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RESEARCH ARTICLE

An integrated approach to measure hunting intensity and assess its impacts on mammal populations

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Abstract

1. Unsustainable hunting of wildlife is one of the greatest threats to diverse and healthy forests, yet our understanding of hunting activity is limited by our methods of accurately identifying its intensity and distribution. Several methods have been used to quantify hunting in past studies (e.g. interviews, ranger patrols and camera traps). However, none of these alone have been able to produce precise spatiotemporal measures of hunting activity.
2. In this study, we used a new method to detect hunters through passive acoustic monitors and developed an integrated approach to measure hunting activity while simultaneously assessing its impacts on mammal populations using camera traps.
3. We applied a hierarchical community occupancy model that accounted for the imperfect detection of species on data from 45 trap locations, surveyed from January to June 2018, to investigate the impacts of spatial variation and intensity in hunting pressure on mammal species richness and occurrence in four protected areas in southern Belize. We developed spatiotemporally explicit indices of hunting activity separately from camera trap and acoustic monitor data and used a Bayesian model selection framework to identify predictors of site occurrence for individual species and three functional groups: carnivores, herbivores and omnivores.
4. We found that camera traps under-detected hunting activity in the region by 939% compared to acoustic monitors.
5. Consistent with our predictions, hunting intensity was negatively correlated with site-level species richness, with an average decrease in richness of 31% across its range of variation. Occurrence patterns for the three functional groups were also negatively associated with hunting intensity. Often the target of hunters, herbivores, displayed the strongest negative response to hunting, while omnivores were least affected.
6. *Synthesis and applications*. Unsustainable hunting of wildlife is a global phenomenon with wide-ranging implications for ecological communities, especially mammals. Our study highlights mammal sensitivity to increasing hunting pressure at the community and species level and emphasizes the necessity for developing robust tools to accurately monitor hunting activity, while also providing a

flexible framework for simultaneously assessing hunting and its impacts on mammal communities.

KEYWORDS
acoustic monitor, Belize, camera trap, hunting, mammal, occupancy, poaching, protected area

1 | INTRODUCTION

Unsustainable hunting of wildlife is one of the greatest threats to diverse and healthy forests (Bennett & Robinson, 2000). Increasing human populations have created a rising demand for bushmeat and wildlife products (Brashares et al., 2004; Zhang, Hua, & Sun, 2008), and expansion into remote areas has made previously isolated forests more accessible to hunters (Laurance et al., 2008). While subsistence hunting is practiced in many regions across the globe, over-hunting can have major impacts on wildlife populations, leading to large population declines or even local extinctions (Benítez-López et al., 2017; Laurance et al., 2006; Madhusudan & Karanth, 2002; Melo, Gadelha, Silva, Júnior, & Pontes, 2015). As a result, many forests are becoming increasingly void of wildlife and are often referred to as 'empty forests' (Redford, 1992), which has prompted further research investigating cascading effects, loss of ecosystem function and a decline in total biomass (Dirzo et al., 2014; Fox, 2006; Peres, Emilio, Schietti, Desmoulière, & Levi, 2016; Wilkie, Bennett, Peres, & Cunningham, 2011).

Mammals are among the taxonomic groups most impacted by unsustainable hunting. For instance, a review of 176 studies revealed that mammal abundances declined by an average of 83% in hunted areas (Benítez-López et al., 2017). However, less is understood about the impacts of hunting on specific functional groups within mammal communities (e.g. carnivores and herbivores). Healthy mammal populations are essential to functioning ecosystems, since they are often keystone species, assist in seed dispersal (Wang, Sork, Leong, & Smith, 2007) and even help facilitate carbon storage (Osuri et al., 2016). Therefore, being able to link precise spatiotemporal measures of hunting activity with mammal species richness and distribution is essential for informing sound conservation planning and management. However, commonly used methods to quantify hunting activity, such as interviews, ranger patrols and camera traps, are often unreliable and may in fact be underestimating hunting intensity and misrepresenting its spatial patterns, potentially leading to incorrect inferences on the impacts of hunting on mammals (Aiyadurai, Singh, & Milner-Gulland, 2010; Burton, Sam, Balangtaa, & Brashares, 2012; Gandiwa, Zisadza-Gandiwa, Mango, & Jakarasi, 2014; Madhusudan & Karanth, 2002). This has created a need for the development of a new methodological approach to more accurately quantify and map hunting distribution and intensity across a landscape.

In recent years, passive acoustic monitors have become increasingly prevalent in ecological studies and present a potential alternative to measure hunting activity in regions where firearms are used as the primary hunting method. They have been widely used to assess diversity in birds, bats, amphibians, marine mammals and even terrestrial mammals by identifying unique vocalizations among species (Enari, Enari, Okuda, Maruyama, & Okuda, 2019; Pieretti, Lo Martire, Farina, & Danovaro, 2017; Russo & Voigt, 2016; Xie et al., 2018; Zhang, Towsey, Xie, Zhang, & Roe, 2016). They have also been implemented to assess anthropogenic sound and its impacts on habitat use and behaviour in birds (Nemeth & Brumm, 2010). Building on these applications, it follows that passive acoustic monitors may also be well suited for identifying gunshots as a proxy metric of hunting activity in regions where accurately measuring hunting is difficult.

Furthermore, better understanding of both the direct and indirect impacts of hunting on mammals is a multi-faceted problem that requires an integrated approach. By pairing acoustic monitors to measure hunting activity with camera traps to observe mammal populations, we can potentially provide better informed inferences on the impacts of hunting intensity across diverse mammal communities. Although potentially less effective in measuring hunting activity, camera traps have been successfully used to study rare and cryptic species (Hegerl et al., 2017; Rovero, Martin, Rosa, Ahumada, & Spitale, 2014; Silver et al., 2004; Sollmann et al., 2012; Tobler, Carrillo-Percastegui, Zúñiga Hartley, & Powell, 2013) and are ideally suited to utilize sampling methods and robust spatiotemporal analyses that can account for the imperfect detection of species (Ahumada, Hurtado, & Lizcano, 2013). This allows for unbiased estimation of ecological indicators and makes camera traps a cost effective and efficient monitoring method for ecological and conservation studies.

