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Local abundances of terrestrial mammal and bird species around indigenous villages in Suriname

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Abstract

Hunting is an important threat to tropical wildlife, yet many people are dependent on forest fauna for protein provisioning. We analyzed abundances of terrestrial mammal and bird species around four indigenous villages in the south of Suriname, using camera trap data and the Royle–Nichols abundance model. We hypothesized that hunting pressure increases with decreasing distance to a village and with increasing village size (expressed as cropland area). We detected 24 animal species in all villages combined, including several rare species. For 11 of the 24 species, we were able to examine if and how distance to a village and village size related to local abundances and found a positive effect of distance to village on local abundances in five species, and a negative effect of village size in one species. Because villages, and thus hunting, affect local abundances of terrestrial bird and mammal species in our study, we recommend monitoring forest fauna in areas where people are highly dependent on animals for food provisioning.

KEYWORDS
camera trapping, detection rates, food security, indigenous people, subsistence hunting

1 | INTRODUCTION

Hunting poses one of the largest threats to tropical wildlife populations (Harrison, 2011; Wilkie et al., 2011). Due to the nonrandom character of most hunting activities, preferred game species, which are typically larger species with lower reproduction rates (Mesquita & Barreto, 2015; Peres, 2000; Peres & Palacios, 2007; Ripple et al., 2016), become less abundant or go locally extinct (Dirzo et al., 2014). In addition to the direct effects of hunting on animal communities, there are also more subtle effects on species' behavior with diurnal species becoming more nocturnal (Gaynor et al., 2018; Wang et al., 2015). Changes in the animal community composition and in activity patterns may lead to changes in competitive processes and predator–prey dynamics (Cruz et al., 2018; Di Bitetti et al., 2010; Paviolo et al., 2009; Wang et al., 2015). Yet, for many forest-dependent human communities, wildlife is the primary source of protein uptake (Cawthorn & Hoffman, 2015).

Persistent game hunting for subsistence, even at small scales, may have serious consequences for forest fauna (Constantino, 2016; Peres, 2000). Hunting intensity is generally higher in the proximity of roads, rivers, and settlements (Bowler et al., 2016; Peres & Lake, 2003), with indigenous hunters usually hunting within 10 km from their village (Alvard et al., 1997; Constantino, 2015;

Iwamura et al., 2014; Ohl-Schacherer et al., 2007). Hunting intensity also increases with the number of households and the number of agricultural fields in a village (Iwamura et al., 2014). Unsustainable levels of hunting could lead to half-empty or empty forests (Benítez-López et al., 2017; Milner-Gulland & Bennett, 2003), thereby threatening local food security (Constantino, 2016; Nasi et al., 2011). In contrast, some animal species, often smaller animals and with higher reproduction rates, seem to benefit from the presence of agricultural fields (Ferreira et al., 2018; Naughton-Treves et al., 2003; Pérez & Pacheco, 2006), or from competitive release or the absence of predators (Di Bitetti et al., 2010), thereby potentially increasing protein availability for humans.

In South Suriname, indigenous people indicated that over the last decade more frequent and longer hunting trips are needed to obtain a sufficient amount of meat (Amazon Conservation Team Suriname, personal communication). Wildlife has been inventoried in the central part of Suriname (Ahumada et al., 2011; Ouboter et al., 2011, 2021; Ouboter & Kadosoe, 2016; Schuttler et al., 2021), but data about animal communities from the less disturbed southern part of Suriname are largely lacking (Gajapersad et al., 2012). In this paper, we report on the presence of terrestrial bird and mammal species occurring around four indigenous villages in South Suriname, using camera trap data. We also research the impact of hunting on a subset of these species.

We hypothesized that hunting pressure would decrease with increasing distance to the village (Hill et al., 1997) and increase with the size of a village (Iwamura et al., 2014), which was confirmed by the hunters in the villages (see also Luzar et al., 2011). We therefore used distance to village and village size, represented by cropland area, as proxies for hunting pressure. We expect that (i) around smaller villages more species with a high body mass occur compared with larger villages, (ii) abundances of hunted animal species will be negatively affected by village size, (iii) abundances of hunted animal species will be higher further away from a village, and (iv) as an exception to (ii) and (iii) species that benefit from the presence of agricultural fields, or species that might benefit from competitive release and/or the lack of predators, have a higher abundance closer to villages and around larger villages.

The probability of detecting species can be affected by differences between surveyed sites, including vegetation structure (Ferreguetti et al., 2015; Rich et al., 2016), which makes comparisons between survey sites based on detection rates unreliable (Sollmann et al., 2013). Therefore, we investigate the effects of hunting pressure on local abundances of our study species, using the Royle–Nichols abundance model (2003). This enables us to take into account imperfect detection that arises due to differences in vegetation structure in our sites.

