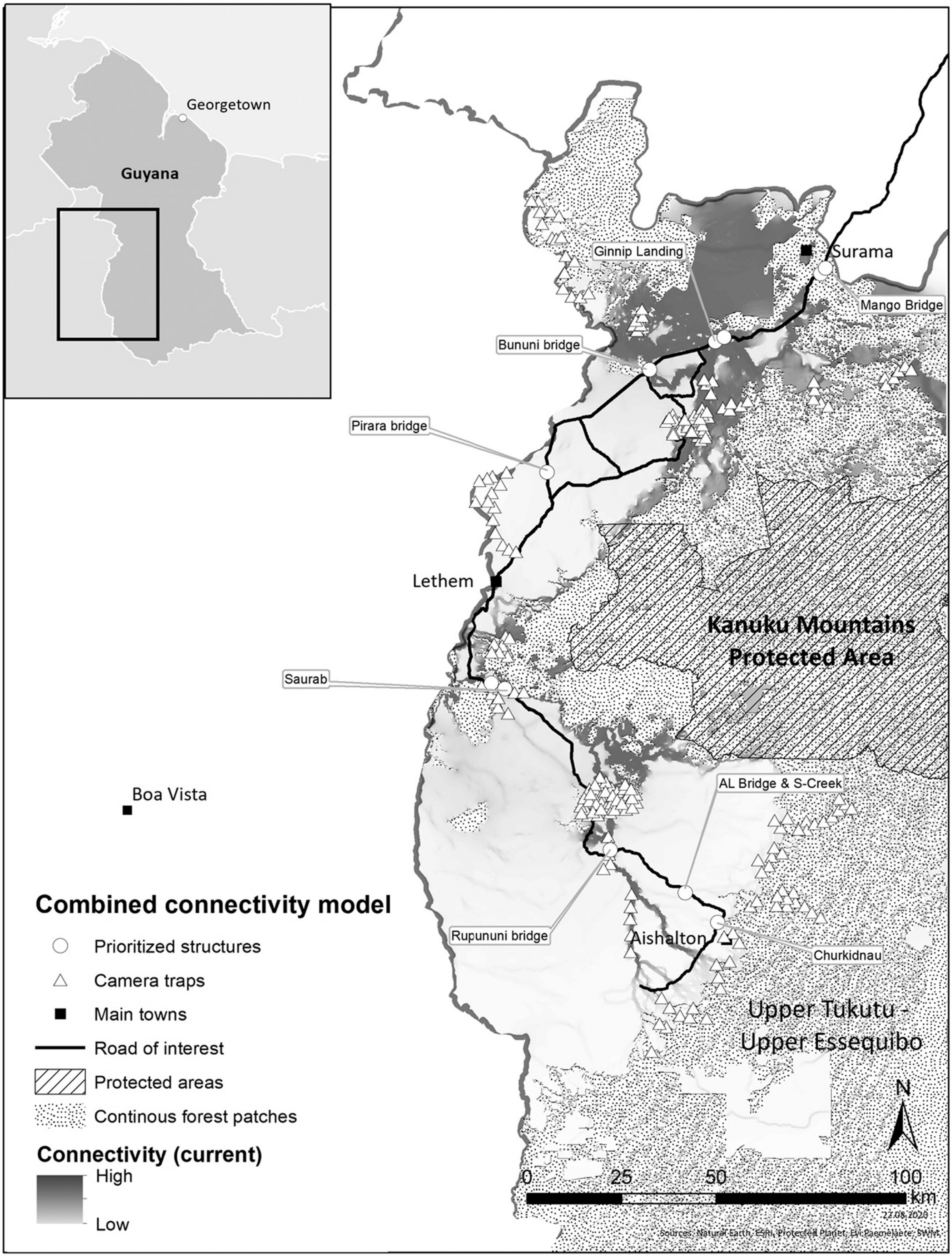


Fig. 3. Combined connectivity map for 17 priority species, indicating crucial road crossing points. Between Saurab and the Rupununi traffic bridges (3 bridges), there are only culverts, in spite of there being two areas of importance for wildlife connectivity across the road (also see Fig. 5).

Table 3

Parameter estimates for the latent variables, detection (p) and habitat-use probability (ψ), based on Bayesian single-species static occupancy models. Mean estimated coefficient (mean), standard deviation (SD), 95% Bayesian credible interval (95% CRI), Gelman-Rubin (R-hat) statistic, and effective sample size (n.eff). Among detection covariates, effort (EFF) was the only observation variable tested and represented the number of days that the camera trap was active during each sampling occasion. Habitat use covariates included: proportion of forest cover (GFC75), distance to nearest forest patch (DFor), distance to nearest water source (DWat), distance to nearest village (DVill), and distance to nearest road (DRoad). In bold are depicted the parameters for which the 95% CRI excluded zero, representing those parameters that had an effect on either detection (p) or habitat-use probability (ψ), for each of the study species.

Crax alector						
	Parameter	Mean	SD	95% CRI	R-hat	n.eff
p	**Intercept**	−2.100	0.490	−3.102 to −1.170	1.000	13,230
	EFF	0.107	0.034	0.042 to 0.177	1.000	11,189
ψ	**Intercept**	−1.558	0.807	−3.314 to −0.194	1.000	11,054
	GFC75	0.884	0.283	0.367 to 1.480	1.000	46,173
	DFor	−6.730	2.911	−13.100 to −1.864	1.000	12,083
Cuniculus paca						
	Parameter	Mean	SD	95% CRI	R-hat	n.eff
p	**Intercept**	−1.677	0.501	−2.698 to −0.731	1.000	60,000
	EFF	0.147	0.043	0.065 to 0.235	1.000	60,000
ψ	**Intercept**	−0.511	0.183	−0.873 to −0.153	1.000	46,207
	GFC75	1.108	0.238	0.661 to 1.596	1.000	60,000
	DVill	0.730	0.198	0.361 to 1.136	1.000	60,000
	DRoad	−0.384	0.223	−0.836 to 0.037	1.000	28,709
Myrmecophaga tridactyla						
	Parameter	Mean	SD	95% CRI	R-hat	n.eff
p	**Intercept**	−1.966	0.462	−2.901 to −1.095	1.000	9124
	EFF	0.064	0.032	0.003 to 0.129	1.000	9713
ψ	Intercept	0.125	0.347	−0.446 to 0.903	1.000	30,757
	GFC75	−0.683	0.330	−1.386 to −0.087	1.000	60,000
	DVill	0.543	0.296	0.028 to 1.192	1.000	60,000
	DFor	−0.872	0.559	−1.735 to −0.013	1.001	14,407
	DRoad	−0.800	0.279	−1.384 to −0.293	1.000	37,144
Panthera onca						
	Parameter	Mean	SD	95% CRI	R-hat	n.eff
p	**Intercept**	−3.137	0.787	−4.781 to −1.676	1.000	60,000
	EFF	0.048	0.053	−0.047 to 0.160	1.000	60,000
ψ	Intercept	0.780	1.441	−1.015 to 4.442	1.000	19,772
	DFor	0.104	2.543	−3.051 to 7.317	1.000	38,951
	DWat	0.973	0.891	−0.099 to 3.383	1.001	3979

3. Results

3.1. Expert based resistance to movement model

We selected 17 species with different habitat requirements and belonging to different crossing guilds to complete the spatial analysis (Supplementary information – Table S1). Key connectivity zones and potential road crossing points were mapped for all species individually. Examples of these maps for the four species used in the habitat model are provided in Figs. 2 a-d. A combined connectivity map for all priority species was produced to identify high priority sites for implementation of wildlife friendly road construction (Fig. 3).

3.2. Expert based model evaluation

We modeled habitat use of the black curassow, lowland paca, giant anteater, and jaguar based on Bayesian hierarchical occupancy models using camera-trap data. For the black curassow, the predicted proportion of occupied sites was 0.52 (95% CRI 0.46–0.58) and site use probability was suggested to be positively correlated to the proportion of forest cover and proximity to forest cover (Table 3, supplementary information Table S4). For the lowland paca the predicted proportion of occupied sites was 0.40 (95% CRI 0.37–0.43), and site use probability was positively related to both proportion of forest cover and distance to villages (Table 3, supplementary information Table S4). The giant anteater was predicted to use 52% of the sampled sites (95% CRI 0.44–0.62) and its site use probability was higher in areas further from forested areas, with low proportion of forest cover, closer to roads, and further from villages (Table 3, supplementary information Table S4). For jaguar, the best model predicted that the species used 58% of the sampled sites, while its site use probability was suggested to be constant along the study area, with no apparent effect from any of the habitat covariates tested (Table 3, supplementary information Table S4). Through predictive mapping from this analysis, we visualized the species' habitat use as shown in Fig. 4.

3.3. Key crossing points and traffic bridges

At priority crossing sites indicated by the connectivity model, we determined the presence of bridges and culverts and identified those that could serve as underpasses for wildlife based on their crossing guild and habitat requirements (Fig. 3, Table 4). Along the Surama-Lethem road, we identified five areas with eight bridges that could serve as underpasses. Along the Lethem-Aishalton road we also identified five areas, with seven bridges, as well as two areas where currently only culverts are installed (Fig. 5). An evaluation of each of these structures is provided in Table 4.

4. Discussion

We applied a resistance model to map movement corridors for priority species and to identify key sites along major roads where measures should be put in place to ensure safe passage of wildlife, and then selected and evaluated traffic bridges within those key sites that could serve as underpasses as part of a wildlife friendly road strategy. To verify that the simple resistance model could be used in road planning and impact mitigation, we compared the output with a habitat use model derived from field data. Overall, the expert-based resistance model resulted in a more conservative identification of key sites for wildlife connectivity compared to the habitat use model, because not all variables considered for connectivity were found to be significant for habitat use of the focal species at the site. An overview of the steps and considerations as discussed here is provided in Fig. 6.