Therefore, in this study, we test a novel integrated approach combining acoustic monitors and camera traps to simultaneously assess hunting intensity and its impacts on terrestrial mammals in a human-dominated tropical ecosystem in southern Belize as a model. We hypothesize that acoustic monitors will capture significantly more hunting events than camera traps, potentially allowing us to estimate more realistic hunting intensities and distributions. To test this, we use both camera traps and acoustic monitors simultaneously to measure hunting activity and compare their data. Second, we hypothesize that observed spatial patterns of mammal species richness and occurrence are heavily influenced by local variations in hunting pressure. We predict that this phenomenon will be most significant for herbivores that are commonly hunted as bushmeat, as well as their primary predators. To investigate this, we implement a community occupancy modelling framework to assess the relative impacts of spatial variation in hunting pressure on mammal species richness and occurrence for individual

species and three functional groups: carnivores, herbivores and omnivores.

2 | MATERIALS AND METHODS

2.1 | Study area

Our study area in southern Belize is a fragmented landscape with a mosaic of community-managed forests and four protected areas (Bladen Nature Reserve, Deep River Forest Reserve, Golden Stream Corridor Preserve and Belize Foundation for Research and Environmental Education [BFREE]; Figure 1). On the periphery of the protected areas, there are five Maya villages (Trio, Bladen, Tambran, Medina Bank and Golden Stream). Residents are mostly farmers and practice a slash-and-burn shifting cultivation technique, commonly known as milpa. In this system, the most common crops produced are maize, beans and squash. Because cattle are rare in Maya communities, residents often hunt game to supplement their diet with protein. The primary method of hunting in this region is firearm-based, and other forms of hunting (e.g. snares) are very rare (Unpublished interviews, MD). In addition to subsistence hunting by local residents, the construction of a new highway and logging roads has made the region more accessible to outside hunters. The spatial distribution and intensity of hunting is largely unknown in the region, and the minimal enforcement inside protected areas, combined with their proximity to roads and villages, facilitates easy access for hunters to exploit protected and vulnerable wildlife.

The topography of the landscape is mostly flat, however, there are some areas of steep slope and moderate elevation (<450 m) in the Bladen Nature Reserve. There are three major land use/cover types in the region: rainforest, savanna and agriculture, with broadleaf rainforest being the most dominant land cover. The mean daily temperature is 30°C in summer and 26°C in winter, and mean annual rainfall is 3,048–3,556 mm, mostly occurring from July to December.

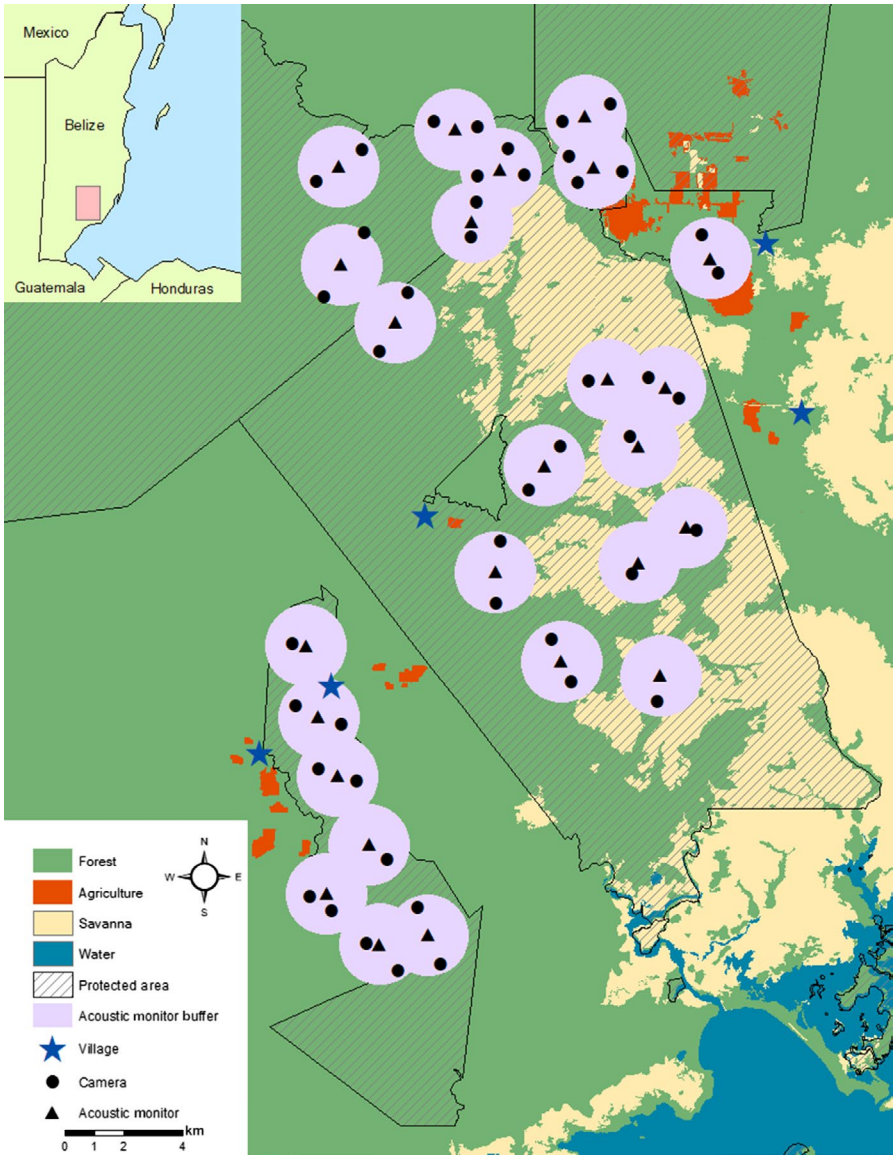

FIGURE 1 The four protected areas, their nearby villages and camera stations ($n = 45$) and acoustic monitors ($n = 25$) with a 1.25-km detection radius surveyed from January to June 2018 in southern Belize