2 | METHODS

2.1 | Study site

We studied animal populations around four isolated indigenous villages in South Suriname (Figure 1a); Kwamalasamutu (KW), Tepu (TP), Apetina (AP) and Curuni (CU). All villages are located in the relatively intact terra firme forest in South Suriname. The villages are inhabited by indigenous Amerindian tribes (Trio in KW, TP, and CU and Wayana in AP) that live in the border areas of Suriname and Brazil. People hunt for meat and use swidden agricultural techniques to grow mainly
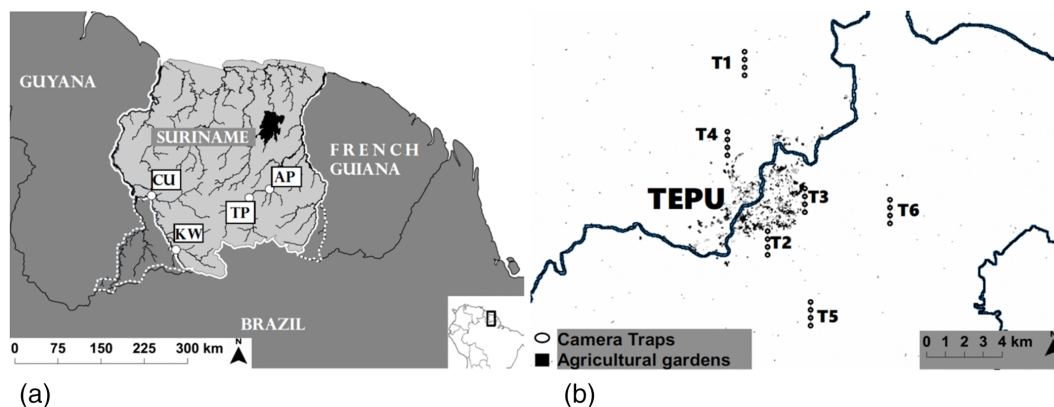

FIGURE 1 (a) Locations of the four indigenous villages in South Suriname in which the study was performed. The dashed lines indicate disputed borders. (b) Set up of the camera transects. The village of Tepu serves as an example here; the transects were of a similar set up in the other villages. The river running through Tepu is the Tapanahony river

cassava in agricultural plots. Until the 1960s, people lived in small, mainly nomadic, clusters comprising between 30 and 50 people. Since then, larger sedentary settlements were created (Nankoe, 2017), which supposedly increased hunting pressure in the area surrounding the villages. A recent coarse estimate by a local medical organization (Medische Zending, personal communication) on the number of inhabitants per village, runs from 40 in CU, 250 in AP, 400 in TP, to 700 in KW.

2.2 | Camera trap set up

Monitoring took place between 2015 and 2017: KW was monitored in 2015, AP in 2016, and CU and TP in 2017. We always monitored between May and August, which coincides with the rainy season. In total 84 unbaited cameras traps (Bushnell HD Trophy Cam, model 119537) were positioned around the villages (24 around KW, TP and CU each, and 12 around AP). The cameras were deployed in 1-km long transects, positioned from north to south (Figure 1b). Per transect, we placed four cameras with 330 m spacing in between. This was done in order to increase detection rates per survey location, since we were expecting low numbers of detections for the majority of the species (Amazon Conservation Team Suriname, personal communication). Survey locations were assigned on a map before going into the field based on information about hunting areas which was provided to us by hunters in the villages. All cameras were placed in intact forest, never in agricultural fields, and always at least at 100-m distance from hunting trails or forest edges. Once in the field, the cameras were attached to a tree close to the predetermined location, 40 cm above the ground, facing the north. Vegetation directly in front of the camera that could trigger the camera into taking pictures was removed. The cameras were set to take three pictures at every trigger with 15 s in between triggers. Every 2 weeks, the cameras were checked for malfunctioning, cleaned of spider webs and dried, and batteries were replaced. Cameras were active in the field for an average of 29 days, adding up to 321 camera days for AP, 569 for TP, 595 for CU, and 882 for KW. Animals on the pictures were identified with the help of the local villagers (Luzar et al., 2011) and by using the book Neotropical Rainforest Mammals (Emmons & Feer, 1997). We also recorded the body masses of all species identified (Bertelli & Tubaro, 2002; Emmons & Feer, 1997; Rossi et al., 2010). If a range of body masses was given, we took the average. Due to logistical issues, we were not able to monitor the animal community in all villages in the same year. We assume that the different years of measurement in our study did not affect our results. Other studies that took place within a time span of up to 6 years also found that "time" largely did not affect occupancy or abundance for a variety of species (Ahumada et al., 2013; Rist et al., 2009; Santos et al., 2019; Xavier da Silva et al., 2018).

To test for the effect of distance to the village, we placed transects at different distances from village centers (range 1.2–8.3 km measured as average distance from the four cameras per transect to the center of the village, as the crow flies). Because there are no accurate estimates of the number of inhabitants per village, we used cropland area (ha) as a proxy for village size (see Iwamura et al., 2014) since all land clearing for agriculture is done to grow food for subsistence. Cropland area was determined by analyzing satellite images (data source: Global Forest Watch) (Hansen et al., 2013) for each village in the year in which the surveys took place. We estimated the cropland area of each village by multiplying the number of pixels of that cover type by pixel size (900 m^2). Due to logistical complications, we could only place three transects in Apetina.

In all villages except for AP, we measured the DBH of all trees of ≥ 5 cm DBH, in 20×20 m plots around each camera. We multiplied the average DBH by the number of trees ≥ 5 cm DBH in each plot to obtain tree density. We counted the number of seedlings (trees with a diameter of <5 cm DBH) in 10×10 m plots around each camera to obtain seedling density.