The habitat model indicated that forest cover is an important predictor in species occurrence, showing a significant positive relationship for lowland paca and black curassow, and a significant negative association for the savanna-dwelling giant anteater. The importance of forest cover has been demonstrated for these and other species throughout their range (e.g., Boron et al., 2019; Hallett et al., 2019; Nagy-Reis et al., 2017; Thompson et al., 2020), justifying the emphasis (high weight) assigned to this variable in the expert connectivity model. We also found that both the paca and anteater were more likely to occur further from villages, which in case of the paca may be associated with nearby hunting (Ferreguetti et al., 2015; Read et al., 2010). Such effect was not found by an earlier study within the same region (Hallett et al., 2019), but has been detected at other sites (Ferreguetti et al., 2019; Motta Lessa et al., 2017; Semper-Pascual et al., 2020; Thompson et al., 2020). Contrary to our predictions, giant anteaters were more likely to occur near roads, thought this trend has been observed in other sites where unpaved roads are prevalent (Gouvea, 2020; Semper-Pascual et al., 2020; Versiani et al., 2021). Anteater occurrence near roads could increase roadkill risk for this species, considering they are categorized as "non-responders" (Cunha et al., 2010; Diniz and Brito, 2013; González-Suárez et al., 2018; Silveira Miranda et al., 2017) and the expansion of road networks is known to decrease habitat suitability for this species (Pinto et al., 2018).

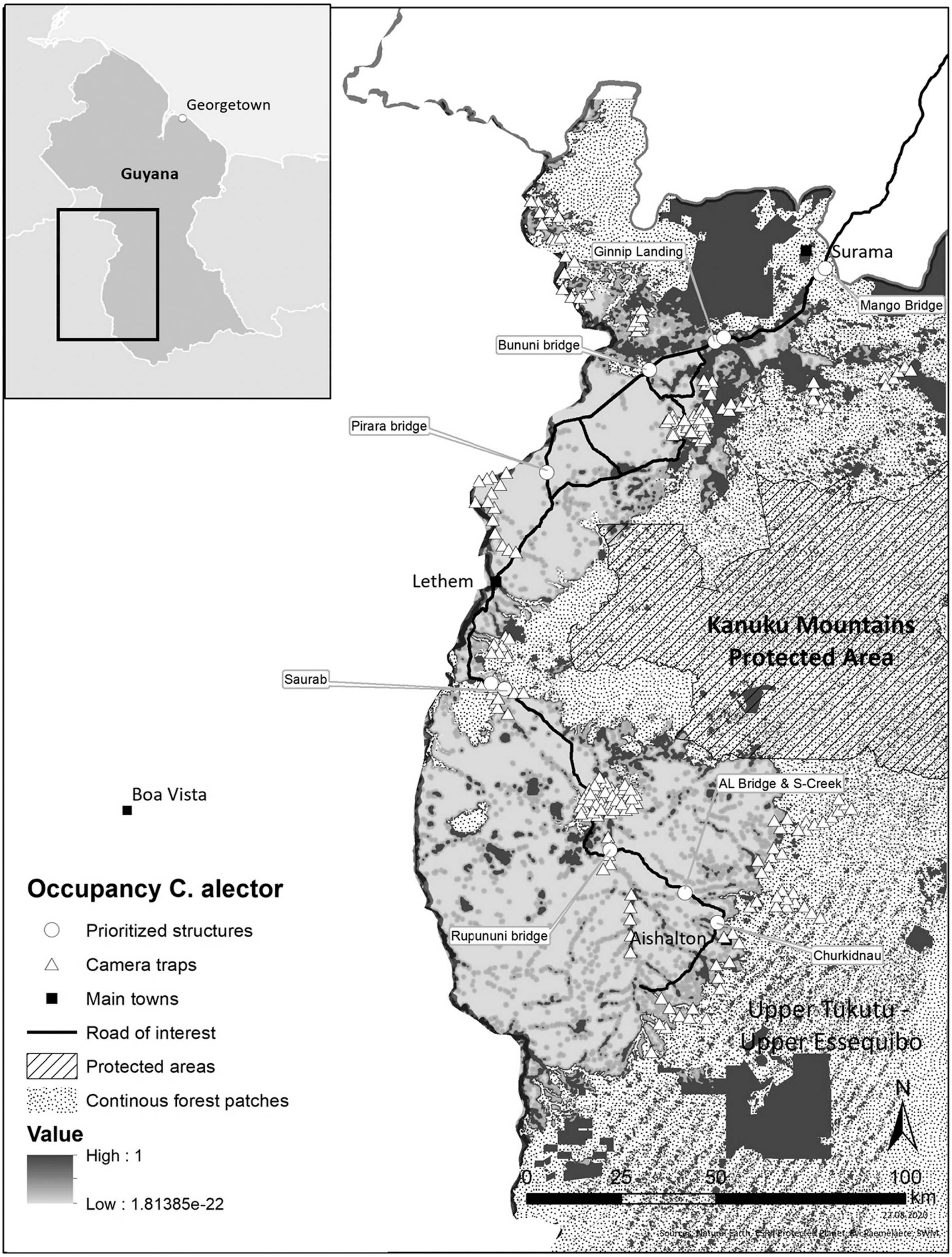


Fig. 4. Habitat use maps for the black curassow (a), giant anteater (b), and lowland paca (c). For the jaguar, none of the habitat attributes showed to be significant, resulting in a predicted distribution throughout the entire landscape.

Jaguar habitat use was not affected by any of the variables in our model for our site, corresponding with earlier findings (Hallett et al., 2019). Researchers from across the jaguar's range have associated jaguar presence with a variety of variables, such as elevation, vegetation cover, distance to water, presence of protected areas, human activities, roads, and prey abundance and richness (Anile et al., 2020; Arroyo-arce et al.,

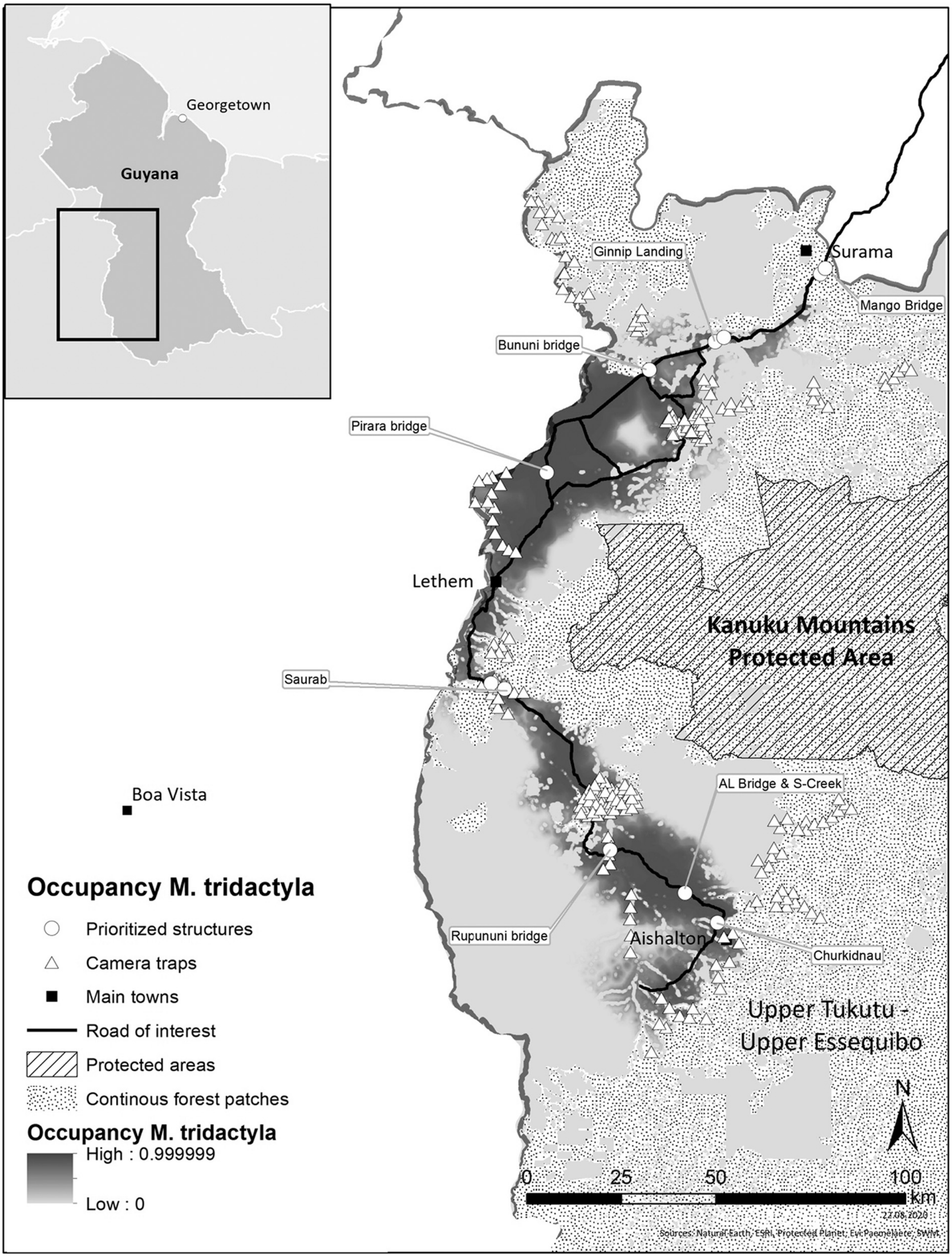


Fig. 4. (*continued*).