2.2 | Camera traps

We deployed camera traps in 45 locations inside four protected areas encompassing 500 km^2 from January to June 2018, corresponding with the dry season (Figure 1). Camera stations were spaced at a minimum of 1 km apart and were not baited. Three brands of cameras were used (Bushnell Trophy Cam HD, Moultrie S-50i and Panthera), and cameras were secured to trees at approximately 40 cm above the ground. Cameras ran 24 hr/day and were checked for maintenance and data collection monthly. Our survey design spanned a gradient of forest areas in varying stages of succession, logging activity and distances from agriculture and villages. We had no prior knowledge of hunting intensity or distribution, so we attempted to allocate camera stations equally among areas of differing human activity and accessibility.

2.3 | Acoustic monitors

To quantify hunting intensity, we deployed 25 passive acoustic monitors (SM4, Wildlife Acoustics Inc.) across the study area. Monitors ran continuously 24 hr/day and audio data were collected in mono, 16-bit WAV format at a sampling rate of 8,000 Hz. Through field tests, we concluded that gunshots could be detected by our acoustic monitors from a maximum distance of 1.25 km. Therefore, we created a buffer around each acoustic monitor to ensure that all camera traps were located within the detection radius of at least one acoustic monitor. Monitors were secured to trees at an approximate height of 5 m and were located away from trails to minimize detection by hunters.

We used the software Kaleidoscope 5 Pro (Wildlife Acoustics Inc.) to process and analyse sound files. To identify gunshots from the data, we performed a cluster analysis based on sample data of 50 test gunshots at varying distances from the acoustic monitor. The cluster analysis function is typically used to separate and group wildlife species based on their unique vocalizations. This analysis is mostly used for bird and bat species identification (Botto Nuñez et al., 2018; Henríquez et al., 2014; Jorge, Machado, da Cunha Nogueira, & Nogueira-Filho, 2018; Mammides, Goodale, Dayananda, Kang, & Chen, 2017; Zhao et al., 2017; Zottesso, Costa, Bertolini, & Oliveira, 2018). However, we used it to isolate gunshots from all other recorded events. Varying signal detection parameters were used to test their effectiveness in creating an accurate cluster of gunshots. We set a minimum and maximum frequency detection range from 1 to 2,000 Hz. In the field, gunshot signatures ranged from 1 to 8,000 Hz (our maximum frequency). However, decreasing the detection parameter of the maximum frequency range to 2,000 Hz eliminated many errant wildlife and environmental recordings, thus significantly reducing the amount of false positive identifications in our gunshot cluster. We set the minimum and maximum length of detection to 0.1–1.5 s, which is slightly longer than the longest detected reverb signature from a gunshot. This ensured that all gunshots were able to be detected and that signals from other sources longer than 1.5 s were excluded. We kept the maximum inter-syllable gap at its default setting of 0.35 s and removed the DC offset.

After performing the cluster analysis, we visibly and audibly identified and selected all gunshots from the generated cluster. This effectively removed the remaining false positive identifications from the test data. From these manual selections, we then used the machine learning advanced classification analysis built into the Kaleidoscope software to train the software to identify gunshots from our actual data. Results generated from the advanced classification were also visibly and audibly checked for accuracy, and confirmed gunshot events were recorded along with their date, location and time. From interviews with local residents and preliminary data from acoustic monitors, we found that hunters would frequently fire many rounds within short time spans. To prevent this from skewing perceived hunting activity, multiple gunshots recorded at the same acoustic monitor within a 1-hr period were considered to be one hunting event. When one hunting event was recorded at multiple acoustic monitors with overlapping buffer areas, the event was counted only once and attributed to the nearest acoustic monitor.

2.4 | Data analysis

We measured hunting activity independently from camera traps and acoustic monitors. Camera traps have been used to identify hunters in previous studies (Brodie et al., 2015; Jenks, Howard, & Leimgruber, 2012). However, the relative effectiveness of acoustic monitors in detecting gunshots is unknown. For camera traps, we assumed any humans carrying guns, animal carcasses, a large bag to transport animals or accompanied by a dog to be hunters (Jenks et al., 2012). For acoustic monitors, we identified hunting by the number of independent gunshot events recorded. We then calculated the total number of hunting events and the proportion of days at each site where at least one hunting event was detected from photographic and acoustic data independently. In addition, we used the point density function in ArcGIS 10.6.1 to map the spatial distribution of hunting events recorded from acoustic monitors and camera traps.

