REVIEW

Using certified timber extraction to benefit jaguar and ecosystem conservation

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Abstract The jaguar *Panthera onca* requires large areas of relatively intact habitats containing adequate amounts of prey to survive. Since a substantial portion of jaguar range occurs outside of strict protected areas, there is a need for economic incentives for habitat conservation, which carefully managed selective logging can provide. Forest Stewardship Council and Pan European Forest Council certifications intended to regulate wood extraction to maintain the ecological functions of forests require evidence of biodiversity and ecosystem conservation. We draw on twelve surveys across four countries and a range of biomes to present evidence that adequate logging management can maintain jaguar populations, but that they are at risk without efficient control of secondary impacts of access and hunting. Where resident, the presence of jaguars can serve as an indication that the ecological requirements of certified timber extraction are being met. We present a gradient of rigor for monitoring, recommending cost-effective options.

Keywords Certified timber extraction · Forest Stewardship Council certification · Jaguars · Pan European Forest Council certification · Selective logging

INTRODUCTION

The jaguar (*Panthera onca*) now occupies 47% of its historic range (Zeller 2007). Large areas of relatively intact habitats containing adequate amounts of suitable prey are requisites for viable jaguar populations over the long-term. Since a substantial portion of jaguar range occurs outside of strict protected areas, and even they do not always control against hunting and encroachment, there is a need

to additional incentives and tools for carefully managed selective logging of valuable hardwoods and ecotourism can provide (Hill and Hill 2011; Salvador et al. 2011).

Extraction of tropical hardwoods has often been viewed as a threat to biodiversity and forest conservation. However, best practices have been developed for reduced-impact selective logging and minimal environmental damages. Considering high deforestation rates throughout the Neotropics in almost all accessible locales where forests do not have an explicit value, timber extraction that generates revenue while leaving most ecological characteristics of a forest intact can be viewed as beneficial for conservation (Putz et al. 2008; Guariguata et al. 2010; Radachowsky et al. 2012; Hodgdon et al. 2015) and a land use that complements areas set aside for strict preservation (Robinson 1993; Fimbel et al. 2001; Marcot et al. 2001; Giam et al. 2011).

Certified hardwood extraction requires evidence of biodiversity and ecosystem conservation. Forest Stewardship Council (FSC) and Pan European Forest Council (PEFC) certifications are intended to regulate forest management and extraction to maintain ecological functions of the forest while ensuring sustainable economic benefits. The Forest Stewardship Council has developed principles and criteria to guide forest management which include social, economic, and environmental considerations, with attention to conservation of species and natural processes in managed forests, and promoting opportunities into the global market for forestry products under FSC certificates (FSC 2013a, b; WWF 2014; FSC 2015a, b).

Economic income from environmentally compatible selective logging can provide an incentive for forest conservation. In Guatemala, forest concessions located in the Multiple Use Zone of the Maya Biosphere Reserve (MBR) have maintained FSC certification (through Rainforest

Alliance-Certification) to permit exportation of timber to overseas markets for an average of 13 years and generate \$10 million annually from sales of rough sawn timber and value added products, such as locally hewn furniture.

In French Guiana, which is an oversea territory of the European Union, PEFC eco-certification has been adopted. A double FSC/PEFC certification process underway for all logged forests mandates in PEFC Criterion 3: *the exploitation of non-timber forest products, including hunting and fishing, shall be regulated, monitored, and controlled*; and Criterion 4: maintenance, conservation, and appropriate enhancement of biological diversity in forest ecosystems: *Forest management planning shall aim to maintain, conserve, and enhance biodiversity on ecosystem, species and genetic levels, and, where appropriate, diversity at landscape level* (PEFC 2010).

Little has been published to document the ecological impact of FSC certification (FSC 2013a, b, WWF 2014, FSC 2015a, b) and compliance with principles and criteria of FSC to wildlife conservation, particularly principles 1.4, 6, 8, and 9 (FSC 2015a, b), all relevant to jaguar conservation. Principle 1.4 emphasizes the need to implement measures, and/or engage with regulatory agencies, to systematically protect the “management unit” from unauthorized or illegal resource harvesting, settlement, and other illegal activities. Principle 6.1 mandates that prior to initiating activities, “the organization” (a certificate applicant or holder) make an assessment of the environmental values of a forest management unit that may be affected, identify potential impacts, and identify and implement preventative actions. Principle 6.4 states that the organization shall protect rare and threatened species in the management unit through conservation zones, protection areas, and habitat connectivity. Principle 6.6 requires that the certificate applicant or holder shall effectively maintain the continued existence on naturally occurring native species and genotypes... and shall demonstrate that effective measures are in place to manage hunting, fishing, trapping, and collection (FSC 2015a, b). Principle 8 includes the condition that management units are monitored and evaluated proportionate to the scales, intensity, and risk of management activities, in order to implement adaptive management.

FSC Principle 9 emphasizes the need to maintain and/or enhance the high conservation values (HCV) of exceptional forests (Finegan et al. 2004) through applying the precautionary approach (FSC 2015a, b). The values defining these HCV forests may include threatened and indicator species such as the jaguar, providing another justification for protecting and monitoring jaguars and their prey (Rumiz et al. 2004).

As the apex predators of low elevation Neotropical forests, jaguars can serve as a testimony to intact trophic chains, validating assertions that timber extraction can

impart only minimal impacts on a site’s ecological characteristic. They thus are ecologically valid and socially emotive indicators that FSC or PEFC standards have been met. We present examples from a range of biomes and management contexts in which the presence of jaguars indicated success in meeting those goals.

Remotely triggered camera traps have become a widely used tool to evaluate furtive animals in forest settings (Kays and Slauson 2008; Nichols et al. 2011; O’Brien et al. 2011; Kelly et al. 2012) including jaguars (Maffei et al. 2011; Foster and Harmsen 2012; Noss et al. 2013; Tobler and Powell 2013). In this paper, we present data (and observations) gathered during jaguar camera trap surveys conducted in forest areas of French Guiana, Guatemala, Bolivia, and Nicaragua (Fig. 1). We draw upon experience to emphasize the management interventions needed to maintain jaguars in areas from which certified timber is extracted, review data from similar studies, discuss using jaguars as an indicator of success in meeting FSC and PEFC goals, and make monitoring recommendations.

MATERIALS AND METHODS

Camera trap surveys followed design recommendations for jaguar capture–recapture population estimation as prescribed in Silver et al. (2004) and updated in Noss et al. (2013) and Polisar et al. (2014a, b). Since our objective was to document within site presence of jaguars and potential prey species, capture frequencies, rather than densities, were considered as a valid common denominator, with comparisons of frequencies only made within each country, avoiding comparisons across surveys of varying size and duration. Photographs were used to identify individual jaguars by spot patterns and to generate capture frequencies by counting independent events—occurred at least an hour apart—for each other species. Capture frequencies of terrestrial species were lumped by groups such as tayassuids, cervids, edentates, tapirids, caviomorph rodents, and procyonid, canid, and mustelid mesocarnivores. Sampling effort was expressed as total trap nights (numbers of stations multiplied by the number of days/nights the stations were operating), while capture frequency for each species was expressed as number of detection events per 1000 trap nights.

French Guiana

Logging practices

Management of forests is under the responsibility of the government Office National des Forêts (ONF). To date, 24 000 km² is managed by the ONF with production and

Fig. 1 Study areas in Bolivia, French Guiana, Nicaragua, and Guatemala

protection areas, including 2400 km² of reserves (Brunaux and Demenois 2003). Selective logging is carried out by small private companies, but opening of logging roads, and identification of wood resources, is under the responsibility of the ONF, preventing illegal harvesting and following PEFC criteria, although the certification process is not yet complete. Management units are small, with a mean size of 300 ha. The average area of cutting blocks (“production units”), defined for 1 or 2 years of activity, is 30–50 ha. More than 60% of timber production was concentrated on only two species, with average logging intensity ranging from 1.5 to 6

trees per hectare and associated canopy damage of 29% (Guitet et al. 2012; Pithon et al. 2013) and cutting cycles of 65 years. The logged areas are located in the north of the country; the southern areas are unoccupied, almost not hunted, unlogged, and nearly pristine, acting as a refuge and potential source for recolonization after logging.

Study sites

The camera trap surveys were in four sites covered by moist evergreen upland forest (Fig. 2a) characterized by

Fig. 2 a, b, c, d Landscape context and forest cover of study areas in French Guiana, Bolivia, Nicaragua, and Guatemala. Specific sample areas are indicated by *solid yellow polygons*, protected areas are illustrated by *green polygons*, and main highways indicated by *numbers in symbols*

high tree diversity (de Granville 1988), with mean elevation of 140 m above sea level (Guitet et al. 2015) and mean annual precipitation between 3100 and 4300 mm.

