



Do responsibly managed logging concessions adequately protect jaguars and other large and medium-sized mammals? Two case studies from Guatemala and Peru

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ABSTRACT

Large areas of tropical forest have been designated for timber production but logging practices vary widely. Reduced-impact logging is considered best practice and third-party certification aims to ensure that strict standards are met. This includes minimizing the number of roads constructed, avoiding sensitive areas and strictly regulating hunting. Large scale camera trap grids were utilized in Guatemala and Peru to evaluate the impact of reduced-impact logging in certified concessions upon the large and medium-sized mammal fauna with special emphasis on jaguars (*Panthera onca*). Spatial capture-recapture models showed that jaguar density in Peru (4.54 ± 0.83 ind. 100 km^{-2}) was significantly higher than in Guatemala (1.52 ± 0.34 ind. 100 km^{-2}) but in both regions, densities were comparable to protected areas. Camera traps detected 22 species of large and medium sized mammals in Guatemala and 27 in Peru and a multi-species occupancy model revealed that logging had no negative impact on any of the species studied and actually had an initial positive impact on several herbivore species. We found no avoidance of logging roads; in fact, many species, especially carnivores, frequently used logging roads as movement corridors. Our results indicate that well-managed logging concessions can maintain important populations of large and medium-sized mammals including large herbivores and large carnivores as long as hunting is controlled and timber volumes extracted are low. Responsible forest management would therefore be an ideal activity in the buffer zones and multiple use zones of protected areas creating much less impact and conflict than alternatives such as agriculture or cattle ranching while still providing economic opportunities. Logging concessions can also play an important role in maintaining landscape connectivity between protected areas.

1. Introduction

Over the last few decades deforestation of humid tropical forests around the world has continuously increased (Achard et al., 2014; Asner et al., 2009; Hansen et al., 2013). In Southeast Asia and Central America over 70% of the original humid tropical forest has been lost or greatly degraded (< 50% tree cover) and in South America this figure is 36% (Asner et al., 2009). About 40% of the remaining forests are affected by commercial logging that often leads to forest degradation, loss of carbon stock, increased vulnerability to fire and increased access to such areas by hunters and small farmers (Asner et al., 2009; Blaser et al., 2011; Laurance et al., 2014; Nepstad et al., 1999).

Management practices of logging operations vary greatly, ranging from clear-cutting to selective reduced-impact logging. Many countries have established forest reserves, logging concessions or other systems for leasing state owned forests to private companies for the extraction of timber with the goal of managing these forests sustainably for long-term production (Blaser et al., 2011). Forest certification was created as an independent third-party verification of responsible forest management with strict standards. The Forest Stewardship Council (FSC), which was established in 1993, has a global forest certification system that accredits companies that use sound social and environmental practices for forest management (FSC, 2016). FSC-certified logging operations are required to practice reduced impact logging, control or

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prohibit hunting within the concession, set aside high conservation value forest, and avoid, repair, or mitigate environmental impacts (FSC, 2016). While this comes at a significant cost for the logging company (Gullison, 2003), certified wood sells for a higher price in international markets and companies get increased market access, resulting in a net financial benefit. Although the global area of certified forests has continuously increased over the last two decades, the largest increases happened in boreal forests in Europe and North America (FSC, 2016; PEFC, 2017). In 2011, only 13% of tropical forests were considered sustainably managed and only 4–5% were certified (Blaser et al., 2011).

The conservation of biodiversity is an explicit goal of the FSC certification scheme (FSC, 2016), but the number of studies that have evaluated how well certified forest management under the FSC label protects biodiversity are few in number. Several studies have looked at responses by either single species or small numbers of species of large and medium-sized mammals to certified forest management approaches, leading to the generation of management recommendations (Clark et al., 2009; Davies et al., 2001; Polisar et al., 2017; Rayan and Mohamad, 2009), but far fewer have examined the effects on the entire mammal community (Roopsind et al., 2017; Sollmann et al., 2017). Moreover, several studies have found negative impacts of logging on species richness with effects varying greatly by taxonomic group, geographic region, and logging intensity (Burivalova et al., 2014; Chaudhary et al., 2016; Gibson et al., 2011). For tropical forests, reduced impact logging has been found to have the least negative effect, with some forests under reduced-impact logging retaining between 80% and 100% of their species richness (Bicknell et al., 2014; Chaudhary et al., 2016; Gibson et al., 2011; Putz et al., 2012).

In this study, we use large-scale camera trap surveys to evaluate terrestrial mammal communities in FSC certified logging concessions in Guatemala and Peru. Camera traps are ideally suited to assess mammal communities in tropical forests and, unlike other methods such as line transects, they are also able to collect data on cryptic and nocturnal species (Ahumada et al., 2013; Tobler et al., 2008; Tobler et al., 2015). We used multi-species occupancy models (Dorazio and Royle, 2005; Dorazio et al., 2006; Yamaura et al., 2011) to examine community structure and distribution of mammals in the logging concessions, and assessed the density of the top predator, the jaguar, using spatial capture-recapture models (Borchers and Efford, 2008; Efford et al., 2009; Royle and Young, 2008).

