Logging and indigenous hunting impacts on persistence of large Neotropical animals

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ABSTRACT

Areas allocated for industrial logging and community-owned forests account for over 50% of all remaining tropical forests. Landscape-scale conservation strategies that include these forests are expected to have substantial benefits for biodiversity, especially for large mammals and birds that require extensive habitat but that are susceptible to extirpation due to synergies between logging and hunting. In addition, their responses to logging alone are poorly understood due to their cryptic behavior and low densities. In this study, we assessed the effects of logging and hunting on detection and occupancy rates of large vertebrates in a multiple-use forest on the Guiana Shield. Our study site was certified as being responsibly managed for timber production and indigenous communities are legally guaranteed use-rights to the forest. We coupled camera-trap data for wildlife detection with a spatially explicit dataset on indigenous hunting. A multi-species occupancy model found a weak positive effect of logging on occupancy and detection rates, while hunting had a weak negative effect. Model predictions of species richness were also higher in logged forest sites compared to unlogged forest sites. Density estimates for jaguars and ocelots in our multiple-use area were similar to estimates reported for fully protected areas. Involvement of local communities in forest management, control of forest access, and nesting production forests in a landscape that includes protected areas seemed important for these positive biodiversity outcomes. The maintenance of vertebrate species bodes well for both biodiversity and the humans that depend on multiple-use forests.

Key words: bush meat; Iwokrama; occupancy model; production forests; reduced-impact logging; selective logging; subsistence hunting; wildlife management.

MANAGED FORESTS CAN EXTEND THE FORMAL 'CONSERVATION ESTATE' BEYOND THE BOUNDARIES OF PROTECTED AREAS (*e.g.*, Clark *et al.* 2009, Putz *et al.* 2012, Edwards *et al.* 2014a). For tropical forests managed principally for timber, the magnitude of this conservation benefit depends on the policies and practices implemented during timber harvests and in the periods between harvests. Control of forest access is of especially high priority to curb the illegal hunting that has contributed to global declines of vertebrate populations (Redford 1992, Wilkie *et al.* 2000, Laurance & Edwards 2014, Bicknell *et al.* 2015a). Faunal loss may affect forest productivity, tree species composition, and the food security of forest-dependent people (Levi *et al.* 2009, Dirzo *et al.* 2014).

Hunting pressure in tropical timber concessions is especially high due to the improved access provided by logging roads and the influx of forestry workers, miners, and other people (Robinson & Bennett 2000, Wilkie *et al.* 2000). The largest vertebrates are the preferred prey of most human hunters and the first to decline due to their characteristically low fecundities and sparse populations (Peres 2000). Their population recovery rates are also

impeded if their home ranges are reduced subsequently by forest conversion into croplands or pastures (Morrison *et al.* 2007). Depletion of large vertebrates may directly affect recruitment and survival of many tree species through loss of their dispersal services (Harrison *et al.* 2013, Caughlin *et al.* 2014). For example, tapirs (*Tapirus spp.*), the largest mammal native to the Neotropics and an often over-hunted herbivore, are important seed dispersers for many large-seeded tree species such as *Manilkara zapota*, a canopy tree species commercially important for both its timber and latex (Fragoso & Huffman 2000, O'Farrill *et al.* 2013). The ability of vertebrates to persist in and move around tropical forests is thus of great importance for natural regeneration processes that contribute to the recovery of timber species and carbon stocks in managed forests (Jansen & Zuidema 2001, Rosin 2014, Osuri *et al.* 2016).

Strictly protected areas are and will remain critical for conservation but many are not large enough to maintain viable populations of vertebrates with large home ranges, including apex predators (Peres 2005, Cantú-Salazar & Gaston 2010). As selective logging leaves most of the forest intact, large production forests adjacent to protected areas will allow continued animal movements and thereby reduce fragmentation (Elkin & Possingham 2008, Edwards *et al.* 2014b). Despite the critical ecological

importance and threatened status of many large vertebrates, knowledge about the impacts of logging on this group of animals remains limited (Vetter *et al.* 2011). For example, a recent meta-analysis of logging impacts on biodiversity that utilized 48 studies included only one study on large vertebrates (Burivalova *et al.* 2014).

Given that the majority of timber concessions experience substantial hunting pressure, it is difficult to untangle the effects of logging from those associated with hunting (Vetter *et al.* 2011, Brodie *et al.* 2015). Hunting is an especially complex issue where subsistence hunting by indigenous people is legally sanctioned and managed forests abut or overlap with their traditional lands. This study was able to address both of these issues because it was conducted in a sustainable-use reserve co-managed by a non-governmental organization (Iwokrama International Centre; http://iwokrama.org) and local indigenous communities (North Rupununi District Development Board; http://nrddb.org) who jointly develop forest use policies. Iwokrama's forest operations were certified by the Forest Stewardship Council (FSC) as responsibly managed, access and hunting by non-indigenous people is strictly controlled, and the permanency of the forest estate is nationally legislated. We assess the biodiversity outcomes specific to large vertebrates that derive in part from these resource-use policies.