Two surveys were implemented in logged forests managed under PEFC certification process (Fig. 2a; Table 1).

- (1) In Counami ($\sim 5^{\circ}16'S$, $53^{\circ}41'W$), logging activity was recent (implemented concomitantly to the survey). Several communities hunt in the site, with documented impacts mainly on large primates (de Thoisy et al. 2005), large frugivorous birds (de Thoisy et al. 2010), and tapirs (de Thoisy, unpublished data).

- (2) Montagne de Fer ($5^{\circ}7'S$, $53^{\circ}16'W$) was logged at a high intensity 20–10 years before the survey performed in 2007. Mixed communities hunt in the site, and there is low-scale illegal wood harvesting in some peripheral areas.

Two surveys were implemented in unlogged forests, facing no or low human pressures (Fig. 2a; Table 1).

- (3) Kaw mountain ($4^{\circ}29'S$, $52^{\circ}13'W$), located in the north of the country, is partly included in the Kaw-Roura natural reserve (94 500 ha, IUCN protected area category I). Small human settlements 5–10 km from the study area resulted in low-intensity hunting pressure and small patches of deforestation.

Table 1 Year sampled, percent area logged, land ownership, and timing of surveys

Country	Study areas	Year of sample	Study duration	Season	% logged area in the study area	Ownership/control	Threats
French Guiana	Counami	2007	4 months	Dry	90	Public forest management institution	Intense hunting
	Montagne de Fer	2008	4 months	Dry	90	Public forest management institution	Intense hunting
	Kaw Mountain	2009	4 months	Dry	10	Public forest management institution	Light hunting
	Nouragues	2010	4 months	Dry	0	Public forest management institution	None
Bolivia	A. Sandoval–San José	2008	2 months	Dry	70	Government land and industrial forest concession	Light hunting
	El Encanto	2006	2 months	Dry	90	Government land and industrial forest concession	Moderate hunting, fires
	Altavista	2009	2 months	Dry–wet transition	90	Private land	Intense hunting, fires, habitat fragmentation
Guatemala	La Gloria	2007	1.5 months	Dry	43	Government land and industrial forest concession	Intense hunting
	AFISAP–Carmelita	2008	1.5 months	Dry	21	Government land with community forest concessions	Moderate hunting
	Árbol Verde–Yaloch	2009	1.5 months	Dry	30	Government land and community forest concessions	Light hunting
	Holmul	2013	3 months	Dry–wet transition	33	Government land and community forest concessions	Light hunting
Nicaragua	Layasiksa	2012	1 month	Dry	90	Indigenous territory and industrial concessionaire	Intense hunting, light habitat fragmentation

- (4) Nouragues natural reserve (4°23'S, 52°27'W) is a 100 000 ha, IUCN protected area category I, in the center of the country, and free of any hunting pressure, access is half-day of river travel, and there were no significant threats closer than 30 km around the reserve.

Surveys

Surveys were implemented successively in the four sites in 2007–2010 during the September–December dry season (Table 1). In each site, 16–18 stations were spaced 2–3 km apart. The respective effort was 1656 trap nights for Montagne de Fer, 1690 for Counami, 1530 for Montagne de Kaw, and 1870 for Nouragues.

Bolivia

Logging practices

By Bolivian law, forest management plans divide management areas into equally sized blocks in which individual

trees larger than a prescribed minimum diameter and belonging to a list of inventoried species can be selectively logged. Cutting cycles in the selected certified areas are 25–35 years with annual harvest areas of 2000–5000 ha. Selective logging of hardwoods included 4–14 species at intensities of 2–6 trees/ha (Mostacedo et al. 2010). Forestry operations in/around the three study sites were performed by private enterprises.

Study sites

Sampling took place in three sites in the eastern Bolivian dry forest ecoregion, characterized by rolling hills and shallow valleys (200–500 m of elevation) covered with Chiquitano dry forests and Cerrado savannas (Fig. 2b). Precipitation is seasonal with 1000–1300 mm between December and March and a pronounced June–September dry season.

- (1) The FSC-certified Angel Sandoval (372 969 ha) and San José (60 024 ha) forestry concessions (~17°49'S, 59°16'W) overlap the San Matias three million

hectare multiple use reserve, IUCN type VI national protected area. This is the largest and most remote study area in the southern Chiquitano forest, with hills (1000 m) in its middle, a few roads on the perimeter and low hunting pressure (Fig. 2b; Table 1).

- (2) The El Encanto FSC-certified forestry concession (87 562 ha; 17°00'S, 59°40'W) is connected to the San Matías multiple use reserve as the first site, but suffers more hunting pressure from local communities and fire risks (Fig. 2b; Table 1).
- (3) The Altavista ranch and private reserve (4000 ha, 16°06'S, 61°52'W) and neighboring properties included a FSC-certified unit INPA Parket Ltd forestry area (30 000 ha). There are communities, agriculture, and cattle ranches around Altavista and INPA, but no large protected areas (Fig. 2b; Table 1). Increased deforestation, fire, new roads, and hunting threaten the integrity of these forests.

Surveys

Sampling comprised 39, 20, and 20 stations, totaling efforts of 2192, 1108, and 1281 trap nights in Angel Sandoval (Venegas et al. 2009), El Encanto (Arispe et al. 2007), and Altavista (Venegas et al. 2010) (Table 1).

Nicaragua

Logging practices

The Layasiksa study area was in legally designated Miskito indigenous territories that had received FSC certification from 2003 (Padilla 2008) and assigned contractual responsibilities to a private company. Layasiksa included 4664 ha under management in blocks in 30-year cutting cycles, with varying harvest intensities depending on tree abundance. The forest management plans include selective logging of up to fifteen species of trees.

Study site

The forest extraction site lays 35.6 km southeast of the Cerro Cola Blanca Natural Reserve, a component of the Nicaragua's 1.9 million ha Bosawás Biosphere Reserve (Fig. 2c; Table 1). The Layasiksa site (84°07'N, 13°50'W) receives 1440–3000 mm precipitation per year (Ineter 1998, 2005) and included a total of 43 481 ha of wet and moist evergreen and semi-evergreen broad-leaved forests (Holdridge 2000; World Bank 2006) and pine savanna on a wide plain with a few dispersed low hills between 34 and 146 meters above sea level.

Surveys

This exploratory survey included ten stations in an effort of 320 trap nights that included an application of the scent Calvin Klein's Obsession for Men. The scent stimulates the curiosity of the cats, and thus facilitates slightly more images and individual identifications. Stations were distributed in a broadleaf forest area at a minimum distance of 1000 m from each other and at least 200 m from logging roads.

Guatemala

Logging practices

Guatemala's 2.1 million hectare Maya Biosphere Reserve (MBR, 17°30'N, 90°00'W) is divided into three zones: (a) the Core Zone consists of national parks, (b) the Multiple Use Zone (MUZ) where low-impact natural resource management activities are permitted, and (c) a 15-km band along the border of the MBR, where agriculture and cattle ranching are allowed (Hodgdon et al. 2015). The study areas covered 315 427 hectares in the center of the MUZ, involving eight forest concessions (7 community, 1 industrial). Recent logging in the survey areas affected only 1.40% of La Gloria and up to 53% in Carmelita–AFISAP concessions. Despite a relatively diverse forest, extraction has focused on the two most precious hardwood species, although more recently secondary species have also been marketed in increasing volumes (Radachowsky et al. 2012). Harvest intensities are 1.2–3.0 m³/ha.

Each forestry concession must prepare a 25-year management plan based on a concession-wide forest inventory, divided into sectors for 5-year-long harvest plans, and annual operation plans (POAs) based on complete censuses of marketable species. Forest management techniques follow reduced-impact logging guidelines such as planning roads and skid trails, directional felling, liberation of lianas, and provisioning of logging crews. Cutting cycles are 25–40 years long, minimum cutting diameters fall between 45 and 60 cm, and post-harvest silvicultural practices are applied in some cases. Annual operation areas ranged from >2400 ha in La Gloria industrial concession to 600 ha in Carmelita–AFISAP, AV–Yaloch, and Holmul community concessions. All of these concessions achieved Forest Stewardship Council certification by Smartwood in fulfillment of their contractual obligation (Radachowsky et al. 2012).

Study sites

Elevation in the four study areas range between 100 and 420 m, and annual precipitation between 1324 and 1350 mm (Moreira et al. 2009), with a December–April dry

season. The MBR is primarily covered by a tall and complex tropical rainforest reaching heights of 25–35 m with interspersed lower seasonally inundated “bajo” forests and transitional forests between the two (Lee 2000).