2. Methods

2.1. Study areas

2.1.1. Peru

Peru has 62.5 million ha of lowland tropical rainforest with historically low annual deforestation rates (around 0.2% per year between 1990 and 2015 (FAO, 2015)). In 2000, the Peruvian government passed a new law of Forestry and Wildlife (Ley Forestal y de Fauna Silvestre, Ley N° 27308) that designated about 8 million ha of permanent production forest. Within these areas the government can grant concessions of between 5000 and 50,000 ha for durations of up to 40 years. The concession holders are required to develop a five-year management plan and an annual operating plan in which they agree to restrictions including limits on timber extraction to 5% of the available basal area and limits on subsistence hunting (commercial hunting is strictly prohibited). Each concession is divided into 20 blocks representing a 20-year harvest cycle with timber being extracted from one block annually.

In the department of Madre de Dios there are 1.3 million ha of logging concessions of which 422,959 ha are FSC certified (DGFFS, 2013). These concessions go through an annual review process undertaken by an outside certification organization that evaluates compliance with all the FSC standards to ensure sustainable management practices.

Our study was carried out in the north-eastern part of Madre de Dios

in two FSC certified logging concessions (Forestal Otorongo and Aserradero Espinoza) south of the Tahuamanu river (Fig. 2). These concessions are part of a large block of logging concessions towards the north, south and west and are bordered by agriculture land and Brazil nut concessions (for the extraction of Brazil nut from mature forests) to the east. Logging in these concessions started in 2003 but was preceded by unregulated selective extraction of mahogany and a few other high-value hard-wood species for almost a decade. The average volume of timber extracted from the concessions is between 2 and 3 m³/ha. Hunting is strictly prohibited within the concessions.

The topography is flat with elevation ranging from 150 m to 300 m and the vegetation is lowland Amazonian moist forest with several areas dominated by large patches of bamboo. The mean annual temperature is 24 °C and mean annual rainfall is between 2500 and 3500 mm.

2.1.2. Guatemala

Over a thousand years ago Guatemala's lowland Department of Petén was the epicenter of the Maya culture. In the 20th century, the economy of the northern Petén was dominated by extraction of gum from chicle trees (*Manilkara zapota*), a market that has since dwindled. Until recently, this, the largest of Guatemala's 22 departments was isolated from the rest of the country due to the lack of well-maintained access routes and long distances from principal cities (Hodgdon et al., 2015).

In 1990, the Guatemalan government via the Consejo Nacional de Áreas Protegidas (CONAP, Guatemala's National Council of Protected Areas) created the Maya Biosphere Reserve (MBR) in the northern portion of the Petén with the goal of “combining the conservation and sustainable use of natural and cultural resources in order to maximize the ecological, economic and social benefits for Guatemala” (Secaira et al., 2015). The reserve was divided into three zones: (a) the core zone (36% of the MBR) is formed by national parks where only scientific investigation and low impact tourism are allowed, (b) a 15 km-wide buffer zone (24% of the MBR) along the southern border of the MBR where agriculture, farming, and other productive activities are permitted with the aim of reducing the pressure on the other two zones, and (c) a 848,440 ha multiple use zone (40% of the MBR) where sustainable and low-impact land uses are allowed including controlled logging of hardwood tree species in forest concessions (Hodgdon et al., 2015; Radachowsky et al., 2012; Secaira et al., 2015).

Between 1994 and 2002, CONAP granted 533,132 ha of the multiple use zone (MUZ) of the MBR to 14 forest concessions for a period of 25 years. They included two industrial concessions (private companies), six non-resident community concessions (communities in the buffer zone), two resident community concessions with forest-based history (communities established as chicle harvesting centers more than a century ago) and four resident community concessions for recent immigrants (Hodgdon et al., 2015; Radachowsky et al., 2012; Secaira et al., 2015). Three of the four resident community concessions for recent immigrants were cancelled or suspended due to a lack of compliance with the contract agreements while the other 11 concessions were granted FSC certification between 1998 and 2004 (Carrera et al., 2006; Hodgdon et al., 2015; Radachowsky et al., 2012). The harvest intensities in these concessions (1.2–3.0 m³/ha) are among the lowest in the world.

Our study was carried out in the territory of five non-resident community concessions: La Unión, Las Ventanas, Chosquitán, Río Chanchic and Yaloch managed by Sociedad Civil Custodios de la Selva, Árbol Verde, Sociedad Civil Laborantes del Bosque, Sociedad Civil Impulsores Suchitecos, and Sociedad Civil El Esfuerzo respectively (Fig. 1). These concessions are exclusively used for logging; no people besides the workers are living inside the concessions and there is no hunting. Forty-three percent of the study area was harvested before the sampling period and the entire area reported 0% of deforestation during 2000–2013 (Hodgdon et al., 2015). The MBR is classified as