2.3 | Data analysis

2.3.1 | Detections

In the analyses, we included pictures of species that are hunted (based on personal communication with the hunters) and that could be identified to the species level. To get a general understanding of species presence, we calculated the detection rate (e.g. the number of detections per 100 camera days) for all detected species in all villages. We excluded detections of the same species if they were recorded within 30 min on the same camera. If multiple individuals appeared on a picture, their total number was counted. Based on these data, we selected species for further analysis on the relationship between local abundances and distance to village, and village size (i.e. species with a detection rate of 5/100 camera days or more) (Shannon et al., 2014). For all identified species, we created rarefied species curves to analyze our sampling effort, using the vegan package (Oksanen et al. 2015) in R (R Development Core Team, 2015).

2.3.2 | Local abundance

Due to the high heterogeneity in detection rates between cameras and the fact that imperfect detection is not taken

into account when solely analyzing detection rates (Iknayan et al., 2014; Sollmann et al., 2013), we decided to estimate abundances with the Royle–Nichols abundance model (Royle & Nichols, 2003) and study the relationship of these estimated abundances with distance to village and village size. This hierarchical detection-based model is an extension of regular occupancy models and assumes that detection probabilities carry information about local abundances. It thus allows us to take imperfect detection into account by simultaneously examining the effects of site-specific covariates—in our case tree density and seedling density—on detection probability (i.e. the observation process) and then estimating abundance in relation to covariates—in our case distance to village (D) and village size (A). We tested whether tree density and seedling density surrounding each camera affected the probability of detection of a species in a transect, where we combined the detections of the four cameras of each transect, and averaged tree density and seedling density per transect. We assumed our sites were closed, meaning that no individuals could enter or leave the population due to birth, death, immigration, or emigration during our measurements. We also assumed our observations to be independent since we grouped the data of four cameras per transect and transects were located at least 2 km apart from each other. Since we monitored in a continuous forest and animals roam around within this forest, we opted to use "local abundance" as a parameter for our analyses (Gilbert et al., 2021; Sollmann, 2018).

Per transect, we recorded the number of 5-day intervals (Royle & Nichols, 2003) in which a species was photographed (w_i), as well as the total number of intervals (T_i). Similar to Royle and Nichols (2003) and Bowler et al. (2016), we made use of the Poisson assumption for abundance at the transect-level, where the number of animals of species i available for detection at transect j (N_{ij}) is described by the Poisson rate parameter λ_{ij}: $N_{ij} \sim$ Poisson(λ_{ij}). We used the average distance from the four camera traps per transect to the village center (D_j) and the amount of cropland area (A_j) as potential explanatory variables in our analysis of local abundance (Bowler et al., 2016):

$$\log(\lambda_{ij}) = \beta_{i,0} + \beta_{i,A} \times \ln(A_j) + \beta_{i,D} \times \ln(D_j) + \beta_{i,A:D} \times \ln(Aj)\ln(Dj),$$

where $\beta_{i,o}$ is the species-specific intercept and $\beta_{i,A}$, $\beta_{i,D}$, and $\beta_{i,A:D}$ are the species-specific regression coefficients of the (log-transformed) covariates A_j and D_j and their interaction effect. Detection probability (r) was modeled as a function of the transects' tree density (TD) and seedling density (SD):

$$\text{logit}(r_{ij}) = \beta_{i,r} + \beta_{i,TD} \times TD_j + \beta_{i,SD} \times SD_j + \beta_{i,TD:SD} \times TD_j SD_j,$$

where $\beta_{i,r}$ is the species-specific intercept, and $\beta_{i,TD}$, $\beta_{i,SD}$, and $\beta_{i,TD:SD}$ are the species-specific regression coefficients of the covariates TD_j and SD_j and their interaction effect. Because we did not measure the vegetation in AP, this village was excluded from these analyses. With the data collected in the other three villages, $y_{i,j}$ was fitted to the binomial distribution that best represents the probability that at least one individual of species i was detected:

$$y_{ij} \sim \text{Binomial}\left(k_j, 1 - (1 - r_{ij})^{N_{ij}}\right),$$

where k_j is the number of sampling occasions. The statistical significance of the covariates was tested by running all 64 possible combinations of the covariates per species, using the r-package unmarked (Fiske & Chandler, 2011) (see Table S1). By running all covariate combinations, we take into account that noncontributing covariates may conceal the effects of other covariates on a species' detection probability or abundance. We compared Akaike Information Criteria (AICs) between the models and selected the three models with the lowest AIC. For those factors significantly affecting detection or abundance, delta AIC was greater than 2 between models with and without this factor.

3 | RESULTS

3.1 | Detections

We identified 24 species in a total of 2367 camera trap days (Table 1). We detected 21 species in KW, 16 in TP, 17 in AP and 20 in CU. The percentage of species detected relative to the species that were estimated to be present, was 88% for KW, 75% for AP and 74% for TP and CU (see Figure S1 for rarefaction curves). Half of the 24 species were detected around all villages and three species were detected in only one village. Species with the highest detection rates included *Dasyprocta leporina* (Red-rumped Agouti), *Myoprocta acouchy* (Red Acouchi), and *Psophia crepitans* (Grey-winged Trumpeter), although their detection rates differed per village (up to almost 15-fold for the Grey-winged Trumpeter). Overall, detection rates were low (average 3.16 ± 0.07 SE detections per 100 camera days).