To test our hypothesis that mammal species richness and distribution in the region would be influenced by variation in hunting intensity, we used a Bayesian hierarchical community occupancy framework (Royle & Dorazio, 2008), which uses detection data from multiple species to estimate both occupancy and detection probability for the community as well as for each species. This framework requires repeated species detection surveys of sites during a period where the species' occupancy states are assumed to be closed (i.e. a site is either occupied or unoccupied throughout all repeated surveys) to estimate the probability that a species is detected, given its presence. The imperfect detection of species (i.e. false negatives) is taken into account to provide unbiased estimates of occupancy. This approach is especially beneficial for species with sparse data, since the model assumes that species' responses are derived from a

community-level distribution, which allows the community data to improve species-specific estimates of occurrence (Zipkin, Dewan, & Andrew Royle, 2009). We treated our 6-month sampling period as one season with twenty-four 1-week surveys (*k*) and assumed closure of the mammal community. To prepare species data for analysis, detection/non-detection matrices were constructed where cells were denoted as 1 (species *i* was photographed at site *j* during survey *k*), 0 (species was not photographed), or NA (camera at site *j* was not active during survey *k*). The occurrence of a species *i* at camera station *j* (0 if absent, 1 if present), z_{ij}, is a Bernoulli process with a success (i.e. occupancy) probability ψ_{ij1}, which can be modelled as a function of covariates using a logit link. Binary detection data were also modelled as a Bernoulli random variable with a success (i.e. detection) probability (*p*), with the inclusion of covariates on *p*, to provide unbiased estimates of occupancy by accounting for heterogeneity in detection probabilities (Royle & Dorazio, 2008).

Hunting intensity derived from acoustic monitors was the primary covariate of interest for the model, but we anticipated other site-specific covariates would also likely influence species occurrence probabilities. Therefore, we included three additional covariates used in Dobbins et al. (2020) that were shown to impact occurrence and detection probabilities for many species in the area: distance to village, distance to logged site and a binary covariate of old versus young-growth forest. We identified and calculated all covariates with ArcGIS 10.6.1, and used an object-based high-resolution (10 m) land cover classification from Dobbins et al. (2020) to identify the various land cover types and assist in covariate calculations. The model for occurrence of species *i* at location *j* was represented by:

$$\begin{aligned}\text{logit}(\psi_{ij}) &= \varphi_i + \alpha 1_i \text{hunting}_j + \alpha 2_i \text{village}_j + \alpha 3_i \text{logging}_j \\ &\quad + \alpha 4_i \text{old\_growth}_j,\end{aligned}$$

where φ_i represents the species-level intercept, and the alpha coefficients indicate the effects of covariates on the occurrence of species *i*. We standardized all continuous covariates to have a mean of 0 and standard deviation of one to help interpret their relative effects. We anticipated that hunting and other site-specific covariates may also affect the detection probability of species. For example, the presence of hunters could make animals more cautious and thus less likely to be detected. Therefore, all occurrence covariates were also included in a general model for detection probability using the logit link function:

$$\begin{aligned}\text{logit}(p_{ij}) &= \eta_i + \beta 1_i \text{hunting}_j + \beta 2_i \text{village}_j + \beta 3_i \text{logging}_j \\ &\quad + \beta 4_i \text{old\_growth}_j,\end{aligned}$$

where η_i is the species-level intercept, and the beta coefficients are the effects of the covariates on the detection probability of species *i*. An additional hierarchical component of the model was added by assuming that the species-level parameters were random effects and derived from a normal distribution, governed by hyper-parameters (mean and variance) that are shared across all species (Kery et al., 2009). Because species richness of the mammal community was unknown, we created a 'super-community' by adding a large number of all-zero encounter histories to our data to account for species that are present but were not detected during sampling. To investigate the relative effects of hunting intensity on functional groups, we contrasted beta estimates from the community model among our three identified functional groups. In addition, summing across all occurrence states, *z*, for a given camera allowed us to estimate the number of species present at particular sample locations (i.e. location level richness), observed or unobserved, and summing all species with $z_{ij} = 1$ for at least one location allowed us to estimate richness for the study area. We further investigated the relationship between richness and hunting pressure using derived species richness estimates by implementing a two-step hierarchical procedure and fitting a simple regression model with two residual components, where the first component estimates the uncertainty in deriving species richness and the second assesses lack of fit estimated from the data (Kéry & Royle, 2015).

The community model was run in the software WinBUGS version 1.4.3 (Spiegelhalter, Thomas, Best, & Way, 2003) using the package R2WinBUGS (Sturtz, Gelman, & Ligges, 2005) in the program R version 3.5.1 (Lunn, Thomas, Best, & Spiegelhalter, 2000). Inference was made from three MCMC chains of 70,000 iterations each with a burn-in of 20,000 and a thinning rate of 30. We checked chain convergence by examining $\widehat{R}$ values and the MCMC chains. Model fit was assessed by computing a Bayesian *p*-value, where values very close to zero or one (<0.05 or >0.95) indicate a lack of model fit (Gelman, Meng, & Stern, 1996).

3 | RESULTS

3.1 | Hunting activity

Acoustic monitors detected significantly more hunting events ($n = 742$, mean per monitor = 37.1) than camera traps ($n = 79$, mean per trap = 1.8), and the point density maps of hunting activity generated contrasting distributions of hunting intensity from photographic and acoustic detections (Figure 2). Photographic detections of suspected hunters were largely uniform with just two areas of relative high intensity. Only one of these high intensity areas was adjacent to a village, while cameras located near the remaining four villages recorded very few hunters. By contrast, acoustic hunting data showed three well-defined centres of hunting intensity, and all were located within close proximity of the five local villages. In addition, hunting intensity appeared to gradually decrease as distance from villages increased, which was expected but not observed with the camera data.