2014; Espinosa et al., 2018; Jędrzejewski et al., 2018; Rabelo et al., 2019; Sollmann et al., 2012; Thompson et al., 2020; Zeller et al., 2011). Moreover, male and female jaguars are known to respond differently to roads, with females avoiding and males favoring roads (Conde et al., 2010). The variables affecting jaguar distribution clearly differ between sites, which may be due to the scale at which their habitat use is being assessed (Zeilhofer et al., 2014), and the amount and distribution of modified landscapes and human activity across the study area and beyond (e.g., Thompson et al., 2020). Considering the relatively intact habitat of our study site, these variables may not yet affect jaguar habitat

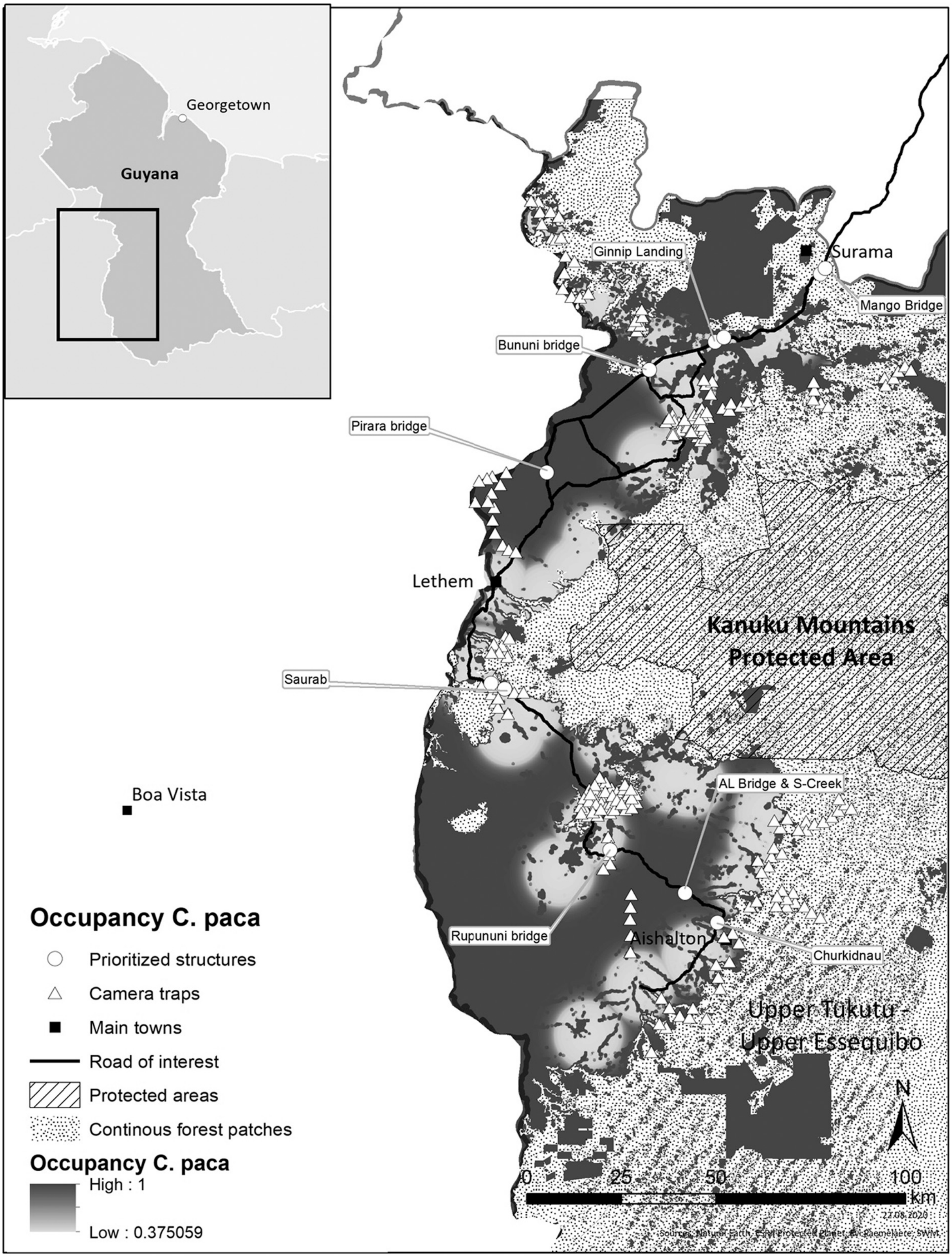


Fig. 4. (*continued*).

use. We did not incorporate prey availability, seasonal variation or sex differences, as this is data intensive and beyond the scope of our prioritization exercise. Rather, we focused on easily available spatial data, as have been used in landscape-level conservation planning (Zeller and Rabinowitz, 2011).

Both connectivity and habitat use (occupancy) models have been used in predicting population connectivity (Fabrizio et al., 2019), with connectivity models corresponding well with movement paths from GPS tracking or genetic markers (Keeley et al., 2017; McRae and Beier, 2007; Reed et al., 2017; Vanthomme et al., 2015). We applied habitat use

Table 4

Bridges along the Surama-Lethem-Aishalton road at key crossing sites identified by the expert-based connectivity model. Bridges situated in the same movement path are grouped between dotted lines. x: applies, (x): may apply, –: does not apply. Functionality indicates whether small generalists (gen_S), large generalists (gen_L), semi-aquatic (semi-aqua) species and certain habitat specialists (Specialists) could pass under the bridge. Openness specialists require clear entrance and exits ways; Cover specialists require vegetation under the bridge; Aerial specialists require high bridges. Recommendations: L: bridge needs to be longer (=wider underpass) for free water flow to reduce structural damage and to provide a dry area for wildlife to walk under the bridge; H: bridge should be higher to permit passage of large species; HA: human activity needs to be controlled (e.g. vehicle access, washing, fishing, hunting); MA: old bridge materials need to be removed; Veg: requires natural vegetation under and near the bridge; canopy: maintain existing roadside canopy/touching canopy for arboreal species or create arboreal passage. Species: HH: Hydrochoerus hydrochaeris; MT Myrmecophaga tridactyla; OC Odocoileus cariacou; PB: Pteronura brasiliensis; SA: Sporophila angolensis.

	Location		Functionality as a wildlife underpass						Recommended Improvements					
Name	Y	X	Gen_S	Gen_L	Semi-aqua	Specialists	Wet	Priority species passage	L	H	HA	MA	Veg	Other
SURAMA – LETHEM ROAD														
Pirara	3.625	−59.677	X	X	X	Openness, cover, (aerial)	–	Semi-aquatic (PB, HH), Savanna (OC, MT)			X	X		
Bunununi	3.870	−59.434	X	–	X	Cover	–	All except SA	X		X	X		
Ginnip landing	3.936	−59.277	X	–	–	Openness	–	Savanna species (OC, MT, SA)	X	X				
Yak3	3.947	−59.256	X	X	–	Openness	–					X		
Yak2	3.947	−59.259	X	X	–	Cover, openness	–					X		
Bush mouth	4.059	−59.059	X	(X)	X	Openness	–	Forest species, semi-aquatic species.	X			X	X	Canopy
Junction bridge	4.098	−59.027	X	–	X	Cover	–		(X)			X	X	Canopy
Mango bridge	4.112	−59.016	X	X	X	(Openness), cover	–						X	Canopy
LETHEM – AISHALTON ROAD														
Saurab	3.114	−59.776	X	X	X	Openness; Cover	x	All			X			
Rupununi_M	2.729	−59.526	X	X	X	Openness; Cover; Aerial	–	All			X			
Rupununi_S1	2.727	−59.523	X	X	–	Cover	–	All						
Rupununi_S2	2.728	−59.522	–	–	X	*None*	–	Only (semi-)aquatic						

models merely to evaluate the variables from the connectivity model and to ensure that connectivity paths fell within the local habitat range. Considering the predictive nature of both models, more research is needed to validate the accuracy of connectivity models for a wide variety of species. Where possible, such empirical evidence should be collected in impact studies (Beier et al., 2008; Zeller et al., 2018), although in EIAs, this is generally not feasible. Road kill data have also been used to evaluate the predictions of such models (Cerqueira et al., 2021; Fabrizio et al., 2019), but these data must be interpreted with caution, considering the behavioral framework (Jacobson et al., 2016a, 2016b; Zimmermann Teixeira et al., 2017). Furthermore, they can only be considered after road construction. Predictive models have the advantage of guiding mitigation at the planning phase, and, unlike empirical data, they allow for scenario modeling of road alignment, traffic conditions, secondary road network expansion, or other developments promoted by the change in accessibility. Moreover, combined with the species evaluation frameworks, they can be used to decide not only on the location but also on the types of bridges and culverts to be built.

The selection of attributes and assigned values are essential to the accuracy of the expert-based connectivity model, and, as exemplified by our focal species, it is clear that the importance of certain attributes as determined in the occupancy model may vary across the species' range. The significance of attributes may depend on the scale of the study (Pitman et al., 2017; Sunarto et al., 2012), and be affected by the level of human disturbance present at the time of the research (Thompson et al., 2020). This explains why the expert-based connectivity model may be more conservative compared to the habitat model in identifying key crossing sites, particularly in our case study at a site with limited human disturbance. Reed et al. (2017), also found that expert-based models perform well compared to empirical data but may overestimate the impact of roads, which adheres to the precautionary principle of conservation.