Body mass of the detected species ranged between 0.38 kg (*Crypturellus variegatus*, Variegated Tinamou) to 238.50 kg (*Tapirus terrestris*, Lowland Tapir). The majority of the species with a body mass below 10 kg were

TABLE 1 Detection rates (# detections per 100 camera days)

Village					KW	TP	AP	CU	
Year of measurement					2015	2017	2016	2017	
Cropland area (ha)					5191	1067	440	142	
Total camera days					882	569	321	595	
Species	Order	Body mass (kg)	IUCN Red List status[a]						Total
Birds									
Black Curassow	*Crax alector*	*Galliformes*	3.05	VU	1.02	0.35		2.35	3.90
Grey-winged Trumpeter	*Psophia crepitans*	*Gruiformes*	1.25	NT	8.62	2.28	28.35	33.77	73.01
Variegated Tinamou	*Crypturellus variegatus*	*Tinamiformes*	0.38	LC	0.91	2.46	0.31	3.53	7.20
Great Tinamou	*Tinamus major*	*Tinamiformes*	0.11	NT	1.36	3.51	9.35	3.36	17.58
Mammals									
White-lipped Peccary	*Tayassu pecari*	*Artiodactyla*	35.00	VU				1.85	1.85
Collared Peccary	*Tayassu tajacu*	*Artiodactyla*	26.00	LC	1.36		2.49	1.51	5.36
Tayra	*Eira barbara*	*Carnivora*	4.85	LC	0.79	1.58	1.87	1.85	6.09
Ocelot	*Leopardus pardalis*	*Carnivora*	11.25	LC	1.36	1.05	0.93	1.01	4.36
Margay	*Leopardus wiedii*	*Carnivora*	6.00	NT		0.18		0.17	0.34
South American Coati	*Nasua nasua*	*Carnivora*	5.10	LC	0.79			1.01	1.80
Jaguar	*Panthera onca*	*Carnivora*	94.50	NT	0.34				0.34
Puma	*Puma concolor*	*Carnivora*	74.50	LC	0.45		0.31		0.76
Jaguarundi	*Puma yagouaroundi*	*Carnivora*	6.75	LC	0.23	0.18	1.25	0.17	1.82
Southern Naked-tailed Armadillo	*Cabassous unicinctus*	*Cingulata*	3.20	LC	0.11				0.11
Greater Long-nosed Armadillo	*Dasypus kappleri*	*Cingulata*	10.15	LC	2.04	0.18	3.43	0.67	6.31
Nine-banded Armadillo	*Dasypus novemcinctus*	*Cingulata*	4.50	LC	0.79	2.81	5.61	1.51	10.72
Giant Armadillo	*Priodontes maximus*	*Cingulata*	25.50	VU	0.11	0.35			0.46
Red Brocket Deer	*Mazama americana*	*Even-toed Ungulates*	36.00	data deficient	3.63	0.53	3.12	2.86	10.13
Amazonian Brown Brocket	*Mazama nemorivaga*	*Even-toed Ungulates*	14.75	LC	0.57		0.62	1.51	2.70
Lowland Tapir	*Tapirus terrestris*	*Odd-toed Ungulates*	238.50	VU	0.45		0.31	0.50	1.27
Giant Anteater	*Myrmecophaga tridactyla*	*Pilosa*	30.50	VU		0.18	0.93	0.50	1.61
Lowland Paca	*Cuniculus paca*	*Rodent*	9.00	LC	4.31	4.57	4.98	1.85	15.71
Red-rumped Agouti	*Dasyprocta leporina*	*Rodent*	4.45	LC	9.64	3.16	41.43	6.38	60.61
Red Acouchi	*Myoprocta acouchy*	*Rodent*	1.25	LC	24.60	15.98	19.94	9.07	69.59

Abbreviations: AP, Apetina; CU, Curuni; IUCN, International Union for the Conservation of Nature; LC, least concern; NT, near threatenedKW, Kwamalsamutu; TP, Tepu; VU, vulnerable.

[a]Data from www.iucnredlist.org, consulted on May 28, 2020.