3.2 | Community occupancy model

The community model fit the data well with a Bayesian *p*-value of 0.44 and estimated a total species richness of 20.22 (95% CI 19–22), which was similar to the number of species we observed during the study ($n = 19$; Table 1). The estimated mammal community response to hunting was negative, showing that community-level occupancy

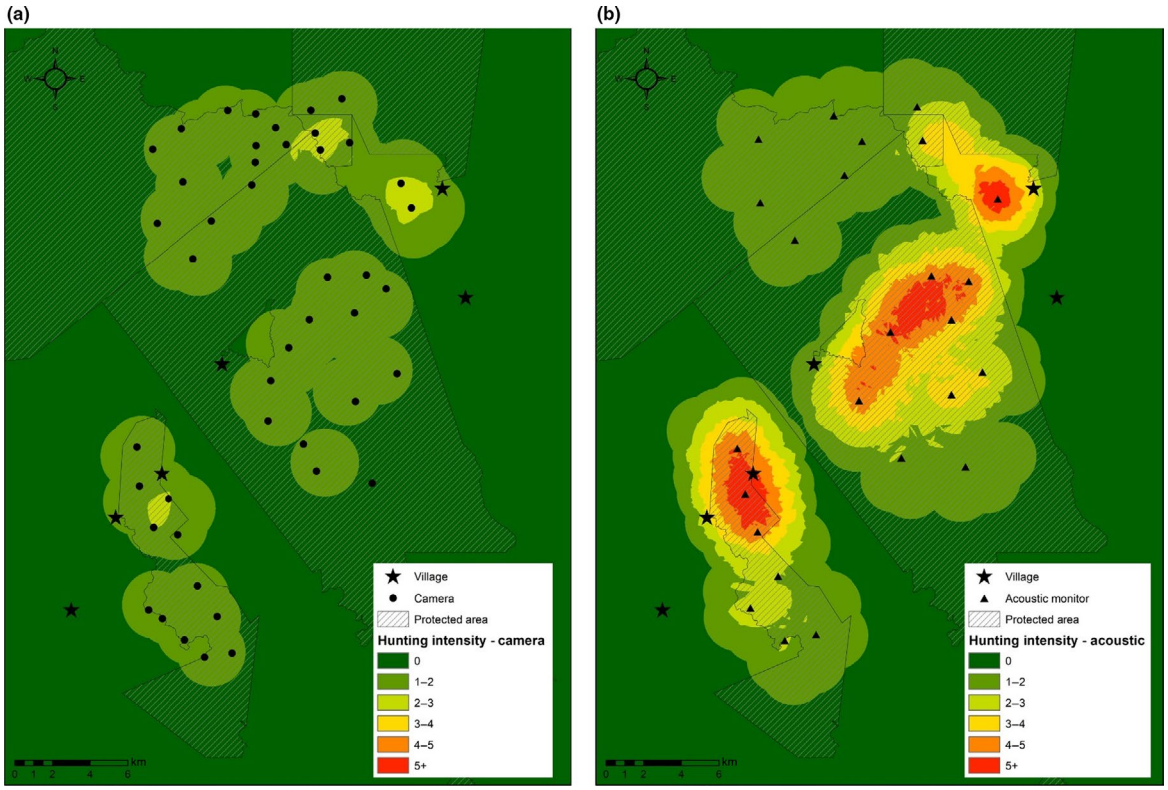

FIGURE 2 Point density functions of hunting distribution and intensity derived from (a) camera traps and (b) acoustic monitors in and around four protected areas in southern Belize. Here hunting intensity is defined as the number of hunting events per hectare recorded independently by camera traps and acoustic monitors

TABLE 1 Mammal species detected via camera traps and their naïve and estimated occurrence (ψ)

Common name	Scientific name	IUCN status	Functional group	Naïve ψ	ψ (*SD*)
Jaguar	*Panthera once*	NT	Carnivore	0.61	0.79 (0.08)
Puma	*Puma concolor*	LC	Carnivore	0.55	0.72 (0.06)
Ocelot	*Leopardus pardalis*	LC	Carnivore	0.81	0.89 (0.03)
Margay	*Leopardus wiedii*	NT	Carnivore	0.13	0.28 (0.08)
Jaguarundi	*Puma yagouaroundi*	LC	Carnivore	0.10	0.19 (0.05)
Greater grison	*Galictis vittata*	LC	Carnivore	0.03	0.09 (0.08)
Brocket deer	*Mazama americana*	DD	Herbivore	0.52	0.76 (0.09)
Collared peccary	*Pecari tajacu*	LC	Herbivore	0.32	0.46 (0.07)
White-lipped peccary	*Tayassu pecari*	VU	Herbivore	0.23	0.31 (0.05)
Tapir	*Tapirus bairdii*	EN	Herbivore	0.68	0.82 (0.04)
Agouti	*Dasyprocta punctata*	LC	Herbivore	0.55	0.68 (0.07)
Paca	*Cuniculus paca*	LC	Herbivore	0.65	0.72 (0.05)
Coati	*Nasua narica*	LC	Omnivore	0.16	0.26 (0.08)
Opossum	*Didelphis marsupialis*	LC	Omnivore	0.23	0.32 (0.06)
Armadillo	*Dasypus novemcinctus*	LC	Omnivore	0.42	0.52 (0.05)
Skunk	*Conepatus semistriatus*	LC	Omnivore	0.10	0.17 (0.08)
Tayra	*Eira barbara*	LC	Omnivore	0.23	0.37 (0.06)
Raccoon	*Procyon lotor*	LC	Omnivore	0.06	0.14 (0.07)
Northern tamandua	*Tamandua mexicana*	LC	Insectivore	0.03	0.07 (0.08)

was lower in areas of increased hunting intensity. This resulted in an average decrease of 31% in mammal species richness across its observed range of variation when all other factors were held constant (Figure 3). For occupancy, the mean effect was significant ($\alpha = -0.22$ 95% CI −0. 45 to −0.04), as Bayesian credible intervals did not overlap zero. However, the effect of hunting intensity on detection probability was not significant at the community level ($\beta = -0.16$ 95% CI −0.64 to 0.31). Community-level summaries of the hyper-parameters for all occupancy and detection covariates are provided in the Supporting Information SI.