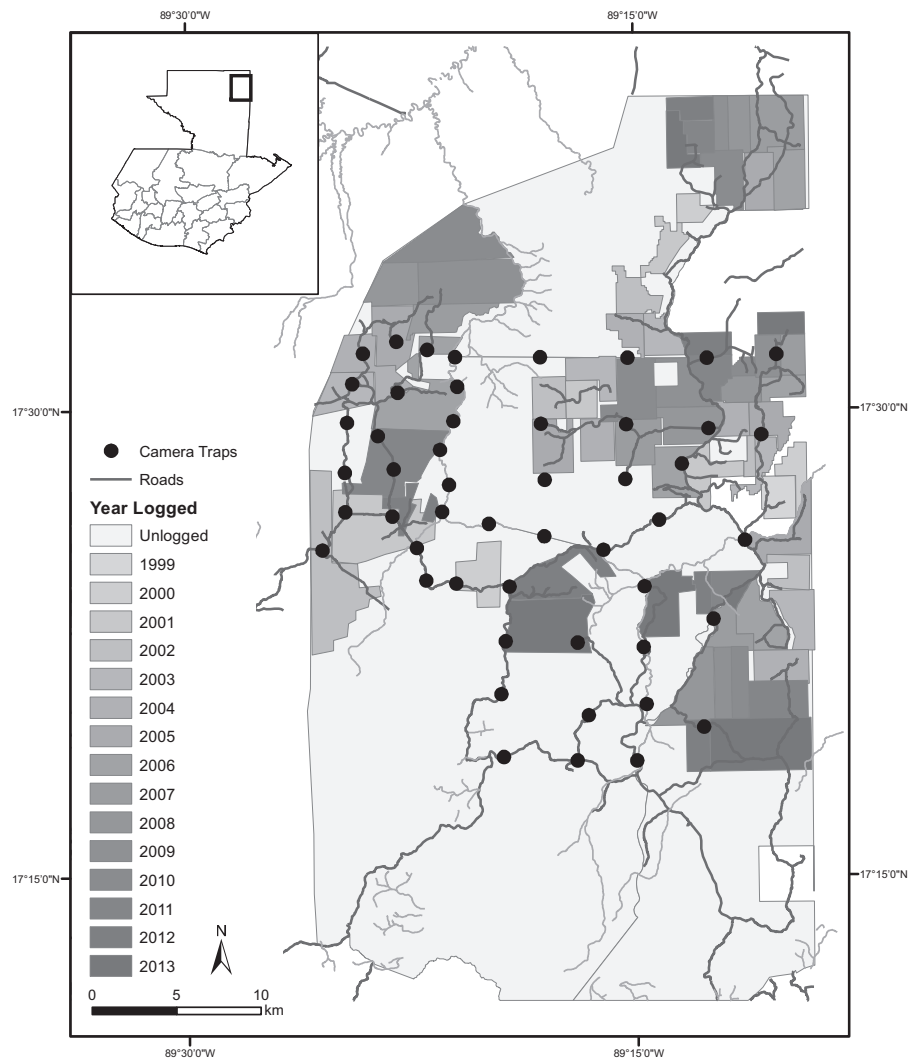


Fig. 1. Guatemala camera trap locations and logging concessions. Colors of logging blocks indicate what year trees were harvested. Unlogged areas are as of 2013.

Petén-Veracruz Moist Forest with trees reaching heights of 25–35 m. Elevations range between 100 and 420 m, average temperatures between 20°–30° and annual precipitation between 1324 and 1350 mm with a dry season from December to April. Forest fires are a major threat to the MBR, registering an average of 2010 MODIS hot points (i.e. fire detected by NASA satellites across the entire MBR) from 2010 to 2015; however only five of those occurred inside the sampling area (CONAP-WCS, 2015).

2.2. Camera trap surveys

Our camera trap survey design followed recommendations by Tobler and Powell (2013) for jaguar surveys. In both study areas we used a paired camera trap setup in a regular grid with cameras spaced 2–3 km apart. In Guatemala we had 50 camera stations with Reconyx Hyperfire RM 45 and HC 500 camera traps whilst in Peru we had 89 camera stations using Bushnell TrophyCam HD (2012 and 2013 models) cameras (Table 1). Camera trap polygons covered an area of 520 km² in Guatemala and 645 km² in Peru. Jaguars normally have higher detection probabilities on roads and trails (Sollmann et al., 2011; Tobler et al., 2013) so we set up cameras along logging roads whenever possible. Camera traps were in the field for between 90 and 120 days during the dry season and were active for 24 h a day. All photos were entered into Camera Base 1.7, a database specifically developed for managing and analyzing camera trap data (Tobler, 2015).

2.3. Jaguar densities

Individual jaguars were identified based on their coat pattern and the sex of each individual was determined whenever possible. If a photo could not be clearly assigned to an individual, it was excluded from the density analysis.