We partition the effects of selective logging and subsistence hunting by indigenous people on large terrestrial vertebrates (>1 kg) with animal surveys using camera traps and spatially explicit surveys of indigenous hunting. We apply a hierarchical multi-species occupancy model to our binary detection data that enables us to account for species-specific differences in detectability associated with behavior and abundance (Iknayan *et al.* 2014). This statistical method quantifies the impacts of both logging and hunting on the occupancy state of large vertebrates in a lowland Neotropical forest in Guyana that is known to harbor substantial populations of game animals such as tapirs (*Tapiris terrestris*), deer (*Mazama spp.*), giant armadillos (*Priodontes maximus*), paca (*Cuniculus paca*), peccaries (Tayassuidae), as well as large predators such as jaguars (*Panthera onca*), and pumas (*Puma concolor*) that are rare or absent in degraded forests (Lim & Engstrom 2005, Read *et al.* 2010).

METHODS

STUDY AREA.—Fieldwork was conducted in Iwokrama Forest in central Guyana (4–5° N, 58.5–59.5°W; Fig. 1), a 370,000-ha conservation area. Iwokrama is zoned into a sustainable-use area where selective logging and other resource-use activities are permitted (*e.g.*, ecotourism and non-timber forest product extraction), a wilderness preserve where anthropogenic disturbances are prohibited, and a titled indigenous community resource-use area. This moist tropical rain forest, with small areas that are seasonally flooded, is located on the Guiana Shield and receives 2693 mm of annual rainfall with a marked September–November dry season (<150 mm/month; Bovolo *et al.* 2012). The area is
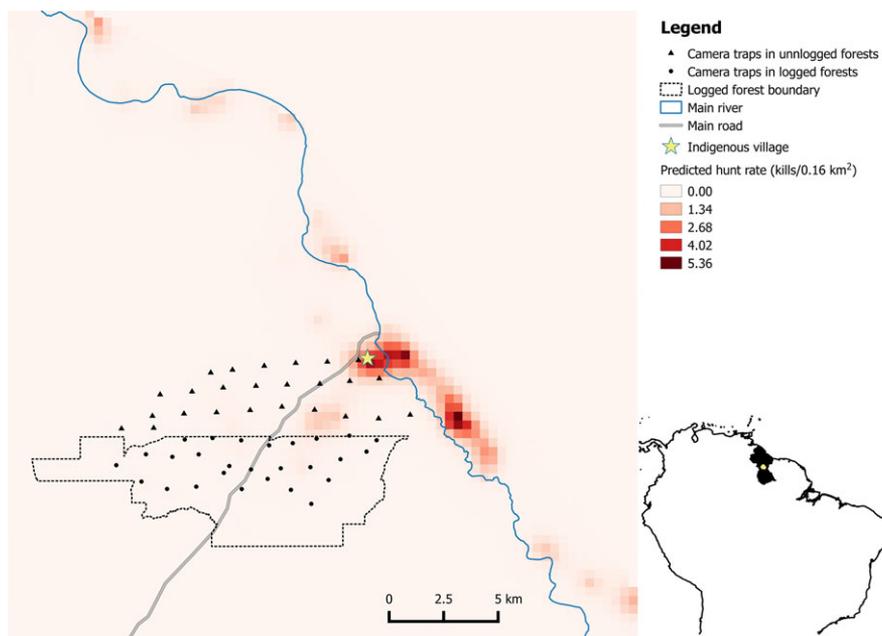

FIGURE 1. Study site location overlain with the predicted hunting surface extracted from a model that uses spatial locations of successful kills over 21 months (2007–2010, total number of kills = 210). Camera traps were installed in 2011 for 808 camera trap nights in logged forests and 805 camera trap nights in unlogged forests. The effective camera trap sample areas were ~ 5747 ha and ~ 6000 ha in logged and unlogged forests, respectively. The indigenous village studied is the only settlement within the sustainable-use reserve. All camera traps outside of the logged forest boundary are located in unlogged forests within Iwokrama. [Inset-map: Guyana is indicated by the filled outline on the South American map, with Iwokrama in the center of Guyana].

characterized by highly weathered and nutrient-poor soils, slow canopy dynamics, and high forest biomass as a result of high densities of trees of species with high density wood that mostly produce large seeds (Hammond 2005, Malhi *et al.* 2009). The canopy of these species-rich forests is dominated by *Catostemma spp., Eperua falcata, Eschweilera spp., Swartzia leiocalycina, Mora excela, Carapa guianensis,* and *Chlorocardium rodiei* (ter Steege 2000). Iwokrama is part of one of the least fragmented lowland tropical rainforests in the Americas and supports an intact community of large vertebrates (Watkins 2010; Fig. S1).

Timber harvesting operations in Iwokrama followed reduced-impact logging (RIL) standards that included a pre-harvest inventory, liana cutting on trees to be harvested, road planning, directional felling, and cable winching. Harvesting is carried out with a 60-year harvest cycle and a minimum cutting diameter of 40 cm dbh (diameter at 1.3 m aboveground). Average harvest intensity in our study area was 12.4 m^3/ha (~6 trees/ha) but was spatially heterogeneous (minimum = 9.1 m^3/ha and maximum = 16.4 m^3/ha) with an average of 72 m/ha of roads and skid trails (Rodney 2013a). Densities of trees ≥20 cm dbh in 12 ha of permanent sample plots in unlogged forest and 169 ha of plots in once logged forests averaged 228 trees/ha and 161 trees/ha, respectively (Rodney 2013b). The forest was FSC certified during the study period.