TABLE 2 Per species, the estimated mean local abundance (λ), estimated mean detection probability (p), weighted AICs of the three best models, and the covariate estimate, standard error, and p-values of the covariates included in these best-fitting models. Underlined AIC values are at least two points higher than that of their respective best model

Species	Mean λ	Mean p	wAIC		Abundance				Detection			
					Intercept	A	D	A:D	Intercept	TD	SD	TD:SD
Grey-winged Trumpeter	3.187	0.324	1.000	Estimate	43.287	−20.618	−9.829	5.044	−2.366		10.007	−4.742
				SE	20.045	8.841	5.351	2.344	0.718		3.881	2.166
				p	.031	.020	.066	.031	.001		.010	.029
			0.597	Estimate	53.139	−23.930	−12.421	5.909	−6.830		17.149	−9.346
				SE	23.313	9.842	6.209	2.602	4.934		8.844	5.694
				p	.023	.015	.045	.023	.166		.052	.101
			0.532	Estimate	42.101	−20.986	−10.019	5.303	2.108	−2.244		
				SE	19.997	8.675	5.287	2.275	1.971	1.160		
				p	.035	.016	.058	.020	.285	.053		
Variegated Tinamou	2.816	0.081	1.000	Estimate	1.035				−1.425			−1.492
				SE	0.690				0.991			0.851
				p	.133				.151			.080
			0.857	Estimate	3.088			−0.162	−2.505			
				SE	1.479			0.085	1.170			
				p	.037			.057	.032			
			0.752	Estimate	0.986				−1.388		−2.197	
				SE	0.674				0.974		1.350	
				p	.143				.154		.103	
Great Tinamou	7.717	0.033	1.000	Estimate	−7.164		2.544		−3.366	1.064		
				SE	4.383		1.146		0.598	0.775		
				p	.102		.026		.000	.170		
			0.572	Estimate	−4.669		1.909		−5.232			
				SE	4.493		1.170		1.438			
				p	.299		.103		.000			
			0.560	Estimate	2.820	−4.077		1.046	−3.331			
				SE	1.296	1.728		0.416	0.538			
				p	.030	.018		.012	.000			
Collared Peccary	5.282	0.198	1.000	Estimate	−21.945		6.376		−15.043	7.778	54.613	−38.500
				SE	11.382		2.952		7.393	4.802	32.251	22.044
				p	.054		.031		.042	.105	.090	.081

TABLE 2 (Continued)

Species	Mean λ	Mean p	wAIC		Abundance				Detection			
					Intercept	A	D	A:D	Intercept	TD	SD	TD:SD
			0.572	Estimate	4.287	−8.392		2.056	−17.964	9.166	71.683	−49.317
				SE	1.361	3.270		0.813	6.983	4.454	31.639	21.432
				p	.002	.010		.011	.010	.040	.023	.021
			0.560	Estimate	−18.744	−0.632	6.119		−14.153	6.706	50.632	−34.954
				SE	11.307	0.540	3.065		6.897	4.466	31.050	21.190
				p	.097	.242	.046		.040	.133	.103	.099
Tayra	9.561	0.035	1.000	Estimate	9.366		−2.058		−7.103	2.163		
				SE	3.710		1.127		1.644	0.992		
				p	.012		.068		.000	.029		
			0.787	Estimate	45.912	−11.443	−13.049	3.392	−6.620	2.041		
				SE	23.232	7.212	6.996	2.097	1.578	1.013		
				p	.048	.113	.062	.106	.000	.044		
			0.653	Estimate	63.024	−17.461	−18.415	5.267	−7.168	2.812		−1.583
				SE	27.287	8.609	8.317	2.544	1.598	1.174		1.136
				p	.021	.043	.027	.038	.000	.017		.163
Greater Long-nosed Armadillo	4.750	0.115	1.000	Estimate	−22.678		6.541		−4.007		13.798	−8.486
				SE	9.935		2.583		0.959		7.266	4.950
				p	.022		.011		.000		.058	.086
			0.883	Estimate	−25.632		7.320		1.111	−3.023		
				SE	9.059		2.358		1.890	1.250		
				p	.005		.002		.557	.016		
			0.550	Estimate	−21.776		6.314		0.371	−3.042	1.398	
				SE	9.509		2.481		2.199	1.330	1.383	
				p	.022		.011		.866	.022	.312	
Nine-banded Armadillo	4.748	0.043	1.000	Estimate	1.558				−2.277			−1.184
				SE	1.273				1.479			0.727
				p	.221				.124			.103
			0.830	Estimate	1.462				−2.169		−1.809	
				SE	1.187				1.394		1.176	
				p	.218				.120		.124	

(Continues)

TABLE 2 (Continued)

Species	Mean λ	Mean p	wAIC		Abundance				Detection			
					Intercept	A	D	A:D	Intercept	TD	SD	TD:SD
			0.588	Estimate	6.573		−1.437		−2.726			
				SE	3.767		0.992		1.273			
				p	.081		.147		.032			
Red Brocket Deer	1.335	0.320	1.000	Estimate	0.289				−0.755			
				SE	0.370				0.451			
				p	.434				.094			
			0.791	Estimate	−4.733		1.414		−0.867			
				SE	4.221		1.165		0.477			
				p	.262		.225		.069			
			0.737	Estimate	0.178				−2.511	1.268		
				SE	0.350				1.555	1.042		
				p	.611				.106	.224		
Lowland Paca	4.969	0.104	1.000	Estimate	1.603				−2.149			
				SE	0.983				1.077			
				p	.103				.046			
			0.914	Estimate	0.566	0.387			−2.322			
				SE	1.504	0.292			1.245			
				p	.706	.185			.062			
			0.778	Estimate	0.760			0.085	−2.269			
				SE	1.389			0.071	1.176			
				p	.584			.227	.054			
Red-rumped Agouti	9.523	0.098	1.000	Estimate	−2.036		1.200		0.173	−1.692		
				SE	3.028		0.777		1.690	0.743		
				p	.501		.123		.918	.023		
			0.756	Estimate	2.096				0.055	−1.485		
				SE	1.143				2.065	0.765		
				p	.067				.979	.052		
			0.637	Estimate	−2.631	−0.282	1.595		0.467	−1.865		
				SE	2.992	0.266	0.857		1.458	0.765		
				p	.379	.290	.063		.749	.015		