We estimated jaguar densities using a spatial capture-recapture (SCR) model (Efford et al., 2009; Royle et al., 2013b; Royle and Young, 2008). SCR models use the spatial information of jaguar detections to estimate the parameters of the half-normal detection function (detection probability at the center of the home range g_0 and movement parameter σ) in order to estimate the density of jaguars. We modeled both detection probability and home-range size independently for males and females. We also included a detection covariate to account for the difference in detection probability for cameras that were placed on active logging roads, on old roads and off roads and modeled an interaction with sex in order to evaluate whether road preference differed for males and females. Old roads are roads that are not used anymore and have vegetation growing back but are still passable (we also included trails within this category). Given that jaguars extensively use the road network for travel we hypothesized that a non-Euclidian distance model would better be able to explain the movement of jaguars in the landscape (Royle et al., 2013a; Sutherland et al., 2015). This model can account for jaguars traveling longer distances along roads than off road. We created a binary cost surface where roads had a value

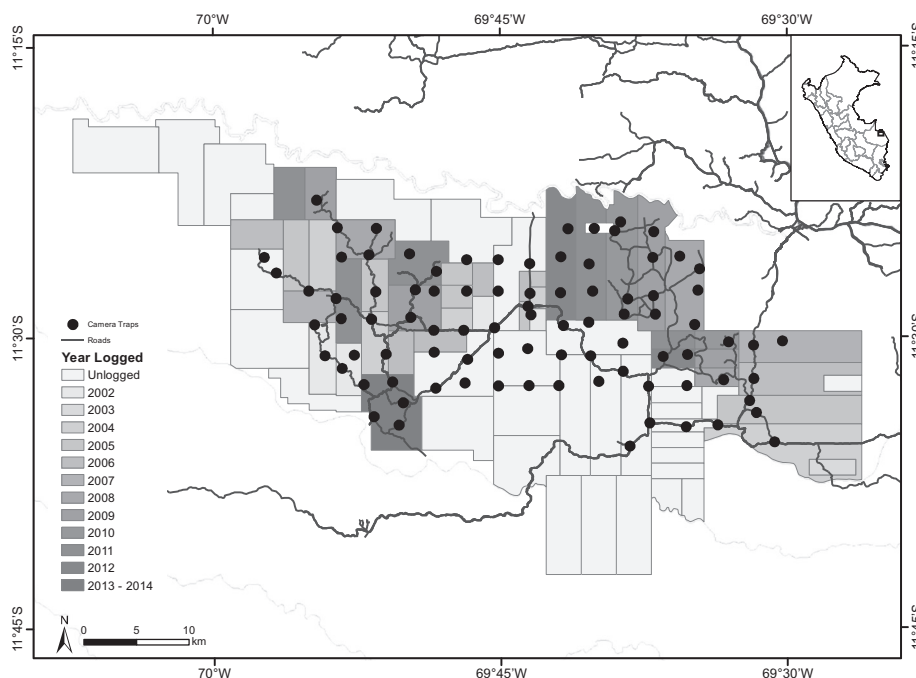


Fig. 2. Peru camera trap locations and logging concessions. Colors of logging blocks indicate what year trees were harvested. Unlogged areas are as of 2014.

Table 1
Data for the camera trap surveys carried out in Guatemala and Peru.

Survey	Start date	End date	Stations	Camera days	Camera polygon ^a (km ²)
Guatemala	18 April 2013	16 July 2013	50	4406	520
Peru	25 June 2014	23 October 2014	89	8688	645

^a Minimum convex polygon without buffer.

of zero and forested areas a value of one. Models were run in a maximum-likelihood framework using the package *secr* (Efford, 2016) in R (R Development Core Team, 2015) and we subsequently compared models using the Akaike Information Criterion (AIC).

2.4. Species richness and occupancy

To evaluate the effect of logging on the whole large and medium-sized mammal community we took advantage of the fact that during each year one or two blocks in each study area were being harvested. This creates a mosaic of unlogged blocks and blocks harvested at different points in time. We used this spatial replication to evaluate the effect of logging over time. While temporal replication would be preferable (evaluating blocks pre- and post-logging), such a design would take 10 to 15 years to carry out. We believe that our study areas are homogenous enough and the logged blocks are distributed enough to not affect our inferences.

For the community analysis we used a Bayesian multi-species occupancy model to estimate community structure and occupancy for all species (Dorazio and Royle, 2005; Dorazio et al., 2006). These models account for imperfect detection and, by combining data from all species of interest, can provide improved parameter estimates for rarer species (Zipkin et al., 2009). To cope with the large level of heterogeneity generally present in camera trap data due to differences in the local abundance or non-random movement of animals we used the Royle-Nichols version of the multi-species occupancy model (Tobler et al., 2015; Yamaura et al., 2011). We used the following occupancy covariates: logged (yes/no), years since logged (zero if the site had not

been logged) and distance from active logging road. We also evaluated distance to the nearest river and the normalized difference vegetation index (NDVI) based on Landsat images but neither was significant for any of the species studied so we dropped them from the model. We included a detection covariate to account for the difference in detection probability for cameras placed on active roads, old roads and off-road. Continuous covariates were standardized to a range between 0 and 1.

We calculated the percentage of area occupied (PAO) across the full extent of the concessions by creating raster grids with a 100 × 100 m resolution for all the covariates, calculating the occupancy probability for each species for each grid cell and then averaging across all cells. We did this for each sample of our MCMC results to estimate credible intervals for the resulting occupancy values. For wide-ranging species such as large carnivores this value is interpreted as the percentage of the area used by the species.

We ran the model in JAGS (Plummer, 2003) through R (R Development Core Team, 2015). We ran three chains with 150,000 iterations, a burn-in of 50,000 and a thinning rate of 100. We visually inspected the chains for convergence. Covariates were considered significant when the 95% Bayesian credible interval did not include zero.