- (1) La Gloria (89°46'W, 17°35'N) is an industrial concession with 15 annual timber extraction plans implemented since 1999 (Fig. 2d; Table 1). It covers 91 094 ha and borders a management unit, not actively managed by any concessionaire although significant extraction of non-timber resource products and hunting occur in that area (Moreira et al. 2007).
- (2) Asociación Forestal Integral de San Andres Petén (AFISAP)–Carmelita site (90°9'W, 17°30'N) includes two community forest concessions (San Andrés and Carmelita) granted 1998–1999, comprising 105 736.84 ha (Fig. 2d; Table 1) with 15–16 annual timber extraction plans implemented since the survey was conducted in the eastern side of AFISAP and south west Carmelita (Moreira et al. 2008). Subsistence hunting by Carmelita community takes place in the area and some illegal hunting takes place in some peripheral areas of AFISAP.
- (3) Arbol Verde (AV)–Yaloch (89°15'W, 17°19'N) includes three community forest concessions with 12–13 annual timber extraction plans implemented the 111 536 ha site since 2001 (Fig. 2d; Table 1). A survey was conducted in the eastern part of Árbol Verde, south of Custodios de la Selva and west of El Esfuerzo concessions, an area with low hunting pressure due to controlled access to the area and managed non-timber extraction (Moreira et al. 2009).
- (4) Holmul (89°17'W, 17°25'N) includes five community forest concessions that have implemented 14–16 annual timber extraction plans (Fig. 2d; Table 1). The 143 099 ha site is subject to low-intensity hunting pressure and controlled extraction of non-timber forest products.

Surveys

- (1) In the La Gloria, survey 33 camera trap stations were placed at a minimum distance of 1.3 km and were active for 46 days for a sampling effort of 1518 days/trap nights between April and June 2007. After 30-sampling days, Calvin Klein Obsession for Men was placed at 17 randomly chosen camera trap stations.
- (2) In the AFISAP–Carmelita survey, 20 camera trap stations were placed at a minimum distance of 0.9 km for 45 sampling days between January and March 2008 for 900 trap nights. After 39-sampling days, Calvin Klein Obsession for Men was placed at 10 camera trap stations.

- (3) In the AV–Yaloch survey, 23 camera trap stations were placed at a minimum distance of 1 km for 45 days between May and July 2009, totaling 1035 trap nights. Calvin Klein Obsession for Men was placed at all stations for the entire study.
- (4) In the Holmul survey, 50 camera trap stations were placed at a minimum distance of 1.6 km for 90 days between April and August 2013, totaling 4500 trap nights.

RESULTS

Jaguars and potential prey items were documented in managed forests in all four countries. Results for each country are presented separately to isolate sampling variation (scale, intensity) that precludes comparisons of jaguar densities across the range of sites.

French Guiana

Jaguars were documented at similar frequencies in the two logged sites Counami and Montagne de Fer (6 and 9 individuals, 11.8 and 17.4 events/1000 trap nights, respectively) and in the two unlogged ones Nouragues and Kaw Mountain (9 and 6 individuals, 26.2 and 13.5 events/1000 trap nights) (Table 2). Prey frequencies were higher in Nouragues, the most pristine site, and uniformly lower in the two logged sites and an unlogged site close to communities that was subjected to hunting (Fig. 2a). Suids, caviomorphs, and xenarthra showed strong inter-site differences, but not related to logged vs unlogged sites. Tapirs, cervids, and meso-carnivores were more abundant in unlogged areas.

Bolivia

At least 6, 4, and 2 individual jaguars were identified in the Chiquitano dry forests of Angel Sandoval, El Encanto, and Altavista sites, and recorded at 11, 6, and 3 events/1000 trap nights, respectively. This rank of abundance reflects the remoteness and connectivity of the two sites located within/near the San Matias protected area *versus* the isolated forest of Altavista subjected to hunting, fragmentation, and fires (Fig. 2a; Tables 1, 2). Encounter rates of tapirs and cervids were high in/near the large protected area and low in the isolated Altavista site, while edentates and rodents were very frequent in the last site.

Nicaragua

Two individual jaguars were documented in the Layasiksa site. The small sample size and duration of the survey

Table 2 Sampling effort, numbers of identified jaguars, and capture rates of jaguars and prey per 1000 trap nights in twelve sites from four countries

Site	Camera trap stations	Size of camera trap polygon in km ²	Duration of study in days/sampling effort in trap nights	# individual jaguars and (captures)	# individual jaguars (and all captures) photos/1000 trap nights	Tayassuids	Caviomorph rodents	Cervids	Edentates	Tapiridae	Nasua + Procyon + Cerdocyon + Eira
French Guiana, Nouragues	17	88	110/1870	9 (49)	4.8 (26.2)	27.3	213.4	66.3	26.2	101.6	20.0
French, Guiana, Kaw	18	87	95/1170	6 (20)	3.5 (13.5)	4.7	21.2	2.9	16.5	1.2	11.0
French Guiana, Counami	15	66	90/1350	6 (16)	4.4 (11.8)	16.3	30.4	6.7	25.9	1.5	0.0
French Guiana, Montagne de Fer	15	63	90/1380	9 (24)	6.5 (17.4)	14.5	46.4s	5.1	14.5	1.4	11.0
Bolivia, A. Sandoval-San Jose	39	125.20	56 (2192)	6 (25)	2.73 (11.40)	1.40	12.30	39.70	3.80	34.70	45.6
Bolivia, El Encanto	20	36.00	58 (1108)	4 (7)	3.61 (6.32)	NP	19.8	107.4	5.4	185.9	148.0
Bolivia, Altavista	20	43.13	64 (1281)	2 (4)	1.56 (3.12)	3.1	79.6	21.9	18.0	4.7	70.0
Nicaragua, Layasiksa	10	9.96	32 (320)	2	2.0 (6.2)	3.1	34.4	3.1	–	12.5	6.25
AFISAP-Carmelita Guatemala	20	50.89	45/900	10 (27)	11.1 (30.0)	2.2	7.8	5.6	1.1	5.6	8.9
La Gloria	33	128	46/1518	6 (22)	3.9 (14.4)	3.3	23.1	5.3	0.0	4.6	34.9
AV-Yaloch	23	67.36	45/1035	9 (45)	8.7 (43.4)	26.1	19.3	23.2	1.0	8.7	65.7
Holmul	50	519	90/4500	25 (204)	5.5 (45.3)	87.8	104.2	48.7	3.6	20.2	98.4

potentially affected the variety of prey species recorded (Table 2). Edentates were not recorded, but tapirs and the rest of the groups were present at rates within the range of other sites sampled in the nearby large Bósawas Biosphere Reserve. Similar sampling effort in an area more isolated from the protected area complex and more vulnerable to uncontrolled hunting of game species, Las Crucetas–Yulukira, 62 km south of Layasiksa, resulted in no jaguar photo-captures (Fig. 2c).

Guatemala

Abundant jaguars (6–25 individuals, 14–45 events/1000 trap nights) and diverse prey were found in the four managed forest sites surveyed in the large habitat block of the Maya Biosphere Reserve (Table 2). During a seven-year span equipment evolved from inexpensive film units to high-performance digital units, survey duration doubled in length, and direct sample areas increased an order of magnitude, from 50 to 519 km². Despite significant differences in effort and detectability, several observations can be made: (1) high prey diversity and frequencies were recorded in the large Holmul site, despite 15 years of annual operating extraction plans and a total of 43% of the sampled area subjected to some history of harvest (Tables 1, 2); (2) high jaguar frequencies were obtained in AFISAP–Carmelita despite 10 years of operating plans, 53% of the area with a history of logging, dated camera trap equipment and a very small sample area; and (3) the lowest frequencies came from La Gloria, where only 2% of the area had been subjected to timber harvest, and only one annual operating extraction plan had been executed, but where the hunting pressure was the greatest of all sites (Table 1).

Landscape context

The data suggest that landscape context is important for jaguars. In French Guiana, all logged sites were connected to large wild areas, and prey frequencies were highest in the most remote area. In the Chiquitano of Bolivia, jaguar frequencies were highest in the area with the greatest overlap with a protected area complex and lowest in the area most isolated from contiguous protected areas. All the Guatemalan sites were within the continuous habitat central block of habitat in the Maya Biosphere Reserve (Fig. 2d), which is connected to the north with Mexico's Calakmul Biosphere Reserve, and to the northeast with the Rio Bravo and Gallon Jug/Yalbac areas in Belize (Kelly and Rowe 2014). La Gloria, the site with the lowest levels of control, had the highest hunting pressure of all surveyed sites and the lowest jaguar frequency (Fig. 2b–d).