TABLE 2 (Continued)

Species	Mean λ	Mean p	wAIC		Abundance Intercept	A	A:D	D	Detection Intercept	TD	SD	TD:SD
Red Acouchi	10.328	0.265	1.000	Estimate	−3.742			1.692	−2.278		5.909	−2.502
				SE	3.187			0.832	0.543		3.015	1.490
				p	.240			.042	.000		.050	.093
			0.791	Estimate	−3.496			1.632	−0.632	−1.070	1.738	
				SE	3.081			0.805	1.151	0.626	0.918	
				p	.256			.043	.583	.088	.058	
			0.737	Estimate	−3.514			1.638	−0.012	−1.440		0.973
				SE	3.065			0.801	1.176	0.693		0.519
				p	.252			.041	.992	.038		.061

Abbreviations: A, cropland area size (ha); D, distance to village (km); SD, seedling density (m^{-2}); TD, tree density (m^{-2}).

detected in all villages. Of the species with a body mass > 10 kg, the majority (eight or nine) were detected in KW, AP, and CU, but only five were detected in TP.

3.2 | Local abundance

We had a sufficient amount of data to reliably analyze local abundance in relation to distance to village and village size using the Royle–Nichols model for 11 species (Royle & Nichols, 2003) (i.e. detection rates of 5/100 camera days or higher, see Table 1) (Shannon et al., 2014): Variegated Tinamou, *Cuniculus paca* (Lowland Paca), Red-rumped Agouti, *Dasypus kappleri* (Greater Long-nosed Armadillo), *Dasypus novemcinctus* (Nine-banded Armadillo), *Eira barbara* (Tayra), *Mazama americana* (Red Brocket Deer), Red Acouchi, Grey-winged Trumpeter, *Tayassu tajacu* (Collared Peccary), and *Tinamus major* (Great Tinamou).

We found statistically significant effects of the covariates tree density and seedling density on detection probabilities for 6 out of 11 species (Table 2). For the Red-rumped Agouti, Greater Long-nosed Armadillo, Grey-winged Trumpeter and Collared Peccary, detection probability decreases significantly with tree density. In contrast, detection probability slightly increases with tree density for Tayra. For the Greater Long-nosed Armadillo, Red Acouchi, and Grey-winged Trumpeter, seedling density was positively related to detection probability. In contrast, the detection probability of Collared Peccary was negatively related to seedling density. We observed nonsignificant trends in two other species: for Variegated Tinamou and Nine-banded Armadillo detection probabilities tended to increase with decreasing seedling densities. For the other three species, we did not find any effects of tree or seedling density on detection probabilities. Further, the increase or decrease of detection probabilities with tree or seedling density, did not seem to be related to body mass.