At the species level, model-predicted responses in occurrence probability to hunting were similar among functional groups (Figure 4), and correspondingly, the posterior mean was negative for 84% ($n = 16$) of the species (Figure 5). Just three species appeared to increase in occurrence in response to hunting: ocelot *Leopardus pardalis*, opossum *Didelphis marsupialis* and coati *Nasua narica*. Four species routinely hunted as bushmeat saw the greatest decrease in modelled occurrence probability: paca *Cuniculus paca*, collared peccary *Pecari tajacu*, brocket deer *Mazama americana*, and armadillo *Dasypus novemcinctus* (Figure 4). All carnivores, except for ocelot, also showed a decrease in occurrence probability in response to hunting. Additionally, we found that 79% ($n = 15$) of species were less likely to be detected in hunted areas, given their presence (Figure 5). White-lipped peccary *Tayassu pecari*, margay *Leopardus wiedii*, and brocket deer had the strongest negative response in detection probabilities.

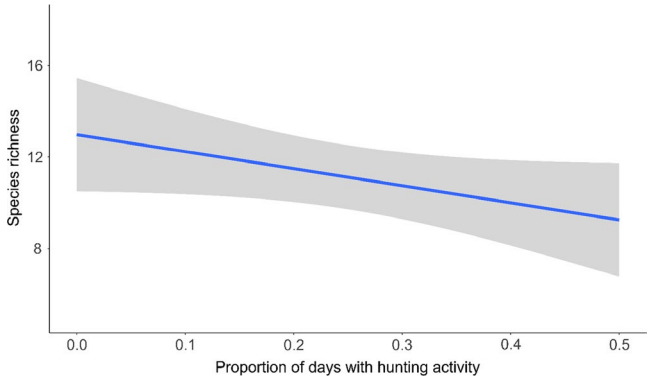

FIGURE 3 Relationship between hunting intensity and estimated species richness in southern Belize across all sample sites, which is conditional on all species being detected at least once during the survey period. The blue line is the regression line estimated in the two-step analysis that accounts for both the estimation error and the residual variation around the regression line. The grey area around the regression line gives the 95% credible interval of the prediction

4 | DISCUSSION

4.1 | Measures of hunting activity

Our study demonstrates a novel integrated approach to estimate hunting intensity and distribution with passive acoustic monitors, while also incorporating species data from camera traps to provide inferences on the relative effects of hunting pressure on mammal communities. Several methods have been used in the past to measure hunting in forested areas, including: resident interviews, camera traps and ranger patrols (De Thoisy, Renoux, & Julliot, 2005; Di Bitetti, Paviolo, Ferrari, De Carlos, & Di Blanco, 2008; Jenks et al., 2012; Remis, 2000; Urquiza-Haas, Peres, & Dolman, 2011). However, each of these methods has significant limitations with the scale and accuracy of hunting data it provides. For example, interviews of residents and potential hunters are often unreliable, as respondents may provide incorrect information (either accidentally or purposefully) regarding their hunting locations and activity (Aiyadurai et al., 2010; Madhusudan & Karanth, 2002). Additionally, interview data rarely provide precise measures of spatiotemporal hunting patterns, which may lead to spatially extensive generalizations of hunting activity that adversely affect inferences on the impacts of hunting pressure on species (unpublished interviews [MD], Aiyadurai et al., 2010). Similarly, ranger patrols are potentially misleading as they rely on a ranger's ability to visually identify evidence of previous hunting events, which is especially challenging in areas

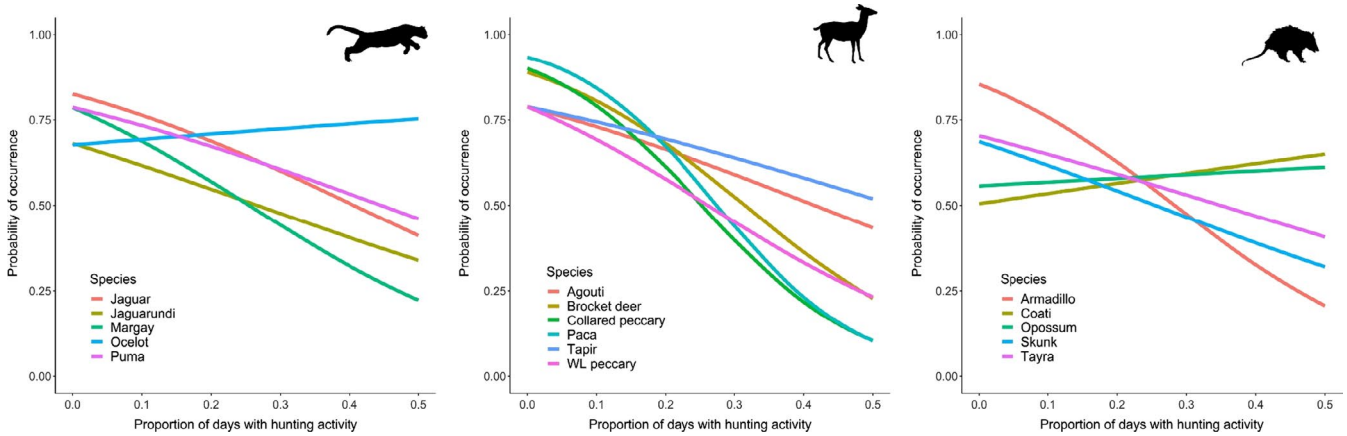

FIGURE 4 Predicted marginal probabilities of species occurrence in relation to hunting intensity for three functional groups: carnivores, herbivores and omnivores