3. Results

3.1. Jaguar densities

We obtained 203 records of 23 jaguars (14 males and 9 females) from Guatemala and 215 records of 43 jaguars (19 males, 22 females and 2 of unknown sex) from Peru. The estimated density in Guatemala was 1.52 ± 0.34 ind. 100 km⁻² and in Peru 4.54 ± 0.83 ind. 100 km⁻² with the highest ranking non-Euclidian distance model and 3.00 ± 0.54 with the Euclidian distance model. For both surveys, detection probability g_0 was higher on active roads than on old roads, much lower off road, and higher for male than for female jaguars (Table 2). The movement parameter σ and therefore the home range size was larger for males than for females, and the respective estimates of σ were similar for the two surveys (Table 2). For the Peru data, the model with the lowest AICc value also included both the non-Euclidian distance as well as an interaction term for road type and sex, indicating

Table 2
Results from spatial capture-recapture models for jaguar surveys in Guatemala and Peru. Values show as mean, standard error and 95% confidence intervals.

Parameter	Guatemala	Peru no-Euclidian	Peru Euclidian
D	1.52 ± 0.34 (0.96–2.25)	4.54 ± 0.83 (2.78–7.44)	3.00 ± 0.54 (2.11–4.26)
σ M	5306 ± 483 (4465–6334)	6922 ± 467 (6066–7899)	5605 ± 382 (4906–6404)
σ F	4073 ± 667 (3043–5673)	4491 ± 574 (3500–5763)	3276 ± 349 (2659–4034)
g0 M road	0.0421 ± 0.0058 (0.0318–0.0540)	0.0522 ± 0.0083 (0.0380–0.0712)	0.0490 ± 0.0072 (0.0366–0.0653)
g0 M old road	0.0230 ± 0.0065 (0.0132–0.0400)	0.0161 ± 0.0040 (0.0099–0.0262)	0.0070 ± 0.0015 (0.0046–0.0107)
g0 M off road	0.0080 ± 0.0042 (0.0029–0.0192)	0.0054 ± 0.0031 (0.0018–0.0164)	0.0010 ± 0.0005 (0.0004–0.0027)
g0 F road	0.0092 ± 0.0029 (0.0047–0.0163)	0.0087 ± 0.0023 (0.0051–0.0147)	0.0091 ± 0.0023 (0.0055–0.0151)
g0 F old road	0.0049 ± 0.0019 (0.0021–0.0098)	0.0037 ± 0.0012 (0.0019–0.007)	0.0029 ± 0.0009 (0.0016–0.0054)
g0 F off road	0.0017 ± 0.0011 (0.0005–0.0045)	0.0019 ± 0.0011 (0.0006–0.0058)	0.0012 ± 0.0006 (0.0005–0.003)
Cost off road M		8.72 ± 1.86 (5.77–13.2)	
Cost off road F		2.49 ± 0.91 (1.25–4.98)	

σ: movement parameter in meters, g₀: detection probability, D: density in ind. 100 km⁻², Cost: cost-estimate for off-road travel by the non-Euclidian distance model, M: male, F: female.

that road use is different for male and female jaguars. Neither of these were included in the highest-ranking model for Guatemala but this could be because of the lower number of cameras and because no female jaguars were detected off-road, making parameter estimates unreliable for the interaction model.

3.2. Species richness and occupancy

In Guatemala we recorded 24 species including 22 species of large and medium-sized terrestrial mammals and two species of terrestrial birds. In Peru, we recorded 27 species comprising of 25 species of terrestrial large and medium-sized mammals and two species of terrestrial birds. In Guatemala, three species showed a significant increase in occupancy in logged areas compared to unlogged areas: red brocket deer (*Mazama temama*), white-tailed deer (*Odocoileus virginianus*) and the tapir (*Tapirus bairdii*). Three species showed an initial increase and then a slow decline over time: paca (*Cuniculus paca*), brown agouti (*Dasyprocta punctata*) and common opossum (*Didelphis marsupialis*, Fig. 3). In Peru, there were seven species that showed a significant increase: paca, brown agouti, ocelot (*Leopardus pardalis*), razor-billed curassow (*Mitu tuberosum*), puma (*Puma concolor*), Brazilian rabbit (*Sylvilagus brasiliensis*) and the lowland tapir (*Tapirus terrestris*; Fig. 4). The initial increase was generally followed by a decrease in occupancy over time after logging. No species showed a negative initial response to logging. We found no species avoiding areas close to logging roads and the jaguar was found more often closer to roads. In Guatemala, nine species had a higher detection probability on active logging roads than on old roads and away from roads: great curassow (*Crax rubra*), brown agouti, common opossum, ocelot, red brocket deer, ocellated turkey (*Meleagris ocellata*), jaguar, puma and the grey fox (*Urocyon*