The average local abundance of the 11 species ranged between 1.34 and 10.33 individuals (Table 2). For 5 of 11 species, we found significant effects of the covariates on local abundance (Table 2; Figure 2). We observed a significant positive relationship between distance to village and local abundances of the Greater Long-nosed Armadillo, Red Acouchi, Grey-winged Trumpeter, Collared Peccary, and Great Tinamou. For the Grey-winged Trumpeter, we also found a negative relationship between village size and local abundance. Nonsignificant trends were observed in two other species: local abundance of the Red-rumped Agouti tends to increase with increasing distance to village, while local abundance of Tayra seems to decrease with increasing distance to
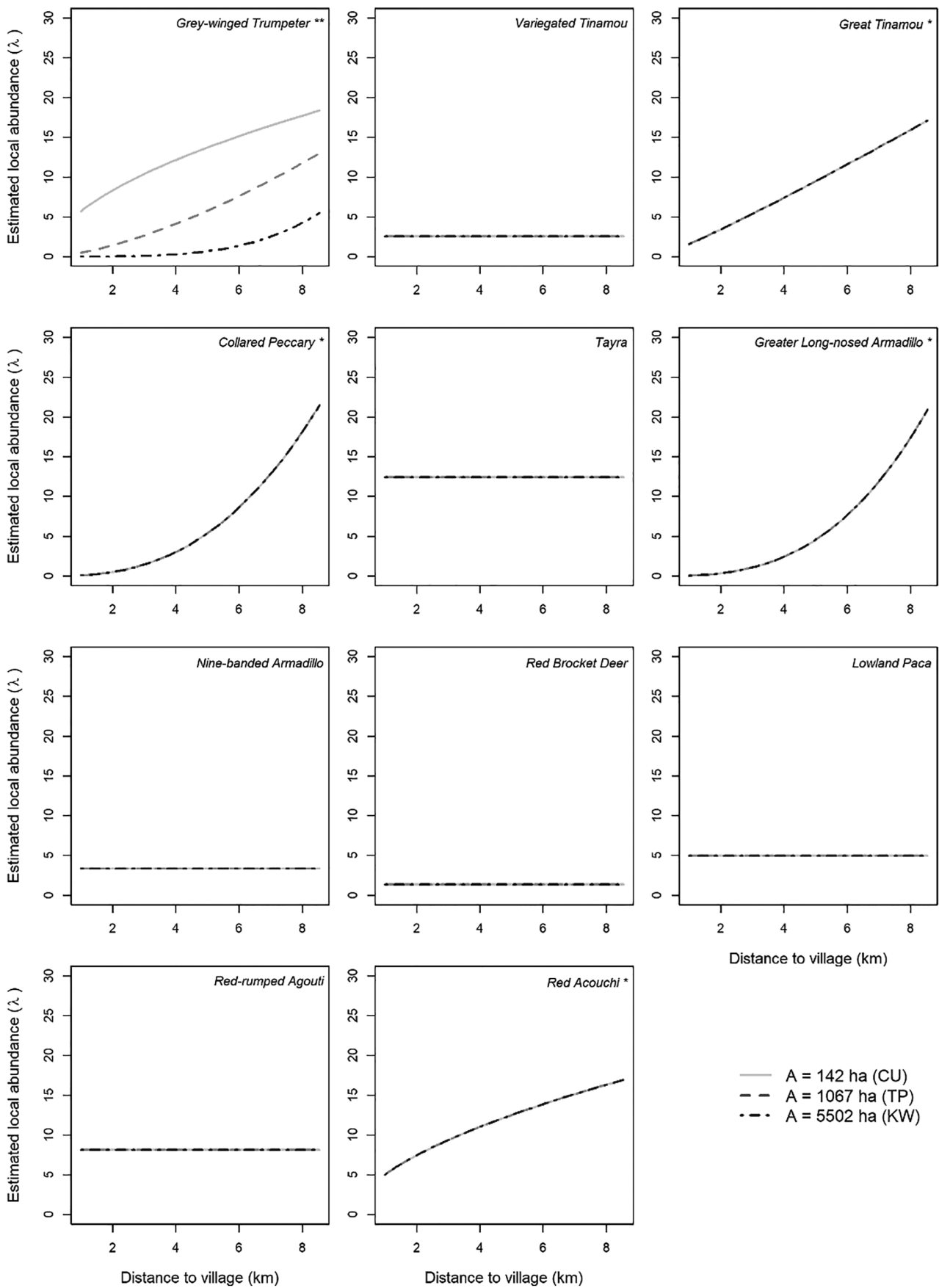
FIGURE 2 Legend on next page.

village. We observed no effects on local abundance for the other four species. Of the 11 species included in this analysis, the species with a body mass between 0.1 and 5 kg and the species with a body mass >10 kg varied in their response to distance and village size. The species with a body mass between 5 and 10 kg did not respond to distance and village size.

4 | DISCUSSION

Assessing the impact of hunting on animal species is important for people who strongly depend on wildlife for protein provisioning (Novaro et al., 2000). Here, we studied the presence and local abundances of terrestrial mammal and bird species around four indigenous villages in South Suriname, using camera trap data. A total of 24 species were detected during our study, including some of the rarest species in the region and species with an IUCN Red List status of "vulnerable" or "near threatened." We examined the relationship between local abundances of 11 species and distance to villages and village size, as proxies for hunting pressure. We found higher abundances further away from villages for five species, and higher abundances in smaller villages for one species.

Despite the relatively low number of cameras and total camera days as compared with other studies that examine animal communities across multiple sites (Rich et al., 2016; Tobler et al., 2015; but see Roopsind et al., 2017), we detected between 74% and 88% of the number of species estimated to be present (see Tobler et al., 2008 for similar results). This included species which the villagers believed were locally extinct, such as *Myrmecophaga tridactyla* (the Giant Anteater). Large bodied species were present in all villages, even in KW where hunting pressure is likely the highest of the four villages. We detected fewer large bodied species in TP (the second largest village) but this may be due to the fact that we detected only 74% of the species estimated to be present. We recorded a similar percentage of species for AP and CU, but it is remarkable that we did not see the Collared Peccary, the Amazonian Brocket and the Tapir in TP, while they were detected in the other villages, albeit with relatively low detection rates. Non-detection does not mean that a species is not present. Some of the species that were not detected in some villages are not

very common in this part of Suriname (Giant Armadillo, White-lipped Peccary) and/or have very large home ranges (e.g. the felid species), which lowers the chance of being captured on camera. Detections of the more elusive species were rare and thus our abundance analysis consequently focused on the more common species.