The weights and scores we assigned to the attributes and their categories can be adopted for other studies with the same species. Nevertheless, local circumstances that may affect key ecological or behavioral traits must be considered. For example, scores for distance to roads may differ based on the current or future road condition to be evaluated, with considerations for pavement, road width, and traffic volume, for which the framework by Jacobson et al., 2016a, 2016b can be used as a guide. Also, study areas with high hunting pressure may increase the resistance intensity of some variables, such as proximity to human settlements and roads (Abrahams et al., 2017; Espinosa et al., 2018).

Furthermore, we did not consider human population density in our models because human population density in the Rupununi Region of Guyana is <1/km2 and this is not expected to change in the next few decades, unlike studies conducted at sites where dense human populations are having a greater impact on wildlife (e.g., Rabinowitz and Zeller 2010). We did include distance to villages, because even low-density human presence has some impact on wildlife, particularly through hunting within a 6 km radius of the village (Read et al., 2010). In study sites with larger towns or cities, it would be good to add human population density. Altitude was also not included here, because within our study area, altitudes are <1000 m and are no limitation for any of the species.

When applying this method in EIAs, it must be noted that our method focused on resolving connectivity issues caused by the road, and would not address certain species-specific impacts that could also affect the population up to more than a kilometer away from the road – the 'road-effect zone' (Forman and Deblinger, 2000), for example, hindered intra-specific communication due to road noise (Parris and Schneider, 2009), or reduced breeding areas or nest success due to filtering light from the road corridor into the forest (Senzaki et al., 2020). Second, it must be recognized that some species will have highly specific needs, which may be identified through the behavioral framework (Jacobson et al., 2016a, 2016b), or in resistance model mapping where they would show limited movement corridors. In locations where such species-specific actions are required, we recommend the use of recent field data for occupancy modeling similar to our verification process with inclusion of factors

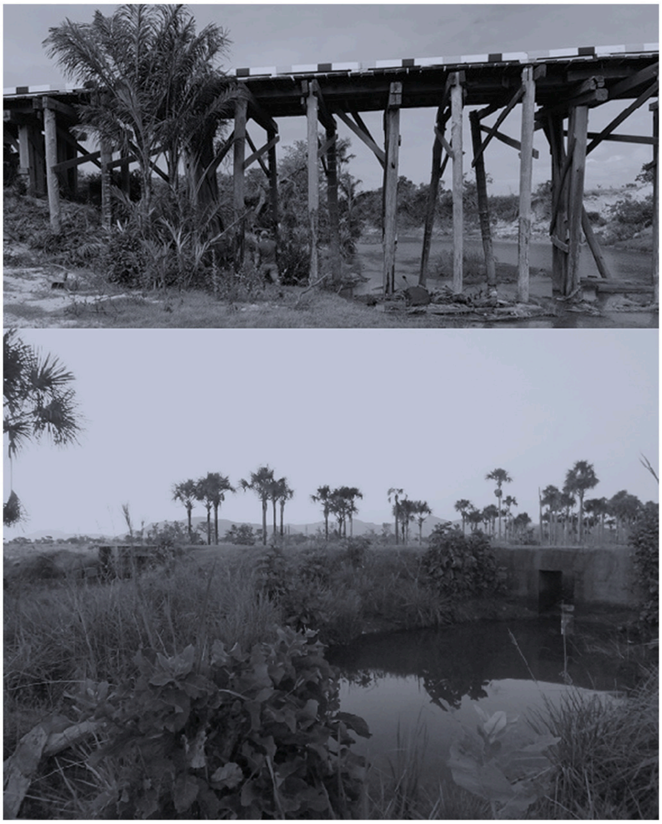


Fig. 5. Structures at priority wildlife connectivity sites across main roads. Top: Pirara bridge, situated at one of the identified priority sites for wildlife connectivity along the GTLR. The bridge is sufficiently high and wide, permitting free water flow and dry area through most of the year; human activity under the bridge, however, may affect its functionality. This bridge will clearly be upgraded in the future, and the new structure should maintain its current dimensions and presence of vegetation. Bottom: One of the priority connectivity sites along the Lethem-Aishalton Road. Here, only two culverts are present, not permitting free water flow or easy passage of aquatic and terrestrial wildlife. A bridge would be a wildlife friendlier option here. Evaluation of structures is clearly an essential component of EIAs.

such as seasonality, species interactions, gender effects and resource availability as applicable to the species at hand. For the purpose of a general prioritization exercise, however, common landscape and human impact variables from freely available spatial data applied to a broad range of species performed well. Third, although our method can make recommendations for road building and post-construction management based on the species frameworks we applied (e.g., reduce human access to areas under bridges, large stretches of undisturbed habitat on either side of the crossing site, particularly for species classified as “avoiders”), follow-up verification of priority species use of the crossing structures is recommended. Additionally, monitoring of road kill should be considered to help avoid traffic accidents and population impacts, which may require additional measures, such as speed reducers or fencing (Ascensão et al., 2013; Rytwinski et al., 2016; Spanowicz et al., 2020).

Landscape and human impact variables, however, are subject to change over time, leading to changes in species presence and movement patterns (e.g., Semper-Pascual et al., 2020). Therefore, it is of utmost importance to consider the prioritization of wildlife crossings within the larger landscape, and to not only provide mitigation measures at the roadside, but also ensure that the same movement corridors remain intact to ensure that the measures remain effective long-term. Such movement corridors could incorporate carefully planned productive areas (e.g., Pardo et al., 2019), and predictive modeling based on a strategy similar to what we presented here could be applied in the decision making process. Moreover, any offset needs associated with development projects could incorporate these measures in the planning phase in an effort to ensure the long-term viability of the movement corridors associated with road impact mitigation measures.

In conclusion, we showed that expert-based species movement models are an excellent easy-to-apply tool in environmental impact assessments, requiring only freely available spatial data and general species knowledge from experts and the literature. Our case study exemplified its use in providing recommendations for modifications of traffic bridges and culverts of an existing road to improve its wildlife friendliness. Nevertheless, these models can be applied to any landscape level development planning, such as road improvements, road alignment planning, road network design, and general land-use development planning. Our method offers a low-cost assessment and a pro-active approach where mitigation measures can be applied during construction to help limit the need for expensive post-hoc measures. Inclusion of this simple process in EIA guidelines should be considered to ensure connectivity in EIAs (Karlsson and Bodin, 2022).

Funding

This research was carried out as part of the SWM Programme, an initiative of the Organization of African, Caribbean and Pacific States, which is funded by the European Union. The SWM Programme is implemented through a consortium partnership, which includes the Centre for International Forestry Research (CIFOR), the Food and Agriculture Organization of the United Nations (FAO), Wildlife Conservation Society (WCS) and the French Agricultural Research Centre for International Development (CIRAD). Additional funding for camera trapping was provided by the Jacksonville Zoo & Gardens Conservation Fund and the Ron Magill Conservation Scholarship. Funders had no role in the concept of the study, nor in the production of the manuscript, or the decision of publication.

Data availability statement

Data are available upon reasonable request from the corresponding author.

Author contributions

- Evi A.D. Paemelaere: Conceptualization of the project, coordination of part of the data collection, participated in decision on statistical analyses, wrote first draft of the manuscript, supervising the project.
- Angela Mejía: contributed to conceptualization of the project, contributed concepts of the spatial analyses involved, and executed the same. Drafted the methodology for the manuscript. Reviewed and edited drafts of the manuscript.
- Simón Quintero: conducted spatial analyses, contributed to the writing of the paper and edited drafts of the manuscript.
- Matt Hallett: designed and coordinated the mammal research project with camera trap data collection, and reviewed and edited drafts of the manuscript.
- Fernando Li: was head coordinator for implementation of the camera trap data collection for all subregions, contributed to research design, and assisted with data management. He was also the lead for the technical team in the evaluations of road structures.
- Asaph Wilson: coordinated camera trap data collection for two subregions (South and Deep South Rupununi), contributed to research design, and assisted with data management.
- Howard Barnabas: coordinated camera trap data collection for a subregion (North Rupununi), contributed to research design, and assisted with data management.