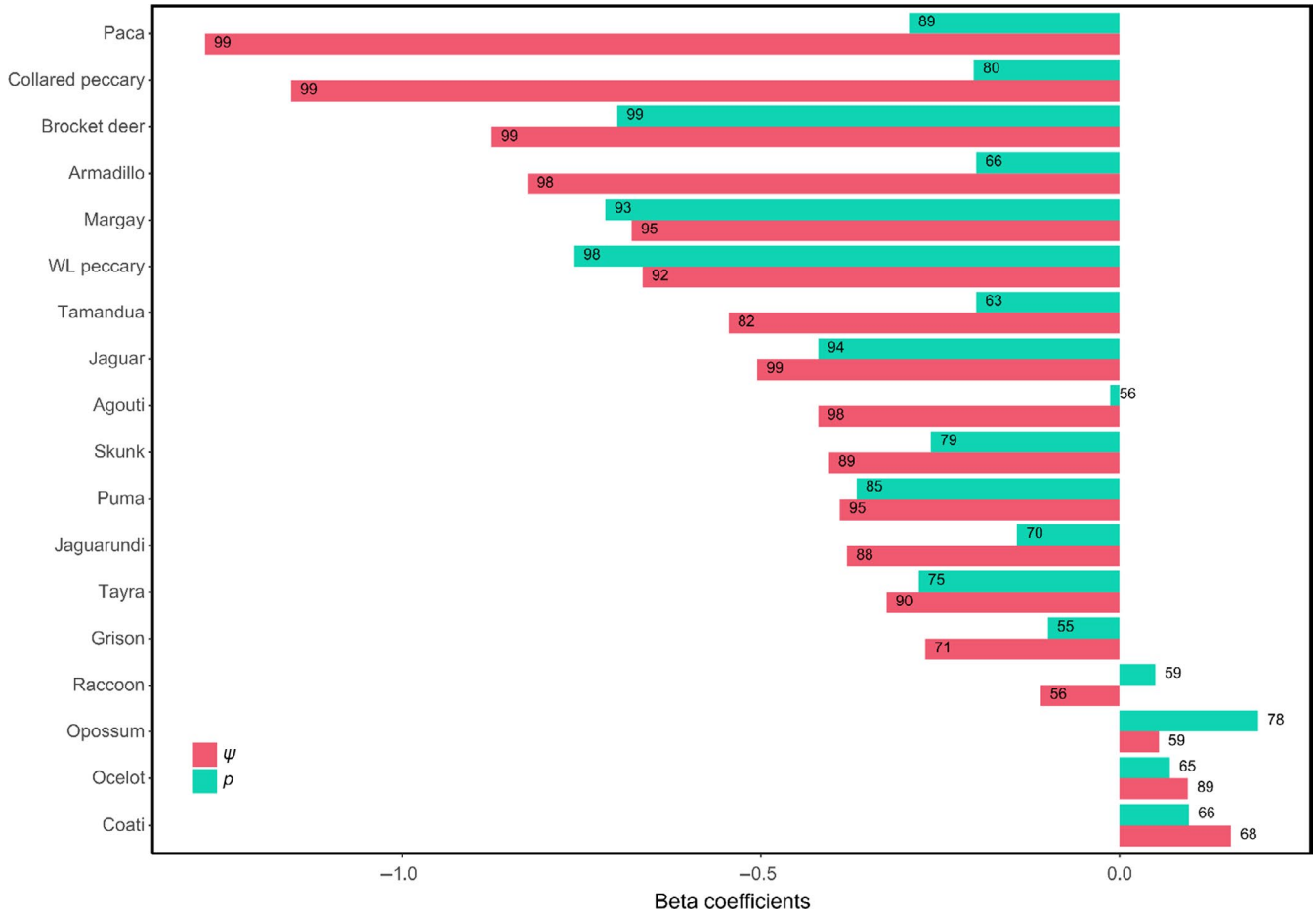

FIGURE 5 Species-specific standardized beta coefficients from the community model in response to hunting intensity for occupancy (ψ) and detection probability (p). Numbers after/inside bars represent the percentage of model runs with the same direction as the mean for each species

where firearm-based hunting is predominant. These observations can be further constrained by the spatial and temporal limitations many rangers face (Brashares & Sam, 2005). For example, park ranger teams are often under-staffed and tasked with monitoring large areas of forest, which makes routine patrols of entire protected areas rare, potentially resulting in spatially autocorrelated hunting distributions around frequent patrol routes. In addition, patrolling at night, when many hunters are typically active, is uncommon, which may result in rangers further underestimating hunting intensity. Furthermore, Burton et al. (2012) used ranger patrols to monitor hunters and found that hunting pressure is particularly difficult to estimate with this method, since hunters actively seek to avoid detection from patrols.

The limitations of human-based monitoring of hunting likely contributed to the implementation of passive monitoring methods that alleviated some of these spatiotemporal constraints. In recent years, camera traps have been used to monitor hunting activity, and while they are cost-efficient and provide precise measures of spatiotemporal hunting activity (e.g. GPS points and timestamps), they also have considerable limitations. Comparing camera traps to acoustic monitors, we found that camera traps under-detected hunting events in our study area by 939%, despite having 20 more locations. Camera traps also misrepresented the distribution of hunting intensity by failing to detect the majority of nearby hunting events. Identifying hunting events with camera traps relies on hunters walking directly in front of a camera, which significantly limits their ability to reliably measure hunting, due to an inherently narrow field of view. It is well-established that hunters actively seek to avoid detection and can simply maneuver around camera traps once they have been spotted. In our study, we also had several cameras stolen or destroyed by suspected hunters in order to avoid detection.

