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Knowledge of Wildlife, Hunting, and Human-felid Interactions in Maya Forest Communities of the Northern Yucatán Peninsula, Mexico

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Abstract
Human-wildlife impacts threaten large-felid persistence in the northern Yucatán Peninsula, triggered largely by livestock depredation. We aimed to explore knowledge and attitudes about local wildlife in relation to husbandry practices, hunting habits, and human-wildlife interactions, in three Maya Forest communities. A questionnaire survey of 30 long-established smallholdings, where livelihood depended on a private fenced plot and surrounding communal forest, found wide knowledge of local wildlife, perception biases for abundances of game species, and preference for living amongst wild herbivores over carnivores. Interviewees had concerns about perceived year-on-year decreases in local wildlife, attributed to regular subsistence hunting by their communities. The few interviewees reporting large-felid attacks on their livestock subsequently altered management practices to prevent further attacks. The region suffers from a poverty trap of subsistence hunting by smallholders needing protein supplement potentially exacerbating depredation on the livestock that sustain their economies by large felids deprived of their natural prey.

Keywords Latin America · Large predators · Mammal conservation · Wildlife knowledge · Rural livelihoods · Yucatán Peninsula, Mexico

Introduction

The forests of the Mexican Yucatán Peninsula face increasingly severe fragmentation and loss from agricultural development and livestock husbandry (Ellis et al., 2017). The vertebrate fauna of remaining forest fragments are threatened by hunting for game species, which is actively and openly practiced in Maya communities throughout the peninsula. Hunting provides food for subsistence, and supplements agriculture, cattle ranching, beekeeping, gardening, fishing, and forest extraction (Barrera-Bassols & Toledo, 2005; Escamilla et al., 2000; León & Montiel, 2008; Terán & Rasmussen, 1994). Hunting uses traditional ecological knowledge, and many wild animal species have been part of the resource-complex managed by traditional Maya practices since historical times, being important elements in their 'cosmovision' of the natural world (Anderson & Medina, 2005; Barrera-Bassols & Toledo, 2005). Currently over 60 terrestrial vertebrate species are extracted for subsistence purposes in rural communities from the Yucatán Peninsula (Jorgenson, 1995; Quijano-Hernández & Calmé, 2002; Naranjo et al., 2004; Rodríguez et al., 2012; Ramírez & Santos-Fita et al., 2012).

Many of the game animals hunted by people are also vital constituents in the diets of jaguars (*Panthera onca*) and pumas (*Puma concolor*) (e.g., Foster et al., 2014; Santos-Fita et al., 2012), the apex predators of this region. These large felids play important roles in the culture and religion of many Native Latin American peoples from Mexico, Central and South America. People have expressed profound emotional bonds with jaguars since the beginning of recorded time, and they continue to be revered and respected in rural communities (Saunders, 1998, 2005). Under Mexican law, the jaguar is considered as threatened, and a top priority species for conservation. In consequence, its hunting is prohibited throughout Mexico (NOM-059-SEMARNAT-2010: CONANP, 2012; SEMARNAT, 2010). However, subsistence hunting of its non-endangered prey species is allowed

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outside protected areas, which in many cases are overexploited due to lack of resources for effective monitoring by local government (Chávez et al., 2016).

Ongoing land-use changes from forest to farming are increasing the overlap of large-felid habitat with livestock and agricultural areas. Competition for limited resources leads to multiple negative impacts on people, including livestock depredation and reduced economic welfare, and negative impacts on felids, including injury or mortality in retaliation shootings and reduced food availability (Amit & Jacobson, 2017). In particular, impacts on jaguars and pumas are aggravated by the unregulated subsistence hunting of their natural prey species, the reduction of forest cover, and the expansion of the cattle frontier (Polisar et al., 2003; Rodríguez-Soto et al., 2011). As large-felid habitats have become increasingly fragmented, these predators have become labelled as dangerous livestock killers and have been persecuted for that reason (Polisar et al., 2003; Weber & Rabinowitz, 1996). The physical impact of jaguar and puma predation on livestock economy is regularly exaggerated, however. Felid predation is usually minor compared to losses caused by theft or sickness (Rosas-Rosas et al., 2008). Nonetheless, veterinary care expenses when domestic animals are injured by an attack are a cause of intolerance towards felids, and a small-scale farmer may not be able to sustain the loss of a cow worth in the order of US$1400 (estimated for southern Mexico: Amit et al., 2013; SNIIM, 2018). Lethal control is thus a dominant component of human-felid impacts. It often occurs illegally in retaliation for a livestock predation event (Creel & Rotella, 2010), when ranchers feel that government restrictions on lethal control impose an intolerable burden on their enterprises (Naughton-Treves et al., 2003). Retaliatory control can achieve high kill rates, resulting in heavy impacts on carnivore populations (Jedrzejewski et al., 2017). If effective conservation measures are not put into place in the next few decades, jaguars and pumas will face a high risk of extinction in the Yucatán Peninsula and, consequently, across the Maya region (Ceballos et al., 2002; Zarco-González et al., 2018).

Many livestock losses are preventable in principle, such as those caused by disease, flooding and theft, and depredation by sick or injured felids. Such losses often result from poor husbandry management practices involving domestic animals being left unattended or allowed to roam freely in forest habitats (Weber & Rabinowitz, 1996). The need for better livestock management illustrates why effective biodiversity management needs a social-ecological perspective. We still lack a comprehensive understanding of the motivations and capabilities of the people living in the rural farming communities, which dictate livestock management practices and retaliatory killings.