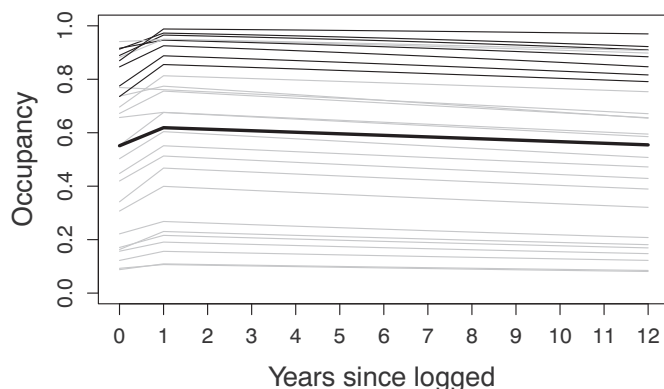


Fig. 4. Marginal occupancy probabilities of 27 species in relation to time after logging in certified logging concessions in the Peruvian Amazon. Zero indicates unlogged blocks. Thin black lines indicate species that have a significant response (95% credible intervals do not include zeroes) and the thick black lines shows the mean response across all species.

cinereoargenteus) (Table S6). In Peru this was the case for six species: ocelot, razor billed curassow, jaguar, puma, Brazilian rabbit and the lowland tapir (Table S4). Of these, three also showed an increased detection probability on old roads and trails. In addition, three species had a lower detection probability on roads in Peru (paca, nine-banded armadillo (*Dasypus* spp.), giant anteater (*Myrmecophaga tridactyla*), pale-winged trumpeter (*Psophia leucoptera*) but none in Guatemala.

In Peru, the total percentage of area occupied across the extent of the concessions ranged from 15% for the pacarana to 95% for the lowland tapir and the red brocket deer (Fig. 5 and Table S1). Jaguars and pumas both used about 75% of the area. Results were similar in Guatemala with values ranging from 19% for the striped hog-nosed skunk to 96% for the ocelot (Fig. 6 and Table S2). Jaguars and pumas used between 70% and 75% of the area.

4. Discussion

4.1. Jaguar densities

Tobler and Powell (2013) found that many jaguar camera trap surveys covered too small an area to collect reliable data on jaguar densities and made a number of design recommendations. We subsequently implemented these recommendations resulting in two of the largest camera trap survey areas for jaguars with some of the highest numbers of individuals recorded to date (review of previous studies in Tobler and Powell, 2013). These robust datasets lead to improved density estimates with smaller confidence intervals for all parameters. While densities were lower in Guatemala (1.52 ± 0.34 ind. 100 km⁻²) than in Peru (4.56 ± 0.83 ind. 100 km⁻²), this is likely due to habitat conditions. The Guatemala study site receives less precipitation than

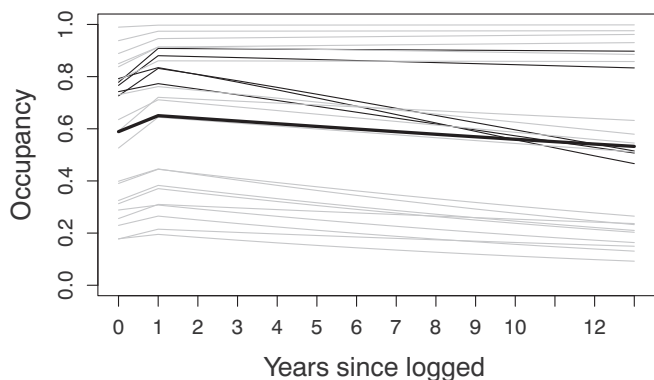


Fig. 3. Marginal occupancy probabilities of 24 species in relation to time after logging in certified logging concessions in the Maya Biosphere Reserve in Guatemala. Zero indicates unlogged blocks. Thin black lines indicate species that have a significant response (95% credible intervals do not include zeroes) and the thick black lines shows the mean response across all species.

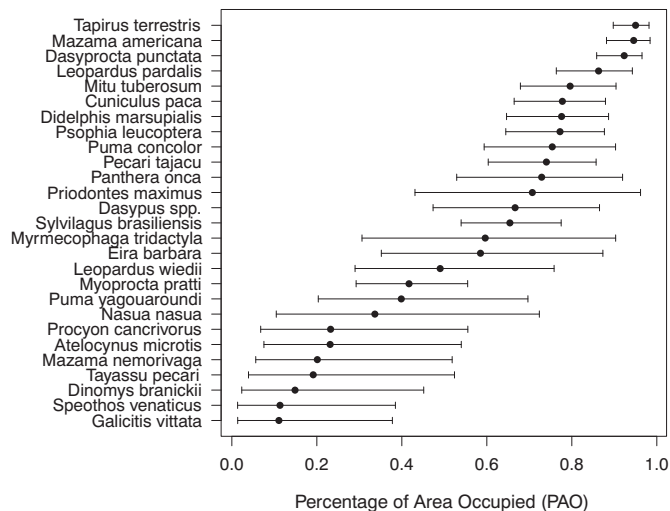


Fig. 5. Percentage of area occupied (PAO) for 27 species in reduced-impact logging concessions in Peru (mean and the 95% credible intervals estimated with a multi-species occupancy model).