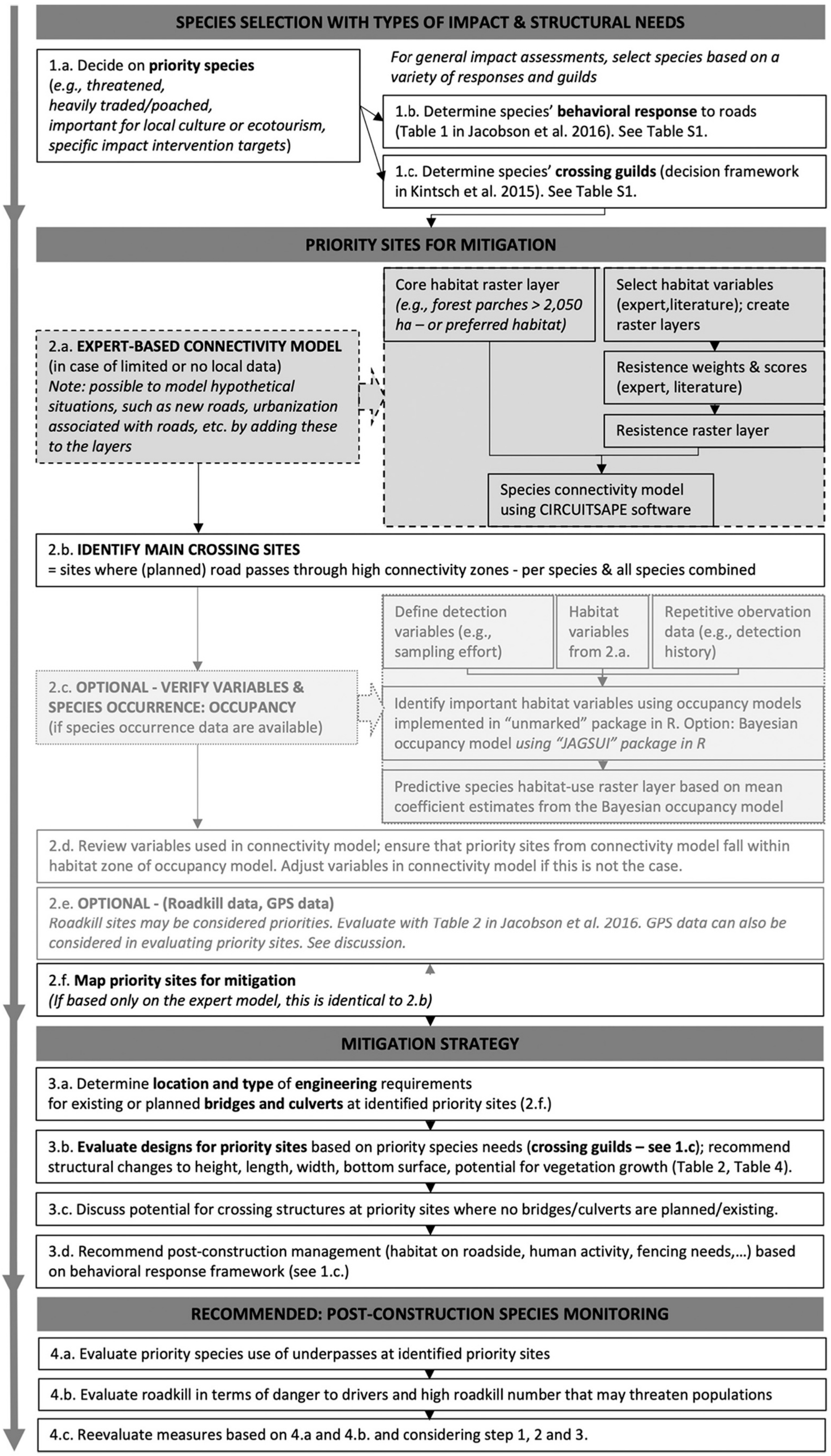


Fig. 6. Overview of the steps and considerations in this road impact mitigation strategy for wildlife friendlier roads.

- Andrew Albert: coordinated camera trap data collection for a subregion (South Pakaraimas), contributed to research design, and assisted with data management.
- Rhomayne Li: coordinated camera trap data collection for a subregion (Deep South Rupununi/Manari), contributed to research design, and assisted with data management.
- Leon Baird: coordinated camera trap data collection for one of the sites (Wichabai ranch), contributed to research design, and assisted with data management.
- Gerard Pereira: coordinated camera trap data collection for one of the sites (Karanambu Ranch), contributed to research design, and assisted with data management.
- Jeremy Melville: coordinated camera trap data collection for a subregion (Central Rupununi), contributed to research design, and assisted with data management.

Declaration of Competing Interest

None.

Data availability

Data will be made available on request.

Acknowledgments

We are grateful to the coordinating team O. David, A. Mahadeo, and N. van Vliet, who also provided feedback to earlier versions of this manuscript. We thank the team who assisted with the evaluation of the structures: L. Fredericks, J. LaRose, and J. Zammett and the team who made the collection of mammal data possible for this study, particularly F. Gomes, J. George, O. Hendricks, J. Lawrence, V. Gomes, N. Atkinson, A. Holland, R. Roberts, B. Duncan, J. George, B. Lawrence, H. Phillips, M. Mandook, A. Roberts, G. Bell, H. Clement, N. Mandook, S. James, M. David, D. DaSilva, Conrad Peters, M. Davis, M. Carter, A. Jackman, Q. DeFreitas, K. Spencer, and E. Gray. We are grateful to the Guyana Environmental Protection Agency, Ministry of Indigenous People's Affairs, Protected Areas Commission and the Kanuku Mountains Community Representative Group for issuing permission and permits to carry out this study. Lastly, we are ever grateful to the leadership and residents of Karasabai, Pai Pang, Tipuru, Taushida, Karabaiku, Kokshebai, Rukumuta, Rewa, Crashwater, Toka, Annai, Kwatamang, Kwaimatta, Yakarinta, Massara, Yupukari, Quatatta, Quarrie, St. Ignatius, Shulinab, Quiko, Katoonarib, Sawariwau, Shea, Maruranau, Awarwanau, and Aishalton villages, as well as Karanambu, Manari, Dadanawa, and Wichabai ranches for their overwhelming kindness, hospitality, generosity, cooperation, support, and participation, without which none of this study could have been carried out. Lastly, we thank the two anonymous reviewers who provided invaluable input into the earlier version of this manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.eiar.2022.107010.

References

Abrahams, M.I., Peres, C.A., Costa, H.C.M., 2017. Measuring local depletion of terrestrial game vertebrates by central-place hunters in rural Amazonia. PLoS One 12, 1–25. https://doi.org/10.1371/journal.pone.0186653.

Anile, S., Greenspan, E., Nielsen, C.K., 2020. Determinants of jaguar occupancy at the northern range edge. Mammal Res. 65, 667–677. https://doi.org/10.1007/s13364-020-00511-0.

Arroyo-arce, S., Guilder, J., Salom-Pérez, R., 2014. Habitat features influencing jaguar *Panthera onca* (Carnivora: Felidae) occupancy in Tortuguero National Park, Costa Rica. Rev. Biol. Trop. 62, 1449–1458. https://doi.org/10.15517/rbt.v62i4.13314.

Ascensão, F., Clevenger, A., Santos-Reis, M., Urbano, P., Jackson, N., 2013. Wildlife-vehicle collision mitigation: is partial fencing the answer? An agent-based model approach. Ecol. Model. 257, 36–43. https://doi.org/10.1016/j.ecolmodel.2013.02.026.

Ascensão, F., Kindel, A., Teixeira, F.Z., Barrientos, R., D'Amico, M., Borda-de-Água, L., Pereira, H.M., 2019. Beware that the lack of wildlife mortality records can mask a serious impact of linear infrastructures. Glob. Ecol. Conserv. 19 https://doi.org/10.1016/j.gecco.2019.e00661.

Bager, A., Fontoura, V., 2013. Evaluation of the effectiveness of a wildlife roadkill mitigation system in wetland habitat. Ecol. Eng. 53, 31–38. https://doi.org/10.1016/j.ecoleng.2013.01.006.

Barber, J.R., Crooks, K.R., Fristrup, K.M., 2010. The costs of chronic noise exposure for terrestrial organisms. Trends Ecol. Evol. 25, 180–189. https://doi.org/10.1016/j.tree.2009.08.002.

Bartoń, K., 2019. MuMIn: multi-model inference. R Package Vers. 1 (43), 6.

Beier, P., Majka, D.R., Spencer, W.D., 2008. Forks in the road: choices in procedures for designing wildland linkages. Conserv. Biol. 22, 836–851. https://doi.org/10.1111/j.1523-1739.2008.00942.x.

Benítez-López, A., Alkemade, R., Verweij, P.A., 2010. The impacts of roads and other infrastructure on mammal and bird populations: a meta-analysis. Biol. Conserv. 143, 1307–1316. https://doi.org/10.1016/j.biocon.2010.02.009.

Bennett, E.L., Milner-Gulland, E.J., Bakarr, M., Eves, H.E., Robinson, J.G., Wilkie, D.S., 2002. Hunting the world's wildlife to extinction. Oryx 36, 328–329. https://doi.org/10.1017/S0030605302000637.

Boron, V., Deere, N.J., Xofis, P., Link, A., Quiñones-Guerrero, A., Payan, E., Tzanopoulos, J., 2019. Richness, diversity, and factors influencing occupancy of mammal communities across human-modified landscapes in Colombia. Biol. Conserv. 232, 108–116. https://doi.org/10.1016/j.biocon.2019.01.030.

Brodie, J.F., Giordano, A.J., Ambu, L., 2014. Differential responses of large mammals to logging and edge effects. Mamm. Biol. 1–7 https://doi.org/10.1016/j.mambio.2014.06.001.

Cerqueira, R.C., Leonard, P.B., da Silva, L.G., Bager, A., Clevenger, A.P., Jaeger, J.A.G., Grilo, C., 2021. Potential movement corridors and high road-kill likelihood do not spatially coincide for felids in Brazil: implications for road mitigation. Environ. Manag. 67, 412–423. https://doi.org/10.1007/s00267-020-01411-4.

Chaves, W.A., Wilkie, D.S., Monroe, M.C., Sieving, K.E., 2017. Market access and wild meat consumption in the Central Amazon, Brazil. Biol. Conserv. 212, 240–248. https://doi.org/10.1016/j.biocon.2017.06.013.

Clevenger, A.P., Wierzchowski, J., Chruszcz, B., Gunson, K., 2002. GIS-generated, expert-based models for identifying wildlife habitat linkages and planning mitigation passages. Conserv. Biol. 16, 503–514. https://doi.org/10.1046/j.1523-1739.2002.00328.x.

Coffin, A.W., 2007. From roadkill to road ecology: a review of the ecological effects of roads. J. Transp. Geogr. 15, 396–406. https://doi.org/10.1016/j.jtrangeo.2006.11.006.