DISCUSSION

We draw on twelve jaguar surveys across four countries to present evidence across a range of biomes that adequate logging management can maintain jaguar populations, but in each country there was also evidence that inadequately controlled secondary impacts could risk not meeting the certification mandate of ecosystem conservation. The observations of secure prey were highest in tightly controlled areas of the Maya Biosphere Reserve and lowest in the sites in the Bolivian Chiquitano that were not well regulated. Even in the most productive sites in French Guiana, it was obvious that controlling access into the area and hunting of prey were paramount considerations for the objectives of preserving biodiversity and ecological functions that are the environmental selling points for certified forests/timber products. In Nicaragua, although the survey was just under an effort of >400 camera trap days/night expected to reach the asymptote of species accumulation curves (Tobler et al. 2008; Meyer et al. 2015), a more full complement of native prey species has been recorded in larger scale, longer duration surveys within the Bosawás Biosphere boundaries.

Logging prescriptions varied among the countries, but within each country, every logged area was part of a mosaic of land use, including designated parks, or remote access areas. From a remote sensing perspective (Fig. 2a–d), landscape context—proximity to, or inclusion in a large block of wild forest, appeared important for maintaining jaguars and prey. Bahaa-el-din et al. (2016) found high densities of forest-dependent golden cats *Caracal aurata* in logged sites with tight controls on hunting, but noted that the study areas were within 10 km of a national park boundary, with possible positive effects on resilience.

Impacts of selective logging and its secondary effects on wildlife

Logging implies primary and secondary impacts. Expanded edge along abandoned roads and additional gaps in primary forest overall might increase rather than decrease terrestrial herbivore biomass. Logging might increase high-quality browse for ungulates. In the absence of hunting, browser-frugivores such as brocket deer and tapir can adapt to the small openings following logging (Fragoso 1991; Davies et al. 2001). Care is needed to not remove food sources for jaguar prey, such as palm fruits or fig trees, (Felton et al. 2013), but controlled selective logging could increase the abundance of select species of jaguar prey and indirectly benefit jaguars.

Careful felling, skidding, and rotations during managed forest harvests will still bring potential negative secondary impacts if they lead to increased entrance by hunters and

establishment of new human settlements (Bennett and Gumal 2001; Wilkie et al. 2001). Uncontrolled road access in the Ecuadorian Amazon has led to diminished numbers of large herbivores (Suárez et al. 2009; Espinosa-Andrade 2012; Espinosa et al. 2014) that play important roles in forest dynamics and sustain jaguars. Increased fragmentation can decrease mammal abundance (Kosydar et al. 2014). Access and hunting need careful control to avoid decreased jaguar prey. Miquelle et al. (1999) stated that logging is compatible with tiger (*Panthera tigris*) conservation, and that selective cutting of appropriate species and age classes can improve tiger habitat in some cases, but that road networks can have severe impacts on tigers and their prey through legal and illegal hunting, with road closures of utmost importance to increase secure habitat for tigers and their prey (Miquelle et al. 1999).

Using camera traps in Malaysia, Rayan and Linkie (2015) found tiger densities three times higher in the protected Royal Belum State Park (RBSP) than in the selectively logged Temengor Forest Reserve (TFR) with controlled road access, anti-poaching patrols, and a military checkpoint the strongest contrasts between the two areas.

Rayan and Mohamad (2009) also obtained density estimates for tigers in the selectively logged Gunung Basor Forest Reserve in Peninsular Malaysia, illustrating the potential of managed forests to accommodate relatively high densities of tigers, a better alternative for tigers than conversion to oil palm. In Malaysian Borneo, logged forests retain high species richness, on average 70% of the species found in primary forest. In contrast, conversion to oil palm dramatically lowers species richness (Edwards et al. 2014).

On a national level, Guatemala retains one of the highest deforestation rates in the Western Hemisphere (Hansen et al. 2013), and the highest rate of protected area degradation in the Americas (Leisher et al. 2013). By comparison, deforestation rates in certified forest concessions are relatively low (Hodgdon et al. 2015). From 2000 to 2013, deforestation rates in areas that were concessioned to recent migrants have been high (1.6%). In other areas, such as concessions with no resident populations or whose communities have been in the MBR for more than 50 years, deforestation rates are next to zero (Hodgdon et al. 2015). The FSC-certified forest concessions have effectively conserved forest cover and jaguars in about a quarter of the MBR, while also producing socioeconomic benefits for local communities (Hodgdon et al. 2015).

Kelly and Rowe (2014) summarized five years in two logged and one unlogged sites in northwestern Belize, the eastern part of the same Selva Maya forest sampled in Guatemala's MBR. Using similar methods across all three of their study areas, no dramatic differences in species

assemblages or species numbers across sites were observed (Kelly and Rowe 2014). Jaguar densities provided little evidence of differences across sites. White-lipped peccaries appeared to have higher trap frequencies in the unlogged sites. The authors considered the similar numbers of species, trapping frequencies, occupancy rates, and densities as testimony to the protection the logging companies provided through controlled access, including full-time manned gates and border patrols.

On all our study sites, the impacts we detected (lower occurrences of large felids and prey) were not the direct consequences of wood extraction, but of hunting. At a local level, logging practices did not present large-scale disturbances: the number of harvested trees was rather low, the network of logging roads optimized, watercourses and flooded forests spared, and the plots where loggers work quite small and separated by areas free of harvest activity. Maintenance of connections between logged forests and pristine areas likely provided refuges for fauna, and allowed rapid recolonization of logged areas after wood extraction.

Historically hunting pressure in the tropics has increased due to roads that provide access to remote areas and commercial wildlife harvest to support human populations (Redford 1992; Peres 2000; Wilkie et al. 2000; Bennett and Gumal 2001; Wilkie et al. 2001; Suarez et al. 2012; Espinosa et al. 2014). Hunting risks a cascade of potential negative ecological consequences. The complex dispersion, pollination, and other processes that organize trophic chains and regeneration dynamics in tropical forests include animal-mediated mutualisms in plant reproduction (Terborgh and Feeley 2004). Changes in forest composition and regeneration dynamics occur when levels of secondary consumers (predators), or primary consumers (herbivores) are dramatically reduced or eliminated (Dirzo and Miranda 1991; Redford 1992; Wright et al. 1994, 2000; Wright 2003; Peres and Palacios 2007; Stoner et al. 2007; Wright et al. 2007a, b; Bello et al. 2015; Peres et al. 2016). Depleted or extirpated populations of frugivores in overhunted areas may result in declines in the availability and quality of seed dispersal services (Bello et al. 2015; Peres et al. 2016). A drastic decline of a particular guild of frugivores can lead to a collapse of seed dispersal services for dependant plant species (Peres and Palacios 2007). Animal seed dispersal agents include preferred game species such as tapirs *Tapirus bairdii* and *T. terrestris*, white-lipped peccaries, paca, *Cuniculus paca*, red brocket deer, and *Mazama americana*, as well as large frugivorous terrestrial birds.

The dietary overlap between jaguars and humans is well documented (McNab 1999; Novack 2003; Novack et al. 2005; Foster et al. 2016). Intensive hunting of medium-sized and large prey species has been shown to reduce an

area's potential for leopard conservation (Henschel et al. 2011) and result in reduced jaguar densities (Espinosa-Andrade 2012). The maintenance of resident jaguars and prey is an unequivocal measure of conservation success and, thus, a logical goal for timber certification.

RECOMMENDATIONS AND CONCLUSIONS

We have provided evidence that forest management to generate income can be compatible with jaguar and ecosystem conservation. In all twelve sites in four Latin American countries, we found jaguars and reasonable assemblages of their prey which are success stories, but one that requires recommendations for management and monitoring. We recognize that in certain cases, certification has started in sites which have already lost jaguars, and/or are so distant from protected area complexes that constant occupancy by jaguars is unlikely. However, maintaining jaguars in managed forests where certification has been initiated can provide jaguars an opportunity to survive outside protected areas.