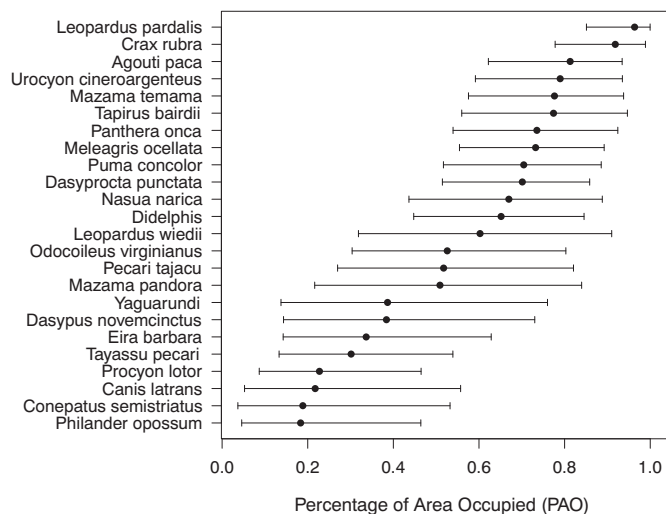


Fig. 6. Percentage of area occupied (PAO) for 24 species in reduced-impact logging concessions in Guatemala (mean and the 95% credible intervals estimated with a multi-species occupancy model).

the Peru site (1324–1350 mm compared to 2500–3500 mm) and due to its porous karstic substrate, that simply filters rain down into aquifers, possesses a scarcity of surface water when compared to the Peru site. However, density estimates from Guatemala were on the high end of estimates from even drier sites such as the Bolivian Chaco (SCR estimate range: 0.46–1.46 ind. 100 km⁻², Noss et al., 2012) and higher than an estimate from the Emas National Park in the Cerrado of Brazil (SCR estimate: 0.29 ± 0.10 ind 100 km⁻², Sollmann et al., 2011). Density estimates for Peru were similar to those from the llanos of Venezuela (4.44 ± 1.16 ind. 100 km⁻², Jędrzejewski et al., 2017) but were higher than jaguar densities along the coast of French Guiana (3.22 ± 0.30 ind 100 km⁻², Petit et al., 2017) and significantly higher than in a logging concession in Guyana (1.72 ind 100 km⁻²; Roopsind et al., 2017). Higher jaguar densities were only found in the Pantanal of Brazil (6.6 ind. 100 km⁻², non SCR estimate, Soisalo and Cavalcanti, 2006). However, estimates were lower than previous estimates from the same area in Peru (4.9 ± 1.0 ind. 100 km⁻²; Tobler et al., 2013) likely due to the increase in the extent of the camera trap polygon.

In agreement with previous camera trap studies (Sollmann et al., 2011; Tobler et al., 2013), male jaguars were found to have much larger

home ranges and higher detection probabilities than females, indicating that they travel further on a daily basis. This is consistent with findings from jaguars tracked with GPS collars (Morato et al., 2016). We also found that detection probabilities on active, open logging roads were higher than on old roads and trails, and much higher than off road. A preference of roads can be seen for both sexes, although it is stronger for males than for females. In Peru, male jaguars had a 10-fold higher detection probability on roads compared to off roads and females had a two-fold higher detection probability. In Guatemala, the detection probability on roads was around five times higher for both sexes but interestingly no females were detected off road. This shows the importance of placing cameras on trails or roads to maximize detection probabilities. At least in the dense forests of the Amazon, roads seem to be important movement corridors for jaguars as reflected by the better fit of the model using non-Euclidian distance and again male jaguars showed a stronger preference for traveling along roads than females. Ignoring these effects of the landscape structure on movement can lead to an underestimation of densities (Royle et al., 2013a; Sutherland et al., 2015).

4.2. Species richness and occupancy

We confirmed previous findings that for large and medium-sized terrestrial mammals the impact of reduced-impact logging is generally small and, in some cases, logging can have positive effects on their diversity and abundance (Azevedo-Ramos et al., 2006; Burivalova et al., 2014; Clark et al., 2009; Gibson et al., 2011; Meijaard and Sheil, 2007; Roopsind et al., 2017). At both study sites we detected all the species known to occur in the region, and in Peru we detected an additional species (Pacarana (*Dinomys branickii*)) that was missed by previous surveys (Tobler et al., 2015). Occupancy rates across the two study sites were very similar with logging resulting in an increase in herbivores including tapir, deer, rabbit, paca and agouti. Logging had no negative effect on any of the other species. The pattern showed an initial increase in occupancy after logging and a slow decrease over the following years back to pre-logging levels. Logging opens up the forest canopy in areas where timber is harvested and along logging roads, which in turn leads to an increase in understory vegetation that is consumed by herbivores. Over time the canopy closes again and understory vegetation diminishes. Similar results have been found in studies in Africa and Southeast Asia where generalist herbivores benefited from low-impact logging but some smaller-bodied frugivores were negatively affected (Clark et al., 2009; Davies et al., 2001).

The cause for the increase in the two large rodent species is less clear since they are mainly frugivores (Dubost et al., 2006). However, an increase of rodents in logged forests can be explained by an increase in microhabitat diversity, increased cover and an increase in resource abundance in the form of fruit and insects (Fredericksen and Fredericksen, 2002; Lambert et al., 2006). Many of the herbivores and large rodents are important prey species for jaguars and pumas (Emmons, 1987; Foster et al., 2010; Weckel et al., 2006) which is reflected by the high density and high occupancy of these large cats in the studied logging concessions. An increase in rodent abundance could also explain the increase in occupancy of ocelots in logged areas.