Iwokrama is remote, approximately 240 km from the nearest non-indigenous settlement, but accessible by an all-weather dirt road with entry controlled at several checkpoints; these characteristics together lead to minimal hunting other than for subsistence purposes by local indigenous people. Other land-use practices such as swidden agriculture are controlled by co-management protocols negotiated with the Makushi and Wapishana tribes, who have utilized these forests for thousands of years (see Plew 2005, Read *et al.* 2010, Luzar *et al.* 2011 for a detailed description of the biophysical and social environments).

CAMERA-TRAP DATA.—A total of 52 camera-trap stations were monitored in June-August 2011 with 27 in logged and 25 in an adjacent unlogged forest (Fig. 1). The unlogged forest is a 6000 ha contiguous buffer zone for the 5747 ha logged area. Timber was harvested during 2007–2011, with the majority completed prior to the study. Camera-trap stations (Cuddeback® Capture, Non-typical Inc., WI, USA) were arranged 1–1.5 km apart at sites with signs of animal activity (*e.g.,* animal tracks, scat) to increase chances of photo captures. Each station comprised two cameras installed on opposite sides of the presumed animal path to increase captures and to buffer against camera failure. The effective sample area of each camera-trap station was assumed to be a circle with a diameter of 1.5 km (see TEAM Network 2011). Frames were captured 24 h per day with a 1-min delay between exposures with the date and time recorded. Consecutive photographs of the same species at the same site were considered new individuals when there was at least a 1-hour interval between 'captures', except for when individuals were identifiable by unique markings (following Bowkett *et al.* 2007). Due to limitations on equipment and personnel, cameras were

deployed sequentially, first in the logged forest and immediately after in the adjacent unlogged forest. Cameras were active for 30–33 days at each site (*i.e.,* 1613 trap nights).

We used spatially explicit capture–recapture models (SECR) to estimate densities of species with uniquely identifiable individuals across the entire multiple-use area surveyed (jaguars and ocelots; Gopalaswamy *et al.* 2012) and mean camera-trapping rates as proxies for densities between logged and unlogged sites for all species (Rovero & Marshall 2009). The SECR density estimates for jaguars and ocelots were not partitioned into logged and unlogged forests due to the large home ranges of these carnivores (*e.g.,* jaguars >10 km^2; Rabinowitz & Nottingham 1986, Maffei *et al.* 2011), and the contiguous spatial nature of the logged and unlogged forests. Our goal of estimating density is to compare overall SECR density estimates from our multiple-use area with protected forests with little to no anthropogenic disturbance.

HUNTING DATA.—Survey data on animal kills by hunters from the indigenous community within Iwokrama Forest were collected from 2007–2010 as part of a wider regional study on subsistence livelihood strategies (see Read *et al.* 2010, Luzar *et al.* 2011, Fragoso *et al.* 2016). Hunting surveys were administered to every household in the community by locally recruited indigenous technicians who were residents of the community and trained by project researchers. A hunting record consisted of a hunter ID, the spatial location of the kill site identified by the hunter on a topographic map, and the species hunted. Quality control checks were carried out throughout the data-collection process to identify mistakes and potential falsification of self-reported hunting events. For a discussion of the strengths and limitations of these self-reported hunting data, see Luzar *et al.* (2011).

We filtered the hunting records to include only large terrestrial vertebrates (>1 kg; Appendix S1: Table S1), which led to the exclusion of mainly aquatic species (*e.g.,* river turtles). Kill sites marked by the hunters on a topographic map were used to estimate hunting rates for 400 m × 400 m grid cells across a minimum convex polygon (39,000 ha) that captured all kills as well as the logged and unlogged forest areas where camera traps were deployed. Total number of kills for the entire study period was then extracted for each grid cell and used as a response variable. As our question here concerns how hunting affects wildlife occupancy, we used total number of kills as a cumulative metric of spatial hunting rates across the 21 months of data from the livelihood study. We used a negative binomial distribution to account for over-dispersion because the number of kills is heavily skewed toward zero with a few large outliers (Bolker 2008, Appendix S1: Fig. S1). We then predicted mean hunting rate (μ) for each grid cell (j) as a function of distance from the village within Iwokrama with an integrated nested Laplace approximation (INLA; Lindgren *et al.* 2011) to account for spatial autocorrelation, where ξ_j represents a spatial random effect. Distance (β_{hunting}^1) from the village was the only fixed effect in our hunting model (distance from the nearest road and river did not improve model fit and were excluded in the final

$$\log(\mu_j) = \alpha_{\text{hunting}} + \beta^1_{\text{hunting}} \times \text{Village}_{\text{distance}_j} + \xi_j.$$

Our analysis improves on recent efforts to decouple hunting and logging effects on wildlife by explicit inclusion of spatially referenced kill locations. This approach contrasts with other studies that relied on categorical classifications of hunting (often just unhunted vs. hunted) or metrics such as hunter encounter rates (Poulsen *et al.* 2011, Brodie *et al.* 2015). The advantage of predicting a mean hunting rate as a covariate in the occupancy model is that the continuous nature of a hunting rate prevents a loss of statistical power compared to when continuous variables are discretized into binary categories such as 'hunted vs. non-hunted' (Gelman & Park 2009). One caveat to our hunting rate approach is that our surveys did not contain information to allow us to define the catch-per-unit-effort. If catch-per-effort is high in areas where animal abundance is low, our simple hunt rate could be misleading. However, agent-based simulations of hunting at our study region found that villages with a confined hunting territory leads to source-sink meta-population dynamics of prey species where forest cover is maintained, potentially leading to relatively constant catch-per-unit-effort (Iwamura *et al.* 2014). In addition, we found that our model-derived hunt rate led to much better model fit of occupancy models, compared to the simpler metric of distance-from-village (Appendix S2).