We recommend that hunting and trapping for timber camp labor and for markets outside the managed area be prevented, and acknowledge that observing that strict laws may work with commercial operators from outside the area, but resident communities need a stake in long-term management of an area (Davies et al. 2001). Additional recommendations include the following: (1) controlled access with roads closed and controlled after logging, (2) alternative sources of animal protein for forest workers, and (3) requiring logging operations to invest in enforcement (Bennett and Gumal 2001; Meijaard et al. 2005). If timber extraction operations allow game consumption by harvesters or lead to uncontrolled access and hunting afterwards, they run the risk of dramatically altering forest dynamics in violation of FSC Principle 6. Hunting is the primary factor to evaluate and control to comply with FSC's Principles 1.4, 6, 8, and 9 and allow the jaguar to play its role in the maintenance of natural forests (FSC 2015a, b). Wherever jaguars occur prior to initiation of certification, and in portions of their range where their presence is expected, jaguars can be considered a HCV attribute (FSC 2015a, b), and cost-effective monitoring of jaguars and their prey can provide evidence that areas are fulfilling FSC Principle 6.

Forest management unit operative plans should include: (1) assessments of wildlife habitat in the landscape context (Richard-Hansen et al. 2015); (2) an assessment of the presence and distribution of key wildlife species and hunting practices and needs of local communities, including tenure and hunting rights at the landscape scale (Renoux and de Thoisy 2016); and (3) plans to address legal requirements for threatened and endangered species, and

management of hunting and wildlife trade (Bennett 2004). FSC Principles 3 and 4 emphasize indigenous people and local community's rights of tenure, access, and use of forest resources, customary rights, and the requirement for free, prior, and informed consent (FSC 2015a, b). These principles mandate that traditional use areas and knowledge are respected. Principle 5 mandates compensation for losses that forest management might bring. Hunting management may involve several levels of complexity, and negotiated agreements or mandatory measures with communities, landowners, and loggers. Locally generated wildlife evaluations should support hunting authorizations to accomplish and monitor Principles 1, 6, 8, and 9.

One solution for local communities with traditional rights might be hunting for local consumption of species that have high reproductive rates, widespread distribution, and are habitat generalists. For example, collared peccaries *Pecari tajacu* and armadillos *Dasypus novemcinctus* would then be candidates for managed hunting. The gray brocket deer *Mazama gouazoubira* seems very resilient to hunting in Bolivian dry forests and in French Guiana (de Thoisy et al. 2010). White-lipped peccaries, *Tayassu pecari*, tapirs *T. bairdii*, and *T. terrestris*, brocket deer *M. americana*, and terrestrial frugivorous birds can decline in number under hunting pressure (de Thoisy et al. 2009, 2010). These species have longer generation times and lower fecundity (Peres 2000) and/or specialized habitat requirements (Reid 2009) that make them more vulnerable.

Jaguars are inspirational indications of success in meeting ecological standards, yet biological monitoring should not imply such high costs that it removes the incentives for certification (Gullison 2013; Carlson and Palmer 2016). We suggest that camera traps can provide irrefutable proof that jaguars are in or using a forest management area, evidence of compliance with certification standards. We are mindful of extra costs this might incur (WWF 2014) and suggest hierarchical spectrum of jaguar monitoring rigor and cost that includes capture–recapture studies, occupancy (presence–absence), and presence (Fig. 3). Long-term capture–recapture studies assess influence of environmental and management factors on density, distribution, survivorship, and numerical trends of female and male jaguars, but require considerable external investments of expertise and resources (Karanth et al. 2011a; Sollman et al. 2011; Tobler and Powell 2013; Polisar et al. 2014a; Royle et al. 2014; Bahaa-el-Din et al. 2016; Boron et al. 2016). The next level down in cost is detection probability-based presence–absence occupancy of jaguar and prey (Karanth et al. 2011b; Sollman et al. 2012; Sunarto et al. 2012; Polisar et al. 2014a; Tobler et al. 2015). At the lowest level of complexity and rigor (Tobler et al. 2008; Sollman et al. 2013; Polisar et al. 2014b), but also the most cost-feasible, is simple proof of the presence

Fig. 3 Hierarchical spectrum of jaguar and prey monitoring

or counts of jaguars in a management area and prey frequencies (Fig. 3).

All levels external require training, guidance, and impartial interpretation of results. Evaluations of the presence and frequencies at regular intervals every two–three years to document jaguars should at least exceed 400 trap nights (Tobler et al. 2008) and a minimum of ten strategically placed camera traps. FSC certification occurs at five-year intervals. Female jaguars reproduce at approximately 2.5 years of age, and their female cubs reproduce 2.5 years later, (Polisar et al. 2014b). The ideal monitoring scenario is detection probability-based capture–recapture or occupancy sampling synchronized with five-year certification cycles to measure trends, but simple proof of the presence is important as well. Jaguars provide evidence that the ecological requirements of certification are being met, but documenting that should not be cost and labor prohibitive.

Landscapes in which carefully managed extraction and human use areas complement areas under stricter protection might provide wild felids the highest chance for long-term large-scale conservation (Davies et al. 2001; Fimbel et al. 2001; Meijaard et al. 2005; Henschel et al. 2011; Jorge et al. 2013; Goswami et al. 2014; Rayan and Linkie 2015; Bahaa-el-Din et al. 2016; Boron et al. 2016). Sound management of protected areas should be viewed as a priority complement to well-managed logging concessions using FSC's principles and criteria (FSC 2015a, b).

Jaguars can prove that forest certification is working as a useful conservation tool when certification principles are followed. Reinforcing the reach of timber certification processes through cost-effective monitoring can help maximize jaguar and ecosystem conservation using forest management as a complementary conservation approach across Latin America.

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REFERENCES

- Arispe, R., D.I. Rumiz, and C. Venegas. 2007. Censo de jaguars y otros mamíferos con trampas cámara en la Concesión Forestal El Encanto. Informe Técnico WCS 173, Santa Cruz.
- Bahaa-el-Din, L., R. Sollman, L.T.B. Hunter, R. Slotow, D.W. Macdonald, and P. Henschel. 2016. Effects of human land-use on Africa's only forest dependent felid: The African golden cat *Caracal aurata*. *Biological Conservation* 199: 1–9.
- Bello, C., M. Galetti, M.A. Pizo, L.F.S. Magnago, M.F. Rocha, R.A.F. Lima, C.A. Peres, O. Ovaskainen, et al. 2015. Defaunation affects carbon storage in tropical forests. *Science Advances* 1: e1501105.
- Bennett, E. 2004. Seeing the wildlife and the trees: Improving timber certification to conserve tropical forest wildlife. A paper for discussion. WCS/World Bank.
- Bennett, E.L., and M.T. Gual. 2001. The interrelationships of commercial logging, hunting, and wildlife in Sarawak: Recommendations for forest management. In *The cutting edge: Conserving wildlife in logged tropical forests*, ed. R.A. Fimbel, A. Grajal, and J.G. Robinson, 359–372. New York: Columbia University Press.
- Boron, V., J. Tzanopoulos, J. Barragan, L. Jaimes-Rodríguez, G. Schaller, and E. Payan. 2016. Jaguar densities across human-dominated landscapes in Colombia: The contribution of unprotected areas to long-term conservation. *PLoS ONE* 11(5): e0153973.
- Brunaux, O., and J. Demenois. 2003. Aménagement forestier et exploitation en forêt tropicale humide guyanaise. *Revue Forestière Française* 55: 260–272.
- Carlson, A., and C. Palmer. 2016. A qualitative meta-synthesis of the benefits of eco-labeling in developing countries. *Ecological Economics* 127: 129–145.
- Davies, G., M. Heydon, N. Leader-Williams, J. MacKinnon, and H. Newing. 2001. The effects of logging on tropical forest ungulates. In *The cutting edge: Conserving wildlife in logged tropical forests*, ed. R.A. Fimbel, A. Grajal, and J.G. Robinson, 93–124. New York: Columbia University Press.
- de Granville, J.J. 1988. Phytogeographical characteristics of the Guianan forests. *Taxon* 37: 578–594.
- de Thoisy, B., F. Renoux, and C. Julliot. 2005. Hunting in northern French Guiana and its impacts on primates communities. *Oryx* 39: 149–157.
- de Thoisy, B., C. Richard-Hansen, B. Goguillon, P. Joubert, J. Obstancias, P. Winterton, and S. Brosse. 2010. Rapid evaluation of threats to biodiversity: Human footprint score and large vertebrate species responses in French Guiana. *Biodiversity and Conservation* 19: 1567–1584.
- de Thoisy, B., C. Richard-Hansen, and C.A. Peres. 2009. Impacts of subsistence hunting on Amazonian primates. In *South American Primates: Comparative perspectives in the study of behavior, ecology, and conservation*, ed. P.A. Garber, A. Estrada, J.C. Bicca-Marques, E.W. Heymann, and K.B. Strier, 389–412. Berlin: Springer.
- Dirzo, R., and A. Miranda. 1991. Altered pattern of herbivory and diversity in the forest understory: A case study of the possible consequences of contemporary defaunation. In *Plant-animal interactions, evolutionary ecology in tropical and temperate regions*, ed. P.W. Price, T.M. Lewinsohn, G.W. Fernandes, and W.W. Benson, 273–287. New York: Wiley.
- Edwards, D.P., A. Magrach, P. Woodcock, Y. Ji, N.T.L. Lim, F.A. Edwards, T.H. Larsen, W.W. Hsu, et al. 2014. Selective logging and oil palm: Multitaxon impacts, biodiversity indicators, and trade-offs for conservation planning. *Ecological Applications* 24: 2029–2049.
- Espinosa, S., L.C. Branch, and R. Cueva. 2014. Road development and the geography of hunting by an Amazonian indigenous group: Consequences for wildlife. *PLoS ONE* 9: e114916.
- Espinosa-Andrade, S.R. 2012. Road development, bushmeat, extraction and jaguar conservation in Yasuni Biosphere Reserve, Ecuador. PhD thesis. University of Florida, Gainesville, Florida.
- Felton, A.M., A. Felton, D.I. Rumiz, N. Villaroel, C.A. Chapman, and D.B. Lindenmayer. 2013. Commercial harvesting of *Ficus* timber—An emerging threat to frugivorous wildlife and sustainable forestry. *Biological Conservation* 159: 96–100.
- Fimbel, R.A., A. Grajal, and J.G. Robinson. 2001. Logging and wildlife in the tropics: Impacts and options for conservation. In *The cutting edge: Conserving wildlife in logged tropical forests*, ed. R.A. Fimbel, A. Grajal, and J.G. Robinson, 667–695. New York: Columbia University Press.
- Finegan, B., J. Hayes, D. Delgado, and S. Gretzinger. 2004. Monitoreo ecológico del manejo forestal en el trópico húmedo: Una guía para operadores y certificadores con énfasis en Bosques de Alto Valor para la Conservación. WWF. Retrieved 16 August 2016, from <https://www.hcvnetwork.org/resources/folder.2006-09-29.6584228415/Guia%20Monitoreo%20en%20BAVC.pdf>.
- Foster, R.J., and B.J. Harmsen. 2012. A critique of density estimation from camera-trap data. *Journal of Wildlife Management* 76: 224–236.
- Foster, R.J., B.J. Harmsen, D.W. MacDonald, J. Collins, Y. Urbina, R. Garcia, and C.P. Doncaster. 2016. Wild meat: A shared resource amongst people and predators. *Oryx* 50: 63–75.
- Fragoso, J.M.V. 1991. The effect of selective logging on Baird's tapir. In *Latin American mammalogy: History, biodiversity and conservation*, ed. M.A. Mares, and D.J. Schmidly, 295–304. Norman: University of Oklahoma Press.
- FSC. 2013a. Celebrating success: Stories of FSC certifications. Retrieved 16 August 2016, from <https://ic.fsc.org/en/smallholders/success-stories>.
- FSC. 2013b. Furniture cooperative in Honduras. Retrieved 16 August 2016, from <https://ic.fsc.org/en/smallholders/success-stories>.