Colchero, F., Conde, D.A., Manterola, C., Chvez, C., Rivera, A., Ceballos, G., 2011. Jaguars on the move: modeling movement to mitigate fragmentation from road expansion in the Mayan Forest. Anim. Conserv. 14, 158–166. https://doi.org/10.1111/j.1469-1795.2010.00406.x.

Conde, D.A., Colchero, F., Zarza, H., Christensen, N.L., Sexton, J.O., Manterola, C., Chvez, C., Rivera, A., Azuara, D., Ceballos, G., 2010. Sex matters: modeling male and female habitat differences for jaguar conservation. Biol. Conserv. 143, 1980–1988. https://doi.org/10.1016/j.biocon.2010.04.049.

Conservation International, 2002. The Kanuku Mountains Protected Area Process: The Community Resource Evaluations. Georgetown, Guyana.

Cramer, P.C., Gifford, S., Crabb, B., Mcginty, C., Ramsey, D., 2014. Methodology for Prioritizing Appropriate Mitigation Actions to Reduce Wildlife-Vehicle Collisions on Idaho Highways.

Cunha, H.F., Moreira, F.G.A., Silva, S.S., 2010. Roadkill of wild vertebrates along the GO-060 road between Goiânia and Iporá, Goiás State, Brazil. Acta Sci. Biol. Sci. 32, 257–263. https://doi.org/10.4025/actascibiolsci.v32i3.4752.

Cushman, S.A., Lewis, J.S., 2010. Movement behavior explains genetic differentiation in American black bears. Landsc. Ecol. 25, 1613–1625. https://doi.org/10.1007/s10980-010-9534-6.

Diniz, M.F., Brito, D., 2013. Threats to and viability of the giant anteater, *Myrmecophaga tridactyla* (Pilosa: Myrmecophagidae), in a protected Cerrado remnant encroached by urban expansion in Central Brazil. Zoologia 30, 151–156. https://doi.org/10.1590/S1984-46702013000200005.

Dulac, J., 2013. Global Land Transport Infrastructure Requirements: Estimating Road and Railway Infrastructure Capacity and Costs to 2050.

Eigenbrod, F., Hecnar, S.J., Fahrig, L., 2009. Quantifying the road-effect zone: threshold effects of a motorway on anuran populations in Ontario, Canada. Ecol. Soc. 14, 24. https://doi.org/10.5751/ES-02691-140124.

Espinosa, S., Branch, L.C., Cueva, R., 2014. Road development and the geography of hunting by an amazonian indigenous group: consequences for wildlife conservation. PLoS One 9, 1–21. https://doi.org/10.1371/journal.pone.0114916.

Espinosa, S., Celis, G., Branch, L.C., 2018. When roads appear jaguars decline : increased access to an Amazonian wilderness area reduces potential for jaguar conservation. PLoS One 13, e0189740.

Fabrizio, M., Di Febbraro, M., D'Amico, M., Frate, L., Roscioni, F., Loy, A., 2019. Habitat suitability vs landscape connectivity determining roadkill risk at a regional scale: a case study on European badger (Meles meles). Eur. J. Wildl. Res. 65 https://doi.org/10.1007/s10344-018-1241-7.

Ferreguetti, Á.C., Tomás, W.M., Bergallo, H.G., 2015. Density, occupancy, and activity pattern of two sympatric deer (*Mazama*) in the Atlantic Forest, Brazil. J. Mammal. 96, 1245–1254. https://doi.org/10.1093/jmammal/gyv132.

Ferreguetti, A.C., Tomas, W.M., Bergallo, H.G., 2019. Patch occupancy and activity pattern of the spotted paca (*Cuniculus paca* Linnaeus, 1766) in a protected area of the Atlantic Forest, Brazil. Mammalia 83, 363–371. https://doi.org/10.1515/mammalia-2017-0095.

Fiske, I., Chandler, R., 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. J. Stat. Softw. 43, 1–23.

Ford, A.T., Clevenger, A.P., Huijser, M.P., Dibb, A., 2011. Planning and prioritization strategies for phased highway mitigation using wildlife-vehicle collision data. Wildl. Biol. 17, 253–265. https://doi.org/10.2981/09-051.

Forman, R.T.T., Deblinger, R.D., 2000. The ecological road-effect zone of a Massachusetts (U.S.A.) suburban highway. Conserv. Biol. 14, 36–46.

Fredericks, P., Buckley, C., Persaud, J., 2016. A natural resource use assessment in the South Rupununi Savannah, Guyana. In: Alonso, L.E., Persaud, J., Williams, A. (Eds.), Biodiversity Assessment Survey of the South Rupununi Savannah, Guyana. BAT Survey Report No. 1. WWF-Guianas, Guyana Office, Georgetown, Guyana, pp. 203–225.

Glista, D.J., DeVault, T.L., DeWoody, J.A., 2009. A review of mitigation measures for reducing wildlife mortality on roadways. Landsc. Urban Plan. 91, 1–7. https://doi.org/10.1016/j.landurbplan.2008.11.001.

Gonzales-Gallina, A., Hidalgo-Mihart, M.G., Castelazo-Calva, V., 2018. Conservation implications for jaguars and other neotropical mammals using highway underpasses. PLoS One 13, e0206614.

González-Suárez, M., Zanchetta Ferreira, F., Grilo, C., 2018. Spatial and species-level predictions of road mortality risk using trait data. Glob. Ecol. Biogeogr. 27, 1093–1105. https://doi.org/10.1111/geb.12769.

Gouvea, J.A., 2020. How Does the Giant Anteater *Myrmecophaga tridactyla* Use a Landscape Featuring High Human Disturbance and Free-Ranging Dogs? Universidade Estadual Paulista "Julio de Mesquita Filho", São José do Rio Preto.

Grilo, C., Bissonette, J.A., Santos-Reis, M., 2008. Response of carnivores to existing highway culverts and underpasses : implications for road planning and mitigation. Biodivers. Conserv. 17, 1685–1699. https://doi.org/10.1007/s10531-008-9374-8.

Grilo, C., Bissonette, J.A., Cramer, P., 2010. Mitigation measures to reduce impacts on biodiversity. In: Jones, S.R. (Ed.), Highways: Construction, Management and Maintenance. Nova Science Publishers, Inc, New York, pp. 73–114.

Grilo, C., Ascensão, F., Santos-Reis, M., Bissonette, J.A., 2011. Do well-connected landscapes promote road-related mortality? Eur. J. Wildl. Res. 57, 707–716. https://doi.org/10.1007/s10344-010-0478-6.

Grilo, C., Sousa, J., Ascensão, F., Matos, H., Leitão, I., Pinheiro, P., Costa, M., Bernardo, J., Reto, D., Lourenço, R., Santos-Reis, M., Revilla, E., 2012. Individual spatial responses towards roads: implications for mortality risk. PLoS One 7, 1–11. https://doi.org/10.1371/journal.pone.0043811.

Guyana Bureau of Statistics, 2016. 2012 Population & Housing Census: Final Results. Georgetown, Guyana.

Hallett, M.T., Kinahan, A.A., McGregor, R., Baggallay, T., Babb, T., Barnabus, H., Wilson, A., Li, F.M., Boone, W.W., Bankovich, B.A., 2019. Impact of low-intensity hunting on game species in and around the Kanuku Mountains protected area, Guyana. Front. Ecol. Evol. 7, 412. https://doi.org/10.3389/fevo.2019.00412.

Holderegger, R., Di Giulio, M., 2010. The genetic effects of roads: a review of empirical evidence. Basic Appl. Ecol. 11, 522–531. https://doi.org/10.1016/j.baae.2010.06.006.

Hollowell, T., Reynolds, R.P., 2005. Checklist of the terrestrial vertebrates of the Guiana shield. Bull. Biol. Soc. Washingt. 13, 106.

Jackson, N.D., Fahrig, L., 2011. Relative effects of road mortality and decreased connectivity on population genetic diversity. Biol. Conserv. 144, 3143–3148. https://doi.org/10.1016/j.biocon.2011.09.010.

Jacobson, S.L., Bliss-ketchum, L.L., De Rivera, C.E., Smith, W.P., 2016a. A behavior--based framework for assessing barrier effects to wildlife from vehicle traffic volume. Ecosphere 7, 1–15.

Jacobson, S., Kintsch, J., Martens, D., 2016b. Training Workshop: Advanced Innovative Approaches to Wildlife and Highway Interactions. Sagehen Creek Field Station, California, USA.

Jaeger, J.A.G., 2015. Improving environmental impact assessment and road planning at the landscape scale. In: Van Der Ree, R., Smith, D.J., Grilo, C. (Eds.), Handbook of Road Ecology. John Wiley & Sons, Ltd, West Sussex, UK, pp. 32–42.

Jaeger, J.A.G., Fahrig, L., 2004. Effects of road fencing on population persistence. Conserv. Biol. 18, 1651–1657.

Jaeger, J.A.G., Bowman, J., Brennan, J., Fahrig, L., Bert, D., Bouchard, J., Charbonneau, N., Frank, K., Gruber, B., Von Toschanowitz, K.T., 2005. Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. Ecol. Model. 185, 329–348. https://doi.org/10.1016/j.ecolmodel.2004.12.015.

Jędrzejewski, W., Robinson, H.S., Abarca, M., Zeller, K.A., Velasquez, G., Paemelaere, E.A.D., Goldberg, J.F., Payan, E., Hoogesteijn, R., Boede, E.O., Schmidt, K., Lampo, M., Viloria, A.L., Carreño, R., Robinson, N., Lukacs, P.M., Nowak, J.J., Salom-Pérez, R., Castañeda, F., Boron, V., Quigley, H., 2018. Estimating large carnivore populations at global scale based on spatial predictions of density and distribution - application to the jaguar (*Panthera onca*). PLoS One 13, 1–25. https://doi.org/10.1371/journal.pone.0194719.