MULTI-SPECIES OCCUPANCY MODEL.—For our occupancy model, we extracted detection records (present/absent) from the camera-trap data and used these binary observations as our response variable. Camera-trap location was used to situate each trap in either logged or unlogged forest and to predict hunting rates from our spatially explicit hunting model. We used standard hierarchical occupancy models that are widely used for wildlife camera-trap data (Ahumada *et al.* 2013, Tobler *et al.* 2015, Rich *et al.* 2016). Our model represents a multi-species approach to obtain composite information by estimating occurrence probabilities for each species (Dorazio & Royle 2005). The hierarchical model structure permits distinction between non-detection and true absence by an explicit and formal representation of the data into constituent models of the observations (detections) and of the underlying ecological processes (occupancy; Clark 2005, Royle & Dorazio 2008, Iknayan *et al.* 2014). The advantage of a community-level approach is that parameter estimates for data-poor species are more precise because they borrow strength from data-rich species (Zipkin *et al.* 2010, Pacifici *et al.* 2014). We refer to community-level occupancy as the mean occupancy rate across all species, with species-level occupancy drawn from this global distribution (Royle & Dorazio 2008, Zipkin *et al.* 2010). The point-level occurrence model is specified as a Bernoulli distribution, $z(i,j) = \text{Bern}(\psi_{i,j})$ where $\psi_{i,j}$ is the probability that species *i* occurs at site *j*. We accounted for species identity in our models of detection and occupancy using species-level random effects for both the intercept term as well as the parameters that describe effects of hunting and logging. Site level effects are incorporated into the model linearly on the logit probability scale:

$$\text{Logit}\left(\psi_{i,j}\right) = \alpha_i + \beta_i^{\text{logged}} \times \text{LOGGED}_j + \beta_i^{\text{Hunt}} \times \mu_j$$

in which α_i is the intercept term for the occurrence probability of species *i* in unlogged forests, and β_i^{logged} and β_i^{Hunt} are parameters that capture the effects of logging and hunting pressure for species *i*. LOGGED_j indicates whether a grid cell is located in logged or unlogged forests and μ_j is the hunting rate predicted by our INLA model. The detection-level model was similar to the occupancy-level model described above insofar as it included the same covariates in a logit-transformed linear model, with intercept, logging, and hunting parameters estimated as species-level random effects. As an additional metric of community-level response to hunting and logging, we calculated species richness as the sum of species occupancy values at each site.

Of the many ways to account for space in this modeling framework, we chose to use spatially varying covariates to address spatial non-independence; we explicitly modeled the environmental factors that drive variability in the response variable. This approach is desirable because parameters that represent the effect size of these spatially varying covariates have direct biological interpretations (Burton *et al.* 2012). Another (non-mutually exclusive) approach is to estimate the effect of space with models for between-point spatial autocorrelation (Royle *et al.* 2009). We found little evidence for additional spatial autocorrelation in our models once the effects of hunting rate and logging were included (Appendix S2: Description of the spatial vs. non-spatial models) and so we present hierarchical occupancy models with hunting rate as a spatially varying covariate. We also compared our occupancy model that used hunt rate derived from our INLA analysis with a model that substituted distance-to-village and found that hunt rate outperformed distance-from-village as a predictor of occupancy (Appendix S3).

We parameterized our models in a hierarchical Bayesian framework, constructed in the R coding platform (R Core Team 2015) using R-INLA and JAGS (Plummer 2011), with non-informative priors (Appendix S4: model description and complete R and JAGS code). We ran three chains of length 1,500,000 after a burn-in of 500,000, thinned the posterior chains by 2,800, and assessed model convergence using the Gelman-Rubin statistic (Gelman & Hill 2007). To assess statistical power, we simulated occupancy data across a range of parameter values and tested whether our sample size was sufficient to estimate parameter values (Appendix S5). We present our data, model, and simulation code as supplementary materials and online in an open access repository (doi:10.5061/dryad.t2s27).