- FSC. 2015a. Forest Stewardship Council. FSC International Standard. FSC Principles and Criteria for Forest Stewardship. FSC-STD-1-001V5-EN. Retrieved 16 August 2016, from <https://ic.fsc.org/preview.fsc-principles-and-criteria-for-forest-stewardship-fsc-std-01-001-v5-2-enwebversion.a-4849.pdf>.
- FSC. 2015b. Forest Stewardship Council. International Generic Indicators. FSC-STD-60-004 V1-0-EN. Retrieved 16 August 2016, from <https://ic.fsc.org/preview.fsc-std-60-004-v1-0-en-international-generic-indicators.a-4566.pdf>.
- Giam, X., R.C. Gopalswamy, S.A. Aziz, K.Y. Hong, and J. Miettinen. 2011. Rethinking the ‘back to wilderness’ concept for Sundaland’s forests. *Biological Conservation* 144: 3149–3152.
- Goswami, V.R., S. Sridhara, K. Medhi, A.C. Williams, R. Chellam, J.D. Nichols, and M.L. Oli. 2014. Community-managed forests and wildlife-friendly agriculture play a subsidiary but not substitutive role to protected areas for the endangered Asian elephant. *Biological Conservation* 177: 74–81.
- Guariguata, M., C. García-Fernández, D. Sheil, R. Nasi, C. Herrero-Jáuregui, P. Cronkleton, and V. Ingram. 2010. Compatibility of timber and non-timber forest products management in natural tropical forest: Perspectives, challenges, and opportunities. *Forest Ecology and Management* 259: 237–245.
- Guitet, S., R. Péliissier, O. Brunaux, G. Jaouen, and D. Sabatier. 2015. Geomorphological landscape features explain floristic patterns in French Guiana rainforest. *Biodiversity and Conservation* 24: 1215–1237.
- Guitet, S., S. Pithon, O. Brunaux, G. Jubelin, and V. Gond. 2012. Impacts of logging on the canopy and the consequences for forest management in French Guiana. *Forest Ecology and Management* 277: 124–131.
- Gullison, R.E. 2013. Does forest certification conserve biodiversity? *Oryx* 37: 153–165.
- Hansen, M.C., P.V. Potapov, R. Moore, M. Hancher, S.A. Turubanova, A. Tyukavina, D. Thau, S.V. Stehman, et al. 2013. High-resolution global maps of 21st-century forest cover change. *Science* 342: 850–853.
- Henschel, P., L.T.B. Hunter, L. Coad, K.A. Abernethy, and M. Mühlenberg. 2011. Leopard prey choice in the Congo Basin rainforest suggests exploitative competition with human bushmeat hunters. *Journal of Zoology* 285: 11–20.
- Hill, J.L., and R.A. Hill. 2011. Ecotourism in Amazonian Peru: uniting tourism, conservation, and community development. *Geography* 96: 75–85.
- Hodgdon, B., D. Hughell, V.H. Ramos, and R.B. McNab. 2015. Deforestation trends in the Maya Biosphere Reserve, Guatemala. Rainforest Alliance, Consejo Nacional de Áreas Protegidas, Wildlife Conservation Society. Retrieved 16 August 2016, from http://www.rainforest-alliance.org/sites/default/files/publication/pdf/MBR-Deforestation_150213-2.pdf.
- Holdridge, L.R. 2000. Ecología basada en zonas de vida. Quinta reimpresión. Instituto Interamericano de Cooperación para la Agricultura (IICA). San José, Costa Rica.
- Ineter. 1988. Instituto Nicaragüense de Estudios Territoriales. Hojas cartográficas 1:50,000, correspondientes al departamento de Jinotega y Región Autónoma del Atlántico Norte. Retrieved 16 August 2016, from <http://ineter.gob.ni/>.
- Ineter. 2005. Instituto Nicaragüense de Estudios Territoriales. Mapa de precipitación media anual en milímetros, período 1971–2000. Retrieved 16 August 2016, from <http://webserver2.ineter.gob.ni/geofisica/mapas/Nicaragua/clima/atlas/index.html>.
- Jorge, M.L.S.P., M. Galetti, M.C. Ribeiro, and K.M.P. Ferraz. 2013. Mammal defaunation as surrogate of trophic cascades in a biodiversity hotspot. *Biological Conservation* 163: 49–57.
- Karanth, K.U., A.M. Gopalaswamy, N.S. Kumar, S. Vaidyanathan, J.D. Nichols, and D.I. Mackenzie. 2011a. Monitoring carnivore populations at the landscape scale: Occupancy modeling of tigers from sign surveys. *Journal of Applied Ecology* 48: 1048–1056.
- Karanth, K.U., J.D. Nichols, N.S. Samba Kumar, and D. Jathanna. 2011b. Estimation of demographic parameters in a tiger population from long-term camera trap data. In *Camera traps in animal ecology*, ed. A.F. O’Connell, J.D. Nichols, and K.U. Karanth, 145–161. Berlin: Springer.
- Kays, R.W., and K.M. Slauson. 2008. Remote cameras. In *Noninvasive survey methods for carnivores*, ed. R. Long, P. MacKay, W.J. Zielinski, and J.C. Ray, 110–140. Washington, D.C.: Island Press.
- Kelly, M.J., and C. Rowe. 2014. Analysis of 5 years data from Rio Bravo Conservation and Management Area (RBCMA) and one year of data from Gallon Jug/Yalbac Ranch on trap rates for predator and prey, including jaguar density estimates in unlogged versus sustainably logged areas. Report for Rio Bravo Conservation and Management Area. Department of Fish and Wildlife Conservation, Virginia Tech., Blacksburg, VA.
- Kelly, M.J., J. Betsch, C. Wulsch, B. Mesa, and L.S. Mills. 2012. Noninvasive sampling for carnivores. In *Carnivore ecology and conservation: A hand book of techniques*, ed. L. Boitani, and R.A. Powell, 47–69. Oxford: Oxford University Press.
- Kosydar, A.J., D.I. Rumiz, L.L. Conquest, and J.J. Tewksbury. 2014. Effects of hunting and fragmentation on terrestrial mammals in the Chiquitano forests of Bolivia. *Tropical Conservation Science* 7: 288–307.
- Lee, J. (ed.). 2000. *A Field Guide to the Amphibians and Reptiles of the Maya World. The Lowlands of Mexico, Northern Guatemala, and Belize*. London: Cornell University Press.
- Leisher, C., J. Touval, S.M. Hess, T.M. Boucher, and L. Reymondin. 2013. Land and forest degradation inside protected areas in Latin America. *Diversity* 5: 779–795.
- Maffei, L., A.J. Noss, S.C. Silver, and M.J. Kelly. 2011. Abundance/density case study: Jaguars in the Americas. In *Camera traps in animal ecology: Methods and analyses*, ed. A.F. O’Connell, J.D. Nichols, and U.K. Karanth, 119–144. Tokyo: Springer.
- Marcot, B.G., R.E. Gullison, and J.R. Barborak. 2001. Protecting habitat elements and natural areas in the managed forest matrix. In *The cutting edge: Conserving wildlife in logged tropical forests*, ed. R.A. Fimbel, A. Grajal, and J.G. Robinson, 523–558. New York: Columbia University Press.
- McNab, R.B. 1999. Comparative impacts of chicle and xate harvests on wildlife of the Maya Biosphere Reserve, Guatemala. MS thesis, University of Florida, Gainesville.
- Meijaard, E., D. Shell, R. Nasi, D. Augeri, B. Rosenbaum, D. Iskander, T. Setyawati, M. Lammertink, et al. 2005. *Life after logging: Reconciling wildlife conservation and production forestry in Indonesian Borneo*. Jakarta: Center for International Forestry Research.
- Meyer, N.F.V., H.J. Esser, R. Moreno, F. van Langeveld, Y. Liefting, D.R. Oller, C.B.F. Vogels, A.D. Carver, et al. 2015. An assessment of the terrestrial mammal communities in forests of Central Panama using camera-trap surveys. *Journal for Nature Conservation* 26: 28–35.
- Miquelle, D., T.W. Merrill, Y.M. Dunishenko, E.N. Smirnov, H.B. Quigley, D.G. Pikunov, and M.G. Hornocker. 1999. A habitat protection plan for the Amur tiger: Developing political and ecological criteria for a viable land-use plan. In *Riding the tiger: Tiger conservation in human dominated landscapes*, ed. J. Seidensticker, S. Christie, and P. Jackson, 273–289. Cambridge: Cambridge University Press.
- Moreira, J., R. García-Anleu, R.B. McNab, G. Ponce-Santizo, M. Mérida, V. Méndez, G. Ruano, et al. 2009. *Abundancia de jaguares y evaluación de presas asociadas al fototrampeo en las Concesiones Comunitarias del Bloque de Melchor de Mencos*,