Most carnivore species showed an increased detection probability on logging roads at both study sites confirming previous results that they actively use trails and roads for travel (Di Bitetti et al., 2014; Harmsen et al., 2010; Sollmann et al., 2012; Tobler et al., 2015). At both sites, the curassow had a higher detection probability on roads than away from them as did the red brocket deer in Guatemala and the tapir in Peru. These findings indicate that even active logging roads with trucks passing several times a day have a relatively small impact upon our study species and do not pose much of a disturbance or barrier for movement. On the contrary, they might actually increase long-distance movement and possibly facilitate dispersal of animals into logged areas. In Peru, we observed jaguars, tapirs and many other species

starting to use a new road only days after it was created by bulldozers.

While we observed a wide variation in PAO values across species, several patterns can be seen at both sites. Large ungulates such as deer and tapirs are common and widespread with the exception of the white-lipped peccary (*Tayassu pecari*) in Peru and Guatemala and the brown brocket deer in Peru (*Mazama nemorivaga*). This results in a healthy prey base for jaguars and puma as indicated by our density estimates. Among the medium-sized carnivores we can see that the ocelot is the most common species followed by the margay (*Leopardus wiedii*) and the yaguarundi (*Puma yagouaroundi*). Occupancy values in our studies were generally higher than in a comparable study from logging concessions in Guyana (Roopsind et al., 2017) which could be due to the complete absence of hunting in our study areas. In Peru occupancy values for many species, especially large mammals, were comparable to values from other sites, including protected areas (Tobler et al., 2015), but comparison is limited by differences in forest composition that can affect species distribution and occupancy independent of logging.

4.3. The importance of sustainably managed logging concessions

The impact of logging on species diversity and abundance has been the subject of much debate (Burivalova et al., 2014; Chaudhary et al., 2016; Edwards et al., 2014; Gibson et al., 2011). However, the value of well-managed logged forest and logging concessions for biodiversity conservation as a complement to protected areas is becoming more recognized (Dent and Wright, 2009; Dickinson et al., 1996; Edwards et al., 2014; Putz et al., 2012; Struebig et al., 2013; Wilson et al., 2010). For larger and more mobile species, existing networks of protected areas alone may not be enough to ensure long-term conservation. Well-managed forests can provide both important habitat and connectivity among protected areas (Chazdon et al., 2009; Clark et al., 2009; Edwards et al., 2014; Wilson et al., 2010).

An exceptionally important aspect for effective wildlife conservation in logging concessions is a strict regulation of hunting inside the concessions and no access to the logging roads for outsiders (Bennett, 2004; Davies et al., 2001; Polisar et al., 2017). Several studies have shown that the largest impact of logging is not the change in forest structure but the increase in hunting due to the easy access by people along logging roads (Meijaard et al., 2005; Poulsen et al., 2011; Robinson et al., 1999; Roopsind et al., 2017). In the concessions studied in Peru and Guatemala all the main access roads to the concessions are gated with a 24-h watchman on guard. This results in virtually no hunting inside the concessions which is better than in most protected areas.

We found a complete terrestrial mammal community and good jaguar populations in all the logging concessions sampled and could not detect negative impacts of logging on any of the study species. However, we would like to make it clear that our results cannot be generalized to all logging concessions across tropical forests. The volume of wood harvested in the concessions studied (1.2–3 m³/ha) is much lower than in many other logging operations around the world where volumes may be as high as 150 m³/ha, and well below the threshold of 10 m³/ha identified by Burivalova et al. (2014) where negative effects on mammals start to be noticeable. Furthermore, the FSC certification ensures that the logging cycles of 20 years are respected and strict reduced impact logging practices are employed. At the time of this study only half of the blocks had been harvested allowing for fast recolonization of logged areas by animals from surrounding blocks.

We believe that well-managed, certified logging concessions have far less negative effects on forest ecosystems than alternative land uses such as cattle ranching, palm plantations and mono-cultures that result in deforestation and drastic reductions in biological diversity (Gaveau et al., 2013; Oliveira et al., 2007; Polisar et al., 2017; Radachowsky et al., 2012). Logging concessions would therefore be ideal in buffer zones and multiple use zones of protected areas, allowing for economic

activities while still protecting intact ecosystems. The key to success is strict control and enforcement of management practices by governments along with third-party organizations such as the FSC or the Program for the Endorsement of Forest Certification. Programs such as the REDD+ (Reducing Emissions from Deforestation and Forest Degradation), that pay concession owners for maintaining high carbon stocks by reducing logging impact, can complement forest certification to ensure the economic viability of low impact forest management and help maintain high biodiversity forests in logging concessions. In conclusion, increasing the area of tropical forests in Latin America that strictly adhere to certification standards has the potential for large conservation benefits.

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Appendix A. Supplementary data

Additional detailed results from the multi-species occupancy models (Appendix S1), and model selection results for the spatial capture-recapture models (Appendix S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author. Supplementary data associated with this article can be found in the online version, at <https://doi.org/10.1016/j.biocon.2018.02.015>.

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