RESULTS

CAMERA-TRAP DATA.—We captured 270 and 180 independent photographs of 17 and 15 species in the logged and unlogged forest, respectively (Appendix S1: Figs. S1 and S2). Detections were highest for frugivores (*e.g.,* agoutis and trumpeters) and lowest for omnivores and insectivores (*e.g.,* armadillos, tayras, and coatis; Table 1). Tayras and coatis were detected in logged but not

TABLE 1. Species photographed in Iwokrama forest arranged by feeding guild (activity period), body size (kg), density (individuals/km²), threatened status (Emmons & Freer 1990, IUCN 2016) and hunting pressure. Hunting rate is based on 21 months of data collection (see methods). Mean camera trapping rates are used as proxies for species abundance and based on independent photo captures over the sample period.

| Scientific name | Common name | Feeding guild (active period) | Size (kg) | Density estimates (individuals/km²) | IUCN Status | Mean (SE) camera trapping rate | | Mean (SE) monthly hunting rate |
						Logged	Unlogged	
Crax alector	Black Curassow	Frugivore (diurnal)	2.4–3.7	6.90*	Vulnerable	4.33 (±0.68)	2.61 (±5.15)	0.24 (±0.19)
Cuniculus paca	Spotted Paca	Frugivore (nocturnal)	5.0–13.0	84.00–93.00	Least concern	0.25 (±5.76)	0.37 (±1.55)	2.24 (±0.63)
Dasyprocta leporina	Red-rumped Agouti	Frugivore (diurnal)	3.0–5.9	10.50*	Least concern	7.80 (±9.36)	6.34 (±9.12)	2.38 (±1.06)
Dasypus sp	Armadillo	Insectivore (nocturnal)	2.7–6.3	Unknown	Least concern	0.25 (±1.35)	0.37 (1.55)	0.86 (±0.28)
Eira barbara	Tayra	Omnivore (diurnal)	2.7–7.0	9	Least concern	0.50 (±1.27)	0 (±0.00)	No hunting record
Leopardus pardalis	Ocelot	Carnivore (nocturno-crepuscular)	8.0–14.5	0.03–0.80 (0.16 ± 0.06)	Least concern	2.10 (±4.40)	0.37 (±1.17)	No hunting record
Leopardus wiedii	Margay	Carnivore (nocturnal)	3.0–9.0	0.01–0.05	Near threatened	0.12 (±0.68)	0.37 (±1.55)	No hunting record
Mazama americana	Red-brocket Deer	Herbivore (nocturno-crepuscular)	24.0–48.0	0.10–0.30	Data deficient	1.36 (±3.12)	0.87 (±2.60)	0.14 (±0.10)
Mazama gouazoubira	Gray-brocket Deer	Herbivore (nocturno-crepuscular)	11.0–18.0	0.35–1.00	Least concern	0.99 (±1.91)	0.62 (±1.76)	0.10 (±0.10)
Myrmecophaga tridactyla	Giant Anteater	Insectivore (diurnal)	22.0–39.0	0.12–0.41	Vulnerable	0.12 (±0.68)	0.25 (±0.98)	0.05 (±0.05)
Nasua nasua	Coati	Omnivore (diurnal)	3.0–7.2	6.20–13.00	Least concern	0.12 (±0.68)	0 (±0.00)	No hunting record
Panthera onca	Jaguar	Carnivore (nocturno-crepuscular)	31.0–158.0	0.01–0.11 (0.02 ± 0.003)	Near Threatened	2.60 (±5.19)	0.12 (±0.70)	No hunting record
Pecari tajacu	Collared Peccary	Frugivore (diurnal)	17.0–35.0	3.00–7.00	Least concern	0.74 (±2.25)	1.12 (±3.20)	1.33 (±0.58)
Priodontes maximus	Giant Armadillo	Insectivore (nocturnal)	18.7–32.3	0.05–0.06	Vulnerable	0.25 (±0.94)	0.5 (±1.32)	0.05 (±0.05)
Psophia crepitans	Gray-winged Trumpeter	Frugivore (diurnal)	1.0–1.5	15.30*	Least concern	4.46 (±8.22)	7.83 (±11.96)	No hunting record
Puma concolor	Puma	Carnivore (nocturnal)	29.0–120.0	0.02–0.05	Least concern	4.95 (±5.10)	0.25 (±0.98)	No hunting record
Tapirus terrestris	Tapir	Herbivore (nocturno-crepuscular)	227.0–250.0	0.20–3.70	Vulnerable	2.35 (±4.23)	0.37 (±1.55)	0.29 (±0.10)

Size and density estimates are minimum and maximum values reported in Emmons & Freer (1990) and IUCN (2016) respectively; Density estimates with '*' are based on studies in unlogged forests in Iwokrama (Bicknell & Peres 2010). Mean densities (individuals/km²) were estimated for ocelots and jaguars with SECR models with our data shown in parenthesis (means and standard deviations). Mean camera-trapping rates are the ratio of independent photo captures to the number of trap days multiplied by 100 (Rovero & Marshall 2009).

unlogged forest. Mean camera-trapping rates were 18 times greater in the logged forest for the largest carnivores (jaguars and pumas) and three times greater for the largest herbivores (tapirs and red-brocket deer) compared to the unlogged forest (Table 1). Animal densities based on uniquely identifiable individuals for jaguars and ocelots across the combined logged and unlogged forests were estimated at 1.72 individuals/100 km^2 (95% CI; 1.55 – 2.32) and 16.20 individuals/100 km^2 (95% CI; 6.92 – 26.7), respectively (Table 1). These values are similar to those reported in the literature for protected areas.