- Reserva de la Biosfera Maya, Petén, Guatemala*. Flores: Wildlife Conservation Society- Guatemala Program.
- Moreira, J., R.B. McNab, R. García-Anleu, V. Méndez, M. Barnes, G. Ponce-Santizo, A. Vanegas, G. Ical, et al. 2008. *Densidad de jaguares dentro de la Concesión Comunitaria de Carmelita y de la Asociación Forestal Integral San Andrés Petén, Guatemala*. Flores: Wildlife Conservation Society- Guatemala Program.
- Moreira, J., R.B. McNab, D. Thornton, R. García-Anleu, V. Méndez, A. Vanegas, G. Ical, E. Zepeda, et al. 2007. *Abundancia de jaguares en La Gloria-El Lechugal, Zona de Usos Múltiples, Reserva de la Biosfera Maya, Petén, Guatemala*. Flores: Wildlife Conservation Society- Guatemala Program.
- Mostacedo, B., M. Peña, D. I. Rumiz, and Z. Villegas. 2010. Hacia un modelo de manejo sostenible del bosque seco chiquitano: propuesta de ajustes a ciertas prácticas forestales. FCBC-IBIF-WCS Unión Europea, Santa Cruz, Bolivia. Retrieved 16 August 2016, from <http://www.fcbc.org.bo/Website/publicaciones.aspx>.
- Nichols, J.D., K.U. Karanth, and A.F. O'Connell. 2011. Science, conservation, and camera traps. In *Camera traps in animal ecology: Methods and analyses*, ed. A.F. O'Connell, J.D. Nichols, and K.U. Karanth, 45–56. Tokyo: Springer.
- Noss, A., J. Polisar, L. Maffei, R. Garcia, and S. Silver. 2013. Evaluating jaguar densities with camera traps. Wildlife Conservation Society. Retrieved 16 August 2016, from <http://www.wcsnorthamerica.org/AboutUs/Publications/tabid/3437/Categoryid/1535/Default.aspx>.
- Novack, A. 2003. Impacts of subsistence hunting on the foraging ecology of jaguar and puma in the Maya Biosphere Reserve, Guatemala. MS thesis, University of Florida, Gainesville.
- Novack, A.J., M.B. Main, M.E. Sunquist, and R.F. Labisky. 2005. Foraging ecology of jaguar (*Panthera onca*) and puma (*Puma concolor*) in hunted and non-hunted sites within the Maya Biosphere Reserve, Guatemala. *Journal of Zoology* 267: 167–178.
- O'Brien, T.G., M.F. Kinnaird, and H.T. Wibisono. 2011. Estimation of species richness of large vertebrates using camera traps: An example from an Indonesian rainforest. In *Camera traps in animal ecology: Methods and analyses*, ed. A.F. O'Connell, J.D. Nichols, and K.U. Karanth, 223–252. Tokyo: Springer.
- Padilla, A. (compilador). 2008. Revalorando la Institucionalidad Indígenas: Gobernanza de bisques por Pueblos Indígenas, Casos de Guatemala, Honduras, y Nicaragua. Retrieved 16 August 2016, from <https://portals.iucn.org/library/node/9275>.
- PEFC. 2010. International standard. Sustainable Forest Management—Requirements. PEFC ST 1003:2010. PEFC council, Geneva, 2010. Retrieved 16 August 2016, from http://www.pefc.org/images/documents/PEFC_ST_1003_2010_SFM_Requirements_2010_11_26.pdf.
- Peres, C. 2000. Effects of subsistence hunting on vertebrate community structure in Amazonian forest. *Conservation Biology* 14: 240–253.
- Peres, C.A., T. Emilio, J. Schiatti, S.J.M. Desmoulière, and T. Levi. 2016. Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. *Proceedings of the National Academy of Sciences* 113: 892–897.
- Peres, C.A., and E. Palacios. 2007. Basin-wide effects of game harvest on vertebrate population densities in Amazonian forest: Implications for animal-mediated seed dispersal. *Biotropica* 39: 304–315.
- Python, S., G. Jubelin, S. Guitet, and V. Gond. 2013. A statistical method for detecting logging-related canopy gaps using high-resolution optical remote sensing. *International Journal of Remote Sensing* 34: 700–711.
- Polisar, J., S. Matthews, R. Sollman, M. Kelly, J.P. Beckmann, E.W. Sanderson, et al. 2014a. Protocol of jaguar survey and monitoring techniques and methodologies. Retrieved 16 August 2016, from <http://www.wcsnorthamerica.org/AboutUs/Publications/tabid/3437/Categoryid/1535/Default.aspx>.
- Polisar, J., T.G. O'Brien, S. Matthews, J. Beckmann, E.W. Sanderson, O.C. Rosas-Rosas, et al. 2014b. Jaguar survey and monitoring techniques and methodologies: A review. Retrieved 16 August 2016, from <http://www.wcsnorthamerica.org/AboutUs/Publications/tabid/3437/Categoryid/1535/Default.aspx>.
- Putz, F.E., P. Sist, T. Fredericksen, and D. Dykstra. 2008. Reduced-impact logging: Challenges and opportunities. *Forest Ecology and Management* 256: 1427–1433.
- Radachowsky, J., V.H. Ramos, R.B. McNab, E. Baur, and N. Kazakov. 2012. Forest concessions in the Maya Biosphere Reserve, Guatemala: A decade later. *Forest Ecology and Management* 268: 18–28.
- Rayan, D.M., and M. Linkie. 2015. Conserving tigers in Malaysia: A science-driven approach for eliciting conservation policy change. *Biological Conservation* 184: 18–26.
- Rayan, D.M., and S.W. Mohamad. 2009. The importance of selectively logged forests for tiger *Panthera tigris* conservation: A population density estimate in Peninsular Malaysia. *Oryx* 43: 48–51.
- Redford, K. 1992. The empty forest. *BioScience* 42: 412–422.
- Reid, F. 2009. *A field guide to the mammals of Central America and southeast Mexico*, 2nd ed, 346. New York: Oxford University Press.
- Renoux, F., and B. de Thoisy. 2016. Hunting management: The need to adjust predictive models to field observations. *Ethnobiology and Conservation*. doi:10.15451/ec2016-6-5.1-13.
- Richard-Hansen, C., G. Jaouen, T. Denis, O. Brunaux, E. Marcon, and S. Guitet. 2015. Landscape patterns influence communities of medium- to large-bodied vertebrates in undisturbed terra firme forests of French Guiana. *Journal of Tropical Ecology* 31: 423–436.
- Robinson, J.G.R. 1993. The limits to caring: Sustainable living and the loss of biodiversity. *Conservation Biology* 7: 20–28.
- Royle, J.A., R.B. Chandler, R. Sollman, and B. Gardner. 2014. *Spatial capture-recapture*. New York: Academic Press.
- Rumiz, D.I., B. Mostacedo, T. Cochrane, and B. Roza. 2004. Guía de identificación de atributos para definir Bosques de Alto Valor de Conservación. Consejo Boliviano para la Certificación Forestal Voluntaria and GTZ. Santa Cruz, Bolivia. Retrieved 16 August 2016, from <http://www.rainforestalliance.org/sites/default/files/publication/pdf/Gu%C3%ADaIdentificaci%C3%B3nBosquesAltoValorLaPaz.pdf>.
- Salvador, S., M. Clavero, and R.L. Pitman. 2011. Large mammal species richness and habitat use in an upper Amazonian forest used for ecotourism. *Mammalian Biology—Zeitschrift für Säugetierkunde* 76: 115–123.
- Silver, S.L., L.K. Ostro, L.K. Marsh, L. Maffei, A. Noss, M.J. Kelly, R.B. Wallace, H. Gómez, et al. 2004. The use of camera traps for estimating jaguar abundance and density using capture-capture analysis. *Oryx* 38: 148–154.
- Sollman, R., M.M. Furtado, B. Gardner, H. Hofer, A.T.A. Jacamo, N.M. Trres, and L. Silveira. 2011. Improving density estimates for illusive carnivores: Accounting for sex-specific detection and movements using spatial capture-recapture models for jaguars in central Brazil. *Biological Conservation* 144: 1017–1024.
- Sollman, R., B. Gardner, and J.L. Belant. 2012. How does spatial study design influence density estimates from spatial capture-recapture models. *PLoS ONE* 7: e34575.
- Sollman, R., A. Mohammed, H. Samejima, and A. Wilting. 2013. Risky business or simple solution—Relative abundance estimates from camera trapping. *Biological Conservation* 159: 405–412.
- Stoner, K.E., K. Vulinec, J. Wright, and C.A. Peres. 2007. Hunting and plant community dynamics in tropical forest: A synthesis and future directions. *Biotropica* 39: 385–392.