Detection probability can differ between survey sites, which is why detection rates are not a suitable parameter when comparisons between sites are made (Sollmann et al., 2013). Even though all of our sites were located within the same forest type, tree and seedling density varied locally and affected detection probabilities (Table 2). All possible patterns were observed with species having both lower or higher or unchanged detection probabilities with increasing tree and seedling density. We expected that trees and seedlings would obscure the view on animals thereby lowering their detectability (Denis et al., 2017; Rich et al., 2016), which is especially valid for smaller species, but they can also attract certain animals by offering food and shelter which would increase their detectability (Ferreguetti et al., 2015). Detection probability did not seem to be related to the body mass of the species in our study. On a larger (landscape) scale some species are attracted to certain habitats (Boron et al., 2019; Rist et al., 2009; Roopsind et al., 2017), but there is not much known on which environmental factors determine detection probability and differences in abundances at smaller scales. A few papers found that elevation explained detection probabilities to some extent (Ahumada et al., 2013; Santos et al., 2019) but a study from French Guiana reports that a variety of environmental variables had only a marginal effect on animal detectability (Denis et al., 2017). The higher abundances further away from villages for the Greater Long-nosed Armadillo, Red Acouchi, Grey-winged Trumpeter, Collared Peccary, and Great Tinamou may be the result of a higher hunting pressure closer to villages. The fact that we did not find this effect for all species might be due to the limited availability of data, or due to the fact that some species are profiting from the agricultural fields close to villages (Naughton-Treves et al., 2003; Pérez & Pacheco, 2006), or from competitive release, thereby counterbalancing the effect of hunting. For two species with large body masses (Greater Long-nosed Armadillo and Collared Peccary) we saw an increase in abundance with distance to village which could indicate that hunting

FIGURE 2 Estimated local abundances in relation to distance to the village center and village size (a). CU = Curuni, KW = Kwamalsamutu, and TP = Tepu. Significant relations between abundance and distance to village are indicated with an *, while ** indicates there is also a significant relation between abundance and village size. Variegated Tinamou, Red Acouchi, Grey-winged Trumpeter and Great Tinamou had a body mass <5 kg. Lowland Paca, Red-rumped Agouti, Nine-banded Armadillo and Tayra had a body mass between 5 and 10 kg. Greater Long-nosed Armadillo, Red Brocket Deer and Collared Peccary had a body mass >10 kg

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particularly affected these larger bodied species, but we did not see this effect for the Red Brocket Deer. In a study in the Atlantic forest, the Red Brocket Deer was found to be resilient to hunting, by adjusting its activity pattern (Di Bitetti et al., 2008). For species with a body mass between 5 and 10 kg, we did not see any effect of distance. For two related Armadillo species, the Greater Long-nosed Armadillo and the Nine-banded Armadillo, we saw different effects. The Greater Long-nosed Armadillo is a bit heavier and thus possibly more sensitive to hunting than the Nine-banded Armadillo, which might explain why that species is more abundant further away from villages. We expected higher abundances around smaller villages, but found this only for the Grey-winged Trumpeter. None of the larger predators were included in the analysis, so we could not draw conclusions for the impact of hunting on these species, or on effects of lower predator abundance on prey species. Further, we did not monitor animals in areas that were completely undisturbed, so we did not have a true reference scenario (i.e. an unhunted area) to compare our data with.

Inhabitants of the villages in our study informed us of their increased hunting efforts over the past decade to obtain a sufficient amount of meat: this notion was partly supported by our study. Higher occupancies or detections of animals further away from hunters' access points were found by Bowler et al. (2016), Peres and Lake (2003), and in a meta-analysis by Benítez-López et al. (2017). In our study we found five of the 11 species to show patterns corresponding to our hypotheses. Perhaps some of the diurnal and crepuscular species that are hunted around the villages have become more nocturnal due to hunting (Gaynor et al., 2018). Hunters usually hunt during daytime and twilight, which makes them miss certain species if the animals have indeed changed activity patterns. Also animals may have moved away far beyond the zones in which hunting takes place (Constantino, 2016; Cruz et al., 2018; Di Bitetti et al., 2008; Wang et al., 2015). We did not have enough data for activity analyses and could not include data from unhunted areas and thus were unable to test these hypotheses. Hunters also indicated that primates have become less easy to find. Since we deployed camera traps positioned on the forest floor, we inherently excluded arboreal species from our study, including primates, which are an important food source for the Trio and Wayana people.

With this study, we showed that distance to villages as a proxy for hunting, had an effect on the abundance of some mammal and bird species in South Suriname which partially explained why local hunters had to increase hunting effort. Because we found that local animal abundances are affected by hunting, we stress that wildlife should be continuously monitored in areas where people are highly dependent on animals for food provisioning, in order to draw conclusions about trends in population sizes of hunted species and thus food availability. In such studies, we recommend to include a reference scenario in which hunting does not occur and/or repeating monitoring studies especially if unhunted survey sites cannot be included, so that hunting impacts can be detected. We also recommend leaving cameras in the field for longer periods of time to increase detection rates, especially of the more elusive species, and to obtain data for analysis on activity patterns. Lastly, we recommend monitoring of *all* species used as food sources using a variety of monitoring methods rather than camera trapping alone (Zwerts et al., 2021).

CONFLICT OF INTEREST
We state there is no conflict of interest.

AUTHOR CONTRIBUTION
Marijke Van Kuijk and Minu Parahoe designed the study and arranged funding; Leen De Laender and Martin Van Oosterhout supervised data collection and processed the data; Monique De Jager and Marijke Van Kuijk analyzed the data; Marijke Van Kuijk wrote the paper with input from all authors.

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are available from the corresponding author (M van Kuijk; m.vankuijk@uu.nl), upon reasonable request.

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