HUNTING DATA.—We recorded 210 spatially unique hunting kill sites for 13 terrestrial species over 21 months of surveys. All species in the hunting data were also detected with camera traps except two tortoise species, accouchi, and white-lipped peccaries that together account for 23% of all reported kills (Appendix S1: Table S1). Seven species, mainly from the order Carnivora (jaguars, pumas, ocelots, margays, coatis, and tayras) and gray-winged trumpeters, accounted for 38% of all photographs but were not recorded in the hunting data. Species with the highest monthly kill rates were agoutis, pacas, and two peccary species (Table 1). Although distance from the village had a non-significant mean effect (−0.0002; 95% CI, −0.0006 to 0.0001), it was a better predictor of hunting intensity than distance from the nearest road or river. The majority of kill sites were <10 km and mostly upstream from the village (Fig. 1; Appendix S1: Fig. S3). Although much of the logged forest was <10 km from the village, it hosted little hunting.

MULTI-SPECIES OCCUPANCY MODEL.—Across all species and sites (logged and unlogged forests), detection had a median value of 4.12% (95% CI, 0.40–28.91%), and occupancy had a median value of 54.43% (95% CI, 8.36–94.01%). Both logging and hunting had relatively small and non-significant effects on occupancy and detection rates (Fig. 2). Logging resulted in a median increase of 8.81% (95% CI, −16.97–34.48%) in community-level occupancy. Species-level effects of logging on occupancy were weak and uncertain, with 50% CI overlapping zero for most species (Fig. 3; Appendix S1: Fig. S4). Results from our power analysis suggest that if there had been a significantly negative effect of logging on occupancy, we would have had sufficient statistical power to detect it (Appendix S5). Community-level occupancy at the sites with the highest hunting pressure declined by a median value of 25.01% (95% CI, −57.04–17.38%) relative to sites that experienced no hunting. Species-level effects of hunting on occupancy were consistently negative for most species, with the strongest (although non-significant) effects on agoutis (Figs. 3 and 4; Appendix S1: Fig. S4). Using posterior samples, we estimate the probability of negative effects of logging and hunting on community-level occupancy as 24.49% and 88.45%, respectively.

We estimated median observed species richness per sample site at 10 species (95% CI, 5–11) in logged forests and 8 species (95% CI, 2–12) in unlogged forests (Fig. 5). Compared to logging, there was a greater effect of hunt rate on estimated species richness, with a median of 10 species at the sites with no hunting
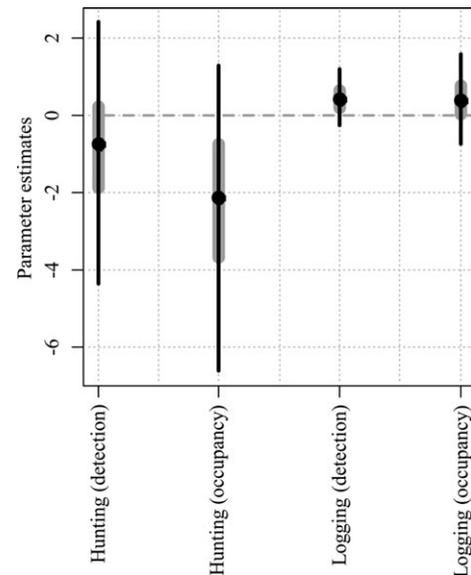

FIGURE 2. Community-level effects of logging and hunting on occupancy and detection. Dark vertical lines represent 95% credible intervals and gray bands represent the 50% credible intervals.

(95% CI, 7–12), compared to a median value of three species (95% CI, 0–6) at the site with the highest hunting rate.

Overall, logging was associated with higher community-level detection of large vertebrates by a median value of 1.76% (95% CI, −0.97–6.08%). The strongest species-level effects of logging on detection were observed for the three terrestrial cat species (*i.e.,* jaguars, pumas, and ocelots), with a significant positive effect of logging on puma and jaguar detection (Appendix S1: Fig. S5). Compared to the community-level effect of hunting on occupancy, the community-level effect of hunting on detection was relatively weak (Fig. 2). Similarly, species-level effects of hunting on detection had a median near zero with wide credibility intervals for all species (Appendix S1: Fig. S5).