- Suárez, E., M. Morales, R. Cueva, V. Utreras Bucheli, G. Zapata-Ríos, E. Toral, J. Torres, W. Prado, et al. 2009. Oil industry, wildlife meat trade and roads: Indirect effects of oil extraction activities in a protected area in north-eastern Ecuador. *Animal Conservation* 12: 364–373.
- Suarez, E., G. Zapata-Ríos, V. Utreras, and S. Strindberg. 2012. Controlling access to oil roads protects forest cover, but not wildlife communities: A case study from the rainforest of Yasuní Biosphere Reserve (Ecuador). *Animal Conservation* 12: 364–373.
- Sunarto, S., M.J. Kelly, K. Parakkasi, S. Klenzendorf, E. Septayuda, and H. Kurniawan. 2012. Tigers need cover; multi-scale occupancy study of the big cat in Sumatran forest and plantation landscapes. *PLoSOne* 7: e30859.
- Terborgh, J., and K. Feeley. 2004. Propagation of trophic cascades via multiple pathways in tropical forest. In *Trophic cascades. Predators, prey, and the changing dynamics of nature*, ed. J. Terborgh, and A. Estes, 125–140. New York: Island press.
- Tobler, M., S. Carrillo-Perceguei, R. Leite Pitman, R. Mares, and G. Powell. 2008. An evaluation of camera traps for inventorying large and medium-sized mammals terrestrial rainforest mammals. *Animal Conservation* 159: 405–412.
- Tobler, M.W., and G.V.N. Powell. 2013. Estimating jaguar densities with camera traps: Problems with current designs and recommendations for future studies. *Biological Conservation* 159: 109118.
- Tobler, M.W., A. Zúñiga Hartley, S.E. Carrillo-Perceguei, and G.V.N. Powell. 2015. Spatiotemporal hierarchical modeling of species richness and occupancy using camera trap data. *Journal of Applied Ecology* 52: 413–421.
- Venegas, C., R. Arispe, D.I. Rumiz, and K. Rivero. 2009. Censo de jaguares (*Panthera onca*) y otros mamíferos con trampas cámara en las Concesiones Forestales Angel Sandóval y San José del Bosque Seco Chiquitano. Informe Técnico WCS-FCBC-Museo NKM, Santa Cruz.
- Venegas, C., D.I. Rumiz, S. Angulo, and K. Rivero 2010. Censo de jaguares (*Panthera onca*) y otros mamíferos con trampas cámara en la propiedad Alta Vista del Bosque Seco Chiquitano. Informe Técnico WCS-FCBC-Museo NKM, Santa Cruz
- Wilkie, D., F. Rotberg, E. Shaw, and P. Auzel. 2000. Roads, development and conservation in the Congo Basin. *Conservation Biology* 14: 1614–1622.
- Wilkie, D.S., J.G. Sidle, G.C. Boundzanga, P. Auzel, and S. Blake. 2001. Defaunation, not deforestation; commercial logging and market hunting in northern Congo. In *The cutting edge: Conserving wildlife in logged tropical forests*, ed. R.A. Fimbel, A. Grajal, and J.G. Robinson, 375–399. New York: Columbia University Press.
- World Bank. 2006. Nicaragua/Honduras: Corazon Transboundary Biosphere Project. Report No. 36072-NI/HN. Global Environment Facility Coordination Team. Environment Department, World bank, Washington, D.C. Retrieved 16 August 2016, from <http://documents.worldbank.org/curated/en/289261468016794134/pdf/36072.pdf>.
- Wright, S.J. 2003. The myriad consequences of hunting for vertebrates and plants in tropical forest. *Perspectives in plant ecology, Evolution and systematics* 6: 73–96.
- Wright, S.J., M.E. Gompper, and B. De Leon. 1994. Are large predators keystone species in Neotropical forest? The evidence from Barro Colorado Island. *Oikos* 71: 279–294.
- Wright, S.J., A. Hernández, and R. Condit. 2007a. The bushmeat harvest alters seedling Banks by favoring lianas, large seeds, and seeds dispersed by bats, birds, and wind. *Biotropica* 39: 363–371.
- Wright, S.J., K.E. Stoner, N. Beckman, R.T. Corlett, R. Dirzo, H.C. Muller-Landau, G. Nuñez-Iturri, C.A. Peres, et al. 2007b. The plight of large animals in tropical forest and the consequences for plant regeneration. *Biotropica* 39: 289–291.
- Wright, S.J., H. Zeballos, I. Dominguez, M. Gallardo, M. Moreno, and R. Ibañez. 2000. Poachers alter mammal abundance, seed dispersal, and seed predation in a Neotropical forest. *Conservation Biology* 14: 227–239.
- WWF. 2014. Building the basis for biodiversity safeguards in Indonesia. WWF Fact Sheet. Retrieved 16 August 2016, from http://d2ouvy59p0dg6k.cloudfront.net/downloads/final_ip_indo_bio_safeguards_web.pdf.
- Zeller, K. 2007. Jaguars in the new millennium, data set updated: the state of the jaguar in 2006. Wildlife Conservation Society, Bronx, NY. Retrieved 16 August 2016, from http://www.catsg.org/fileadmin/filessharing/3.Conservation_Center/3.2._Status_Reports/Jaguar/Zeller_2007_Jaguars_in_the_new_Millennium_Update.pdf.

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