Kang, W., Minor, E.S., Woo, D., Lee, D., Park, C.R., 2016. Forest mammal roadkills as related to habitat connectivity in protected areas. Biodivers. Conserv. 25, 2673–2686. https://doi.org/10.1007/s10531-016-1194-7.

Karlsson, M., Bodin, Ö., 2022. Ten years of experience with ecological connectivity analysis and urban planning in Sweden. Impact Assess. Proj. Apprais. 40, 146–155. https://doi.org/10.1080/14615517.2022.2031551.

Keeley, A.T.H., Beier, P., Keeley, B.W., Fagan, M.E., 2017. Habitat suitability is a poor proxy for landscape connectivity during dispersal and mating movements. Landsc. Urban Plan. 161, 90–102. https://doi.org/10.1016/j.landurbplan.2017.01.007.

Kellner, K., 2018. jagsUI: A wrapper around "rjags" to streamline "JAGS" analyses. In: R Package Version 1.5.0.

Kintsch, J., Jacobson, S., Cramer, P., 2015. The wildlife crossing guilds decision framework: a behavior-based approach to designing effective wildlife crossing structures. In: Proceedings of the 2015 International Conference on Ecology and Transportation (ICOET 2015), p. 34044.

Kor, L., O'Hickey, B., Hanson, M., Coroi, M., 2022. Assessing habitat connectivity in environmental impact assessment: a case-study in the UK context. Impact Assess. Proj. Apprais. 40, 495–506. https://doi.org/10.1080/14615517.2022.2128557.

Laurance, W.F., Goosem, M., Laurance, S.G.W., 2009. Impacts of roads and linear clearings on tropical forests. Trends Ecol. Evol. 24, 659–669. https://doi.org/10.1016/j.tree.2009.06.009.

Laurance, W.F., Camargo, J.L.C., Luizão, R.C.C., Laurance, S.G., Pimm, S.L., Bruna, E.M., Stouffer, P.C., Bruce Williamson, G., Benítez-Malvido, J., Vasconcelos, H.L., Van Houtan, K.S., Zartman, C.E., Boyle, S.A., Didham, R.K., Andrade, A., Lovejoy, T.E., 2011. The fate of Amazonian forest fragments: a 32-year investigation. Biol. Conserv. 144, 56–67. https://doi.org/10.1016/j.biocon.2010.09.021.

Linkie, M., Smith, R.J., Leader-Williams, N., 2004. Mapping and predicting deforestation patterns in the lowlands of Sumatra. Biodivers. Conserv. 13, 1809–1818. https://doi.org/10.1023/B:BIOC.0000035867.90891.ea.

MacKenzie, D.I., Royle, J.A., 2005. Designing occupancy studies: general advice and allocating survey effort. J. Appl. Ecol. 42, 1105–1114.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83, 2248–2255.

MacKenzie, D.I., Bailey, L.L., Nichols, J.D., 2004. Investigating species co-occurrence patterns when species are detected imperfectly. J. Anim. Ecol. 73, 546–555.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., Hines, J.E., 2006. Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence. Academic Press, London.

Magioli, M., Ribeiro, M.C., Ferraz, K.M.P.M.B., Rodrigues, M.G., 2013. Thresholds in the relationship between functional diversity and patch size for mammals in the Brazilian. Anim. Conserv. 2–13 https://doi.org/10.1111/acv.12201.

Mazerolle, M.J., 2017. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). In: R Package Version 2.1.1.

McClure, M.L., Hansen, A.J., Inman, R.M., 2016. Connecting models to movements: testing connectivity model predictions against empirical migration and dispersal data. Landsc. Ecol. 31, 1419–1432. https://doi.org/10.1007/s10980-016-0347-0.

McGregor, R.L., Bender, D.J., Fahrig, L., 2008. Do small mammals avoid roads because of the traffic? J. Appl. Ecol. 45, 117–123. https://doi.org/10.1111/j.1365-2664.2007.01403.x.

Mcguire, T.M., Clevenger, A.P., Ament, R., Callahan, R., Jacobson, S., 2021. Innovative Strategies to Reduce the Costs of Effective Wildlife Overpasses.

McRae, B.H., Beier, P., 2007. Circuit theory predicts gene flow in plant and animal populations. Proc. Natl. Acad. Sci. U. S. A. 104, 19885–19890. https://doi.org/10.1073/pnas.0706568104.

Motta Lessa, I.C., Ferreguetti, Á.C., Kajin, M., Dickman, C.R., Godoy Bergallo, H., 2017. You can't run but you can hide: the negative influence of human presence on mid-sized mammals on an Atlantic island. J. Coast. Conserv. 21, 829–836. https://doi.org/10.1007/s11852-017-0544-2.

Nagy-Reis, M.B., Estevo, C.A., Setz, E.Z.F., Ribeiro, M.C., Chiarello, A.G., Nichols, J.D., 2017. Relative importance of anthropogenic landscape characteristics for Neotropical frugivores at multiple scales. Anim. Conserv. 20, 520–531. https://doi.org/10.1111/acv.12346.

Pardo, L.E., Campbell, M.J., Cove, M.V., Edwards, W., Clements, G.R., Laurance, W.F., 2019. Land management strategies can increase oil palm plantation use by some terrestrial mammals in Colombia. Sci. Rep. 9, 1–12. https://doi.org/10.1038/s41598-019-44288-y.

Parris, K.M., Schneider, A., 2009. Impacts of traffic noise and traffic volume on birds of roadside. Ecol. Soc. 14, 29.

Patterson, C., Torres, A., Coroi, M., Cumming, K., Hanson, M., Noble, B., Tabor, G., Treweek, J., Jaeger, J.A.G., 2022. Treatment of ecological connectivity in environmental assessment: a global survey of current practices and common issues. Impact Assess. Proj. Apprais. 40, 460–474. https://doi.org/10.1080/14615517.2022.2099728.

Peres, C.A., 2000. Effects of subsistence hunting on vertebrate community structure in Amazonian forests. Conserv. Biol. 14, 240–253. https://doi.org/10.1046/j.1523-1739.2000.98485.x.

Pfaff, A., Robalino, J., Walker, R., Reis, E., Perz, S., Bohrer, C., Aldrich, S., Arima, E., Caldas, M., Laurance, W., Others, 2007. Road investments, spatial intensification and deforestation in the Brazilian Amazon. J. Reg. Sci. 47, 109–123. https://doi.org/10.1111/j.1467-9787.2007.00502.x.

Pierre, M., Paemelaere, E., 2018. Wildlife Management Assessment: Region 9 - Upper Takutu - Upper Essequibo, Guyana - Plan of Action for Regional Development (PARD), Region 9. Unpubl. Rep.

Pinto, F.A.S., Bager, A., Clevenger, A.P., Grilo, C., 2018. Giant anteater (*Myrmecophaga tridactyla*) conservation in Brazil: analysing the relative effects of fragmentation and mortality due to roads. Biol. Conserv. 228, 148–157. https://doi.org/10.1016/j.biocon.2018.10.023.

Pinto, F.A.S., Clevenger, A.P., Grilo, C., 2020. Effects of roads on terrestrial vertebrate species in Latin America. Environ. Impact Assess. Rev. 81, 106337 https://doi.org/10.1016/j.eiar.2019.106337.

Pitman, R.T., Fattebert, J., Williams, S.T., Williams, K.S., Hill, R.A., Hunter, L.T.B., Robinson, H., Power, J., Swanepoel, L., Slotow, R., Balme, G.A., 2017. Cats, connectivity and conservation: incorporating data sets and integrating scales for wildlife management. J. Appl. Ecol. 54, 1687–1698. https://doi.org/10.1111/1365-2664.12851.

Plummer, M., 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. In: 3rd International Workshop on Distributed Statistical Computing (DSC 2003). Vienna, Austria, p. 124.

Polak, T., Rhodes, J.R., Jones, D., Possingham, H.P., 2014. Optimal planning for mitigating the impacts of roads on wildlife. J. Appl. Ecol. 51, 726–734. https://doi.org/10.1111/1365-2664.12243.

R Core Team, 2017. R: A Language and Environment for Statistical Computing.

Rabelo, R.M., Aragoón, S., Bicca-marques, J.C., 2019. Prey abundance drives habitat occupancy by jaguars in Amazonian floodplain river islands. Acta Oecol. 97, 28–33. https://doi.org/10.1016/j.actao.2019.04.004.

Read, J.M., Fragoso, J.M., Silvius, K.M., Luzar, J., Overman, H., Cummings, A., Giery, S. T., de Oliveira, L.F., 2010. Space, place, and hunting patterns among indigenous peoples of the Guyanese Rupununi region. J. Lat. Am. Geogr. 9, 213–243. https://doi.org/10.1353/lag.2010.0030.

Reed, G.C., Litvaitis, J.A., Callahan, C., Carroll, R.P., Litvaitis, M.K., Broman, D.J.A., 2017. Modeling landscape connectivity for bobcats using expert-opinion and empirically derived models: how well do they work? Anim. Conserv. 20, 308–320. https://doi.org/10.1111/acv.12325.

Roesch, M.J., 2010. Identifying Wildlife Crossing Zones for the Prioritization of Highway Mitigation Measures Along U . S . Highway 2: West Glacier, Mt To Milepost 193. University of Montana.