DISCUSSION

Our results shed light on conservation-compatible policies for managed forests for species susceptible to extirpation from anthropogenic impacts due to intrinsic demographic and life history traits correlated with body size (Bodmer *et al.* 1997). The community of large vertebrate species at our study site remained intact in areas subjected to both reduced-impact logging and traditional indigenous hunting. Community partnerships, like the one in this case study, can increase conservation gains through improved forest management while they contribute to local livelihoods and achievement of development aspirations. Although generalizations based on a study in a single logging operation and a single community need to be made with caution (Ramage *et al.* 2013), our results contribute to knowledge about the conservation benefits to large vertebrates of improved forest management. More specifically, the benefits for biodiversity conservation are clear for policies that require RIL and restrict forest access to
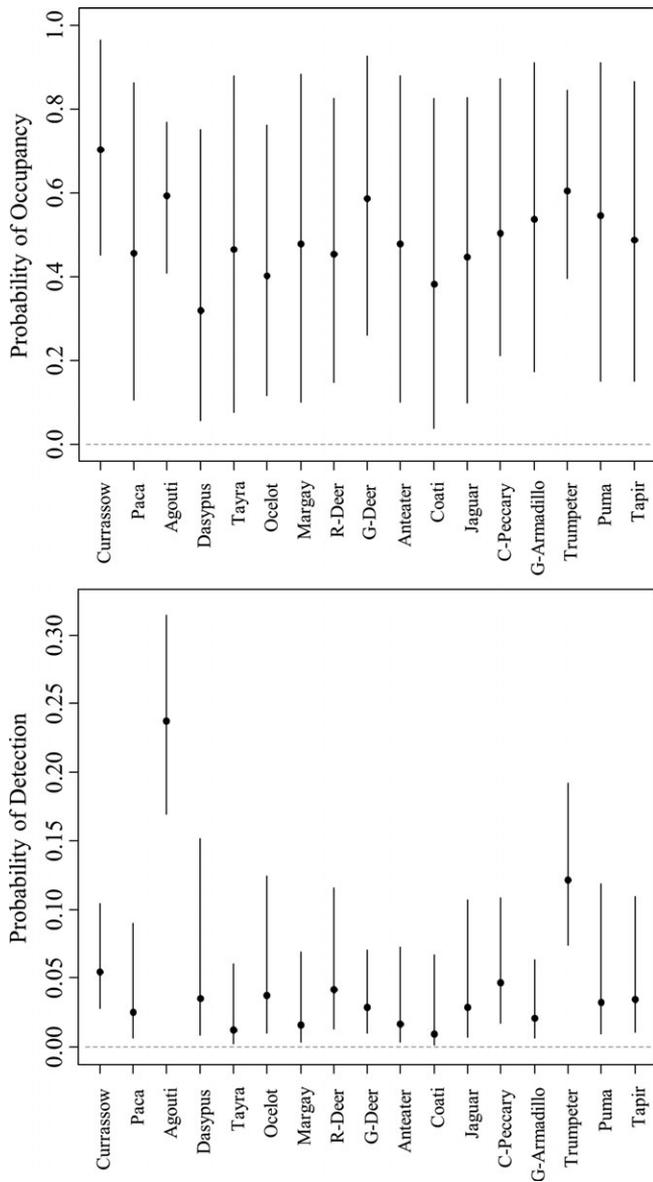
FIGURE 3. Probability of occupancy and detection in unlogged forests for all species recorded in camera traps.
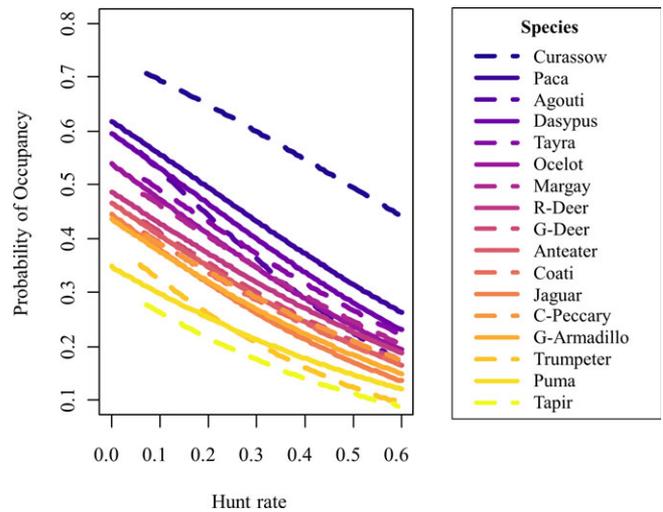

FIGURE 4. Changes in probability of occupancy at the species level across the range of observed hunting rates. Each colored line represents a single species.

people without legitimate claims on forest resources (Edwards et al. 2012, Putz et al. 2012, Bicknell et al. 2014).

In forests that do not benefit from the community partnerships and ecologically sound management practices employed in Iwokrama Forest, the potential loss of ground-dwelling vertebrates can affect the nutrition of local people, forest dynamics, and biodiversity (Iwamura et al. 2014). The large-bodied vertebrates that were retained in our study area are especially important in Guiana Shield forests where seeds of most canopy tree species are too large to be dispersed by wind or small animals (Hammond et al. 1996). Loss of these dispersers will result in decreased populations of these large-seeded tree species, a guild that accounts for the above-average carbon content of the forests at our study site that is so important for national climate

mitigation programs associated with REDD+ (Malhi et al. 2009, Johnson et al. 2016). From a sustainable timber production perspective, regeneration of commercial timber species depends on the maintenance of these plant-animal interactions due to the high costs of silvicultural interventions to promote the regeneration and growth of commercial timber species (Rosin 2014). Avoidance of conversion of production forest to non-forest land uses, which leads to massive biodiversity losses and carbon emissions, is to some extent dependent on the continued regeneration of these commercially important species (Edwards et al. 2014b).

The observed lack of a negative effect of RIL on large vertebrates is in line with other studies on birds, bats, amphibians and primates conducted in Iwokrama Forest (Bicknell & Peres 2010, Bicknell et al. 2015b, Holting et al. 2016). Similar to those studies, we attribute our finding to the low intensity of timber harvests coupled with the use of specific harvesting practices that minimize undesirable logging damage. With planned roads and skid trails coupled with directional felling and log extraction by trained workers, much of the area designated for logging suffers no direct impacts from RIL (Arevalo et al. 2016) and therefore remains suitable for species that normally avoid disturbed forests. It should be noted, however, that the higher animal detections observed in logged forests, especially of carnivores, might be a result of the changes in forest structure that improves visual animal detection, animals making use of logging roads, and/or potential increases in food resources (Fragoso 1991, Costa & Magnusson 2003).