In contrast to camera traps, we found passive acoustic monitors to be quite effective in measuring hunting activity, largely due to their significantly larger detection radius. While camera traps have a ~120° effective field of view and a range of approximately 5 m, acoustic monitors have a 360° field of view and range of 1.25 km. This advantage exponentially improves an acoustic monitor's ability to detect hunting events in a given area and makes them better suited for studies at multiple spatial extents. Another benefit is that acoustic monitors can be hidden off-trail and high off the ground, making them virtually impossible for hunters to find. During our 6 months of data collection, we did not lose any acoustic monitors to theft or damage. Moreover, by utilizing available analysis software (e.g. Kaleidoscope), researchers and park managers can create

classification algorithms to identify gunshots, making the identification process relatively straightforward and viable for both ecological and enforcement applications. Still, there are some limitations worth considering. First, the upfront cost of combining acoustic monitors with camera traps may make the method unfeasible for some, but we believe the medium- and long-term benefits of this approach outweigh the initial monetary investment by significantly increasing spatiotemporal monitoring capacity for both law enforcement and research applications. Second, the only form of hunting detected by acoustic monitors is in the form of gunshots. Therefore, if hunters in a region regularly use alternative methods to hunt (e.g. snares), then acoustic monitors are not a viable option. Nevertheless, acoustic monitors show considerable promise to link firearm-based hunting metrics with wildlife data and as a potential applied conservation tool to help rangers and conservation groups track and combat illegal hunting.

4.2 | Hunting impacts

Our model results provide valuable insight into the impacts of hunting pressure on mammal species richness and spatial patterns. By implementing a hierarchical community model, we were able to analyse patterns across the mammal community while also identifying species-specific responses. Obtaining reliable community and species-specific data in response to anthropogenic disturbances is a topic of considerable interest, especially for phenomena that are difficult to measure, such as hunting. Furthermore, being able to draw reliable inferences on the impacts of hunting activity for rare or elusive species with few detections is increasingly valuable and makes hierarchical models attractive for addressing both ecological and conservation questions (Zipkin et al., 2009). Still, responses to covariates are generally more apparent among species with a greater number of detections, as was the case in our study, which likely also influenced community-level effects (Burton et al., 2012).

Across the mammal community, our findings suggest that hunting has a significant negative impact on species richness and occurrence. The general trend across all three functional groups was similar, but groups differed in the severity of their responses (Figure 4). Herbivores showed the strongest negative response to hunting. All herbivores, except for tapir, are commonly hunted as bushmeat in the region, and potential overhunting may be causing a significant local reduction in these populations, especially in forests adjacent to villages. Nevertheless, tapirs still showed a significant negative response to hunting, which may indicate that the presence of hunters alone is enough to cause adverse effects on species spatial patterns.

Although carnivores and omnivores are not typically hunted, they too showed reduced occurrence probabilities in hunted areas. For carnivores, this could be in part due to a decrease in prey availability or a negative response to the noise of gunshots, which may further suggest that species not targeted by hunters can also be negatively impacted by hunting activity, potentially leading to a cascading effect in the localized loss of species richness. Additionally, some carnivores (e.g. jaguars and to a lesser extent puma and ocelot) are persecuted for attacks on livestock and may be more wary around villages and agricultural lands. Ocelots were the only carnivore species to have a positive response to increased hunting pressure, while the two other small cats, margay and jaguarundi, showed strong negative responses to hunting. For ocelots, this positive response could be in part due to decreased competition for prey with larger cats. Ocelot prey varies widely in size from birds and small mammals <1 kg to large mammals (e.g. brocket deer), while margay and jaguarundi predominantly prey on birds and small mammals <1 kg and squamates (Oliveira et al., 2010). Therefore, it is possible that reduced availability of medium and large mammals potentially due to elevated hunting pressure facilitates increased competition for prey between ocelots and the two smaller cats, which may explain their strong negative response in areas with increased hunting intensity.

Although armadillos are hunted opportunistically, the remaining omnivores in our study are not regularly targeted by hunters (unpublished interviews [MD]). There was a larger variation in responses among omnivores than other functional groups, with coati and opossum both showing positive responses to increased hunting intensity. These species are very successful generalists and have been shown to be tolerant of human activities (Dobbins, 2020), which likely contributed to their positive responses. In a meta-analysis of over 100 studies investigating the relationship between hunting and mammal abundance, Benítez-López et al. (2017) found that smaller mammals were more abundant than large mammals in areas of high hunting intensity, likely due to a decrease in both competition and predation pressure.

4.3 | Conservation significance

Previous studies have largely found that hunting is contributing to the decline of many mammal species across the globe (Cuthbert, 2010; Kumara & Singh, 2004; Mesquita & Barreto, 2015; Naughton-Treves, Mena, Treves, Alvarez, & Radeloff, 2003; Ripple et al., 2016) and that hunting often creates 'halos of defaunation' around settlements (Beirne et al., 2019), which makes gathering precise spatiotemporal hunting data essential for ecological studies and conservation management. Because researchers employ many different methods to measure hunting activity, understanding their limitations and potential impacts on species occurrence patterns is increasingly relevant. For example, if we had used hunting data from camera traps to inform species occurrence models, we likely would have drawn very different conclusions about the impacts of hunting on the mammal community, potentially leading to misinformed management and policy decision-making. From a protected areas management perspective, generating well-informed, spatially extensive maps of hunting distribution and intensity is invaluable to inform patrolling effort and monitoring strategies.

In this study, we have shown that using camera traps to measure hunting may significantly underestimate hunting activity and contribute to unreliable inferences on hunting intensity, distribution and its subsequent impacts on species. As the human population continues to grow and expand, the demand for bushmeat and other wildlife products will increasingly pressure already-depleted mammal communities. The severity and magnitude of this situation has been repeatedly reported in the scientific literature, but what is lacking, and perhaps is this works' most significant contribution, is a means of simultaneously providing a flexible framework for investigating the impacts of firearm-based hunting on mammal communities, while also allowing for the near real-time monitoring of hunting activity and distribution over large areas for parks and law enforcement.

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AUTHORS' CONTRIBUTIONS

M.D. conceived of the study design and methodology; M.D. and S.M. collected the data; M.D. analysed the data; M.D., R.S., E.B. and A.A.Z. contributed to the writing of this manuscript.

DATA AVAILABILITY STATEMENT

Data are available via the Dryad Digital Repository https://doi.org/10.25338/B84K77 (Dobbins, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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