Ruediger, W., Jacobson, S., 2013. Multiple-use crossing structures for providing wildlife habitat connectivity. In: Proc. 2013 Int. Conf. Ecol. Transp. 14.

Russo, L.F., Barrientos, R., Fabrizio, M., Di Febbraro, M., Loy, A., 2020. Prioritizing road-kill mitigation areas: a spatially explicit national-scale model for an elusive carnivore. Divers. Distrib. 26, 1093–1103. https://doi.org/10.1111/ddi.13064.

Rytwinski, T., Soanes, K., Jaeger, J.A.G., Fahrig, L., Findlay, S., Houlahan, J., Van Ree, R., Der, Grift, Van Der, E.A., Findlay, C.S., Houlahan, J., van der Ree, R., van der Grift, E.A., 2016. How effective is road mitigation at reducing road-kill? A meta-analysis. PLoS One 11, e0166941. https://doi.org/10.1371/journal.pone.0166941.

Semper-Pascual, A., Decarre, J., Baumann, M., Camino, M., Di Blanco, Y., Gómez-Valencia, B., Kuemmerle, T., 2020. Using occupancy models to assess the direct and indirect impacts of agricultural expansion on species' populations. Biodivers. Conserv. 29, 3669–3688. https://doi.org/10.1007/s10531-020-02042-1.

Senzaki, M., Barber, J.R., Phillips, J.N., Carter, N.H., Cooper, C.B., Ditmer, M.A., Fristrup, K.M., McClure, C.J.W., Mennitt, D.J., Tyrrell, L.P., Vukomanovic, J., Wilson, A.A., Francis, C.D., 2020. Sensory pollutants alter bird phenology and fitness across a continent. Nature 587, 605–609. https://doi.org/10.1038/s41586-020-2903-7.

Serronha, A.M., Mateus, A.R.A., Eaton, F., Santos-Reis, M., Grilo, C., 2013. Towards effective culvert design: monitoring seasonal use and behavior by Mediterranean mesocarnivores. Environ. Monit. Assess. 185, 6235–6246. https://doi.org/10.1007/s10661-012-3020-3.

Shah, V.B., Mcrae, B.H., 2008. Circuitscape: A tool for landscape ecology. In: Varoquaux, G., Vaught, T., Millman, J. (Eds.), Proceedings of the 7th Python in Science Conference (SciPy 2008), pp. 62–66.

Shepard, D.B., Kuhns, A.R., Dreslik, M.J., Phillips, C.A., 2008. Roads as barriers to animal movement in fragmented landscapes. Anim. Conserv. 11, 288–296. https://doi.org/10.1111/j.1469-1795.2008.00183.x.

Sijtsma, F.J., van der Veen, E., van Hinsberg, A., Pouwels, R., Bekker, R., van Dijk, R.E., Grutters, M., Klaassen, R., Krijn, M., Mouissie, M., Wymenga, E., 2020. Ecological impact and cost-effectiveness of wildlife crossings in a highly fragmented landscape: a multi-method approach. Landsc. Ecol. 35, 1701–1720. https://doi.org/10.1007/s10980-020-01047-z.

Silveira Miranda, J.E., Keichi Umetsu, R., Rodrigues de Melo, F., Silveira Alves Melo, F. C., Pereira, K.F., Oliveira, S.R., 2017. Roadkill in the Brazilian cerrado savanna : comparing five highways in southwestern Goiás. Oecol. Aust. 21, 337–349. https://doi.org/10.4257/oeco.2017.2103.10.

Smith, Daniel, J., Kintsch, J., Cramer, P., Jacobson, S.L., Tonjes, S., 2008. Modifying structures on existing roads to enhance wildlife passage. In: Andrews, K.M., Nanjappa, P., Riley, S.P.D. (Eds.), Roads and Ecological Infrastructure: Concepts and Applications for Small Animals. Johns Hopkins University Press, Baltimore, pp. 208–228.

Sollmann, R., Malzoni, M., Hofer, H., Jácomo, A.T.A., Tôrres, N.M., Silveira, L., 2012. Using occupancy models to investigate space partitioning between two sympatric large predators, the jaguar and puma in Central Brazil. Mamm. Biol. 77, 41–46. https://doi.org/10.1016/j.mambio.2011.06.011.

Spanowicz, A.G., Teixeira, F.Z., Jaeger, J.A.G., 2020. An adaptive plan for prioritizing road sections for fencing to reduce animal mortality. Conserv. Biol. 34, 1210–1220. https://doi.org/10.1111/cobi.13502.

Sunarto, S., Kelly, M.J., Parakkasi, K., Klenzendorf, S., Septayuda, E., Kurniawan, H., 2012. Tigers need cover: multi-scale occupancy study of the big cat in Sumatran forest and plantation landscapes. PLoS One 7. https://doi.org/10.1371/journal.pone.0030859.

Taddia, A., Tamayo, C., Gomez, J.R., Vicentini, V.L., Frigerio, G., Persaud, C., Cardona, I., 2005. Guyana - Pre-Investment Georgetown-Lethem Road (Guyana Segment): Plan of Operations.

Thacker, S., Adshead, D., Fay, M., Hallegatte, S., Harvey, M., Meller, H., O'Regan, N., Rozenberg, J., Watkins, G., Hall, J.W., 2019. Infrastructure for sustainable development. Nat. Sustain. 2, 324–331. https://doi.org/10.1038/s41893-019-0256-8.

Thompson, J.J., Martí, C.M., Quigley, H., 2020. Anthropogenic factors disproportionately affect the occurrence and potential population connectivity of the Neotropic's apex predator: the jaguar at the southwestern extent of its distribution: landscape-scale drivers of jaguar occurrence. Glob. Ecol. Conserv. 24, e01356 https://doi.org/10.1016/j.gecco.2020.e01356.

Torres, A., Patterson, C., Jaeger, J.A.G., 2022. Advancing the consideration of ecological connectivity in environmental assessment: synthesis and next steps forward. Impact Assess. Proj. Apprais. 40, 451–459. https://doi.org/10.1080/14615517.2022.2134619.

Trombulak, S.C., Frissell, C.A., 2010. Review of ecological effects of roads on terrestrial and aquatic communities. Conserv. Biol. 14, 18–30. https://doi.org/10.1046/j.1523-1739.2000.99084.x.

Unnithan Kumar, S., Cushman, S.A., 2022. Connectivity modelling in conservation science: a comparative evaluation. Sci. Rep. 12, 1–12. https://doi.org/10.1038/s41598-022-20370-w.

Van Der Ree, R., Smith, D.J., Grilo, C., 2015. The ecological effects of linear infrastructure and traffic: Challenges and opportunities of rapid global growth. In: Van Der Ree, R., Smith, D.J., Grilo, C. (Eds.), Handbook of Road Ecology. John Wiley & Sons, Ltd, New Jersey, USA, pp. 1–9. https://doi.org/10.1002/9781118568170.ch1.

Vanthomme, H., Kolowski, J., Nzamba, B.S., Alonso, A., 2015. Hypothesis-driven and field-validated method to prioritize fragmentation mitigation efforts in road projects. Ecol. Appl. 25, 2035–2046. https://doi.org/10.1890/14-1924.1.

Veríssimo, A., Cochrane, M.A., Souza Jr., C.M., Salomão, R., 2002. Priority areas for establishing national forests in the brasilian Amazon. Conserv. Ecol. 6, 4 (online]. doi: Artn 4).

Versiani, N.F., Bailey, L.L., Pasqualotto, N., Rodrigues, T.F., Paolino, R.M., Alberici, V., Chiarello, A.G., 2021. Protected areas and unpaved roads mediate habitat use of the giant anteater in anthropogenic landscapes. J. Mammal. 102, 802–813. https://doi.org/10.1093/jmammal/gyab004.

Wilkie, D., Shaw, E., Rotberg, F., Morelli, G., Auzel, P., 2000. Roads, development, and conservation in the Congo Basin. Conserv. Biol. 14, 1614–1622. https://doi.org/10.1046/j.1523-1739.2000.99102.x.

Zeilhofer, P., Cezar, A., et al., 2014. Jaguar *Panthera onca* habitat modeling in landscapes facing high land-use transformation pressure 2014;findings from Mato Grosso, Brazil. Biotropica 46, 98–105.

Zeller, K., Rabinowitz, A., 2011. Using geographic information systems for range-wide species conservation planning. Biol. Conserv. 144, 892–901.

Zeller, K.A., Nijhawan, S., Salom-Pérez, R., Potosme, S.H., Hines, J.E., 2011. Integrating occupancy modeling and interview data for corridor identification: a case study for jaguars in Nicaragua. Biol. Conserv. 144, 892–901. https://doi.org/10.1016/j.biocon.2010.12.003.

Zeller, K.A., McGarigal, K., Whiteley, A.R., 2012. Estimating landscape resistance to movement: a review. Landsc. Ecol. 27, 777–797. https://doi.org/10.1007/s10980-012-9737-0.

Zeller, K.A., Jennings, M.K., Vickers, T.W., Ernest, H.B., Cushman, S.A., Boyce, W.M., 2018. Are all data types and connectivity models created equal? Validating common connectivity approaches with dispersal data. Divers. Distrib. 24, 868–879. https://doi.org/10.1111/ddi.12742.

Zimmermann Teixeira, F., Kindel, A., Hartz, S.M., Mitchell, S., Fahrig, L., 2017. When road-kill hotspots do not indicate the best sites for road-kill mitigation. J. Appl. Ecol. 54, 1544–1551. https://doi.org/10.1111/1365-2664.12870.