The current level of subsistence hunting in Iwokrama may in time reduce the animal populations within the hunting catchment area, as evident from the negative effect of hunting on detection and occupancy. Nevertheless, our overall results and those from other studies in the same area indicate that hunting at our study site is and has been sustainable (Read et al. 2010, Iwamura et al. 2014). Hunting may reduce animal abundances in
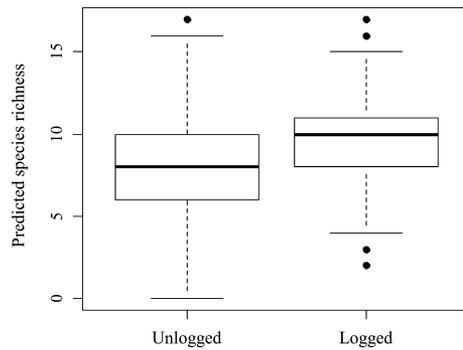
FIGURE 5. Predicted species richness for sites in unlogged and logged forests. The upper and lower edges of the box plots represent first and third quartiles, the thick black line within each box represents the median value, 'whiskers' represent minimum and maximum observations within 1.5 times of the upper and lower quartiles, and dots represents outliers.

areas that experience the highest hunting rates, but these same areas may also represent favorable habitats for wildlife and continue to receive dispersing individuals from surrounding forests (Mayor et al. 2015, Iwamura et al. 2016). Thus, repeated kills at specific sites likely reflect both traditional hunter knowledge and locations favored by their preferred bush meat species. We believe this effect to hold true over time as the hunting data cover multiple years that span the first 4 years of logging in the area during which the 30-year old village experienced a 150% population increase (Iwokrama, unpublished data).

The negative effect of hunting on occupancy and detection that we observed perhaps indicates the sensitivity of this region to overhunting. For example, mean camera-trapping rates were highest for agoutis, a small bodied rodent that comes to dominate community composition as overall species diversity and animal abundance declines within village hunting zones (Shepard et al. 2012). In addition, the density estimated for jaguars, the apex predators at our study site, across the multiple-use forest that included both logged and unlogged forests, falls at the lower end of the range of values reported for protected areas (Maffei et al. 2011). The low densities of jaguars may indicate larger individual home ranges that might reflect population reductions of prey species hunted by humans (Novack et al. 2005) or inherently low animal densities associated with Guiana Shield forests (Eisenberg 1979, Emmons 1984). Density estimates for ocelots, a meso-predator, in contrast, were similar to those reported for protected areas, 80% higher than the minimum values reported (Di Bitetti et al. 2008). The lack of photo captures of white-lipped peccaries, though recorded in the hunting surveys, may reflect the range-wide declines reported for this species (Fragoso 2004, Richard-Hansen et al. 2014, Mayor et al. 2015).

CONCLUSIONS

Our results provide support for the conservation value of managed forests for large vertebrates that are sensitive to human-induced environmental changes (Laurance et al. 2012). The

policies and practices specific to our study site that enabled such an outcome included: (1) the ability to exclude non-sanctioned uses that can lead to forest cover loss and degradation; (2) co-management institutions with indigenous communities who are legally guaranteed access for hunting and other traditional forest uses and benefit financially from the timber business; (3) adherence to high standards of RIL with third-party certification; and, (4) forest zoning so that protected areas equal in size to timber production forests are established in adjacent wilderness reserves. The existence and enforcement of such policies might serve as indicators of good forest management under global conservation initiatives such as REDD+. An outcome that leads to well-managed tropical forests will be good for biodiversity, enhance indigenous people's livelihoods, and contribute to national development, but only where supported by strong policies and effective enforcement.

The impact of selective logging on tropical biodiversity is dependent on the policies, practices, and enforcement contexts in which forest management occurs. Logging and other forest uses such as subsistence hunting by indigenous people are important livelihood activities that can be conducted in ways that do not result in losses of forest cover. Control of forest access through road closure coupled with co-management mechanisms with indigenous communities can clearly serve to improve forest management and prevent illegal hunting, unplanned colonization, and deforestation that leads to massive biodiversity loss (Robinson et al. 1999, Fimbel et al. 2001, Bicknell et al. 2015a). To better understand the suite of policies that would lead to the most conservation gains in managed tropical forest, future research should aim to quantity wildlife densities across multiple sites governed by a range of policies (Ferraro 2013, Angrist & Pischke 2014).

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DATA AVAILABILITY

Data deposited in the Dryad Repository: https://doi.org/10.5061/dryad.6n65q (Roopsind et al. 2017).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

APPENDIX S1. Supplemental figures and tables for main text.

APPENDIX S2. Description of the spatial vs. non-spatial models.

APPENDIX S3. Model results using distance-to-village as a metric of hunting rather than hunt rate.

APPENDIX S4. Hierarchical community occupancy model – JAGS code.

APPENDIX S5. Power analysis.

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