Only one study to date has assessed human-felid impacts in rural communities from the Northern Yucatán Peninsula (Hernández, 2009). It precedes more recent data on frequency of reports of large felid depredation events, which have recognized their effects as one of the main threats to large felid conservation (Reyna-Sáenz et al., 2019). The now 13-year old survey by Hernández (2009) found that one third of interviewees reported attacks by large felids and coyotes in a period of 5 years, and perceived large carnivore predation as the main cause of loss.

Local communities and ejidos (i.e., aggregations of land parcels entrusted by the Mexican government to rural communities for tenure as farmland) in the Yucatán Peninsula of Mexico have access to the Livestock Insurance Fund, developed by the Secretariat of Agriculture and Rural Development (SAGARPA) and managed by the National Confederation of Livestock Organizations (CNOG, 2016). This is the only program established by the government aimed at tackling human-wildlife impacts of large felids to livestock farmers. The fund has been available to farmers since 2009, to cover losses of livestock to all medium-sized or larger predators. It can thus function as a form of adaptation. In the Yucatán Peninsula, Mexican NGO Pronatura acts as a facilitator for some communities to access this program (Pronatura, 2017).

On the other hand, the government of Mexico currently has no scheme aimed at mitigating human-wildlife impacts with preventative measures. General mitigation actions have been suggested, including confinement of livestock, construction or improvement of livestock enclosures and improvement of management practices (Reyna-Sáenz et al., 2019). However, effective mitigation requires a detailed assessment of the impact factors at each location, to inform a situation-specific management strategy (Amit et al., 2013; Inskip & Zimmermann, 2009; van Eeden et al., 2017). Such assessments are currently lacking for the Yucatán Peninsula.

Here we aim to address the gap in our understanding of factors impacting human-wildlife interactions for rural communities of the northern Yucatán Peninsula. We used a questionnaire survey firstly to assess knowledge and attitudes about jaguars and pumas and their prey, and secondly to obtain information on local livestock management, hunting and wild meat consumption habits, and human-predator interactions. The purpose of this descriptive survey was to better understand perceptions by rural communities about nature's contributions to their food security, both in benefits from game meat and in threats from crop losses to herbivores and livestock depredation by predators. Through the communication of outcomes from this study to researchers and NGOs working on sustainable rural biodiversity from Maya communities in Yucatán forests, we are taking steps towards giving a voice to the people most reliant on rural biodiversity, and hearing their needs for sustainable wellbeing.

Methods

Focal Populations

We sampled three small communities (Supplementary Information 3: Fig. S1) adjacent (ca. 2–5 km) to the privately-managed tropical forest of El Zapotal Conservation Area (Pronatura, 2015), and contiguous with the wider forest block of Yum Balam, sustaining populations of both jaguars and pumas at densities of 2–3 adults per 100 km^2 (Piña-Covarrubias, 2019).

We interviewed residents from the rural Maya communities of Nuevo Tesoco (180 inhabitants), Santa María (420) and San Pedro Bacab (200). They belong to Tizimín municipality (ca. 73,100 inhabitants) in Yucatán, which holds the largest number of cattle in the Yucatán Peninsula (Hernández et al., 2004). The nearest centers of economic development for the municipality of Tizimín are the cities of Cancún and Mérida, at distances of 90 and 170 km respectively. Amongst the inhabitants of Tizimín, 43% have only primary-school education (INEGI, 2010). The Human Development Index (HDI) of 0.651 in the municipality of Tizimín falls well below the average of 0.739 for the State of Yucatán (OIDH, 2014; PNUD, 2015). By comparison, the Mexican national HDI is 0.774, and the HDIs for USA and Canada exceed 0.9 (UNDP, 2018).

Sampling Design

We organized the questionnaire survey in collaboration with local NGO Pronatura as a way to raise trust in the interviewer, and thus to facilitate participation in our study, which included sensitive questions. Local communities in the area can be wary of academic researchers, but they have a positive relationship with Pronatura, which facilitates their access to government funds. Pronatura identified a key recruiter living in each community, who was tasked with identifying potential smallholdings in their community.

Suitable smallholders had lived in the community for at least 10 years, with livelihoods that depended on the forest. The head of each smallholding identified one adult ($\geq$ 18 yrs.) from their family with availability for interview. These individuals were approached during weekday working hours (Mondays to Fridays 8:00 am – 6:00 pm), in their workplaces or home. The approach was always made in the presence of personnel from Pronatura, who acted as gatekeepers, facilitating access and trust in the process (Singh & Wassenaar, 2016).

After completing the questionnaire, the interviewer used a 'snowball' technique to identify further interviewees, in order to amplify the study sample (Biernacki & Waldorf, 1981). The final sample of 23 men and 7 women interviewees achieved through this process was constrained in size by logistics of transport for interviewers and gatekeepers to these remote communities, and by seasonal migrations of male householders to urban centers in search of work. It was constrained in sex ratio by a limited freedom for women from childcare and household duties. Interviews were conducted in Spanish, the first or second language after Maya of most people in these communities.

Questionnaire Design

The structured questionnaire (Supplementary Information 1) was designed as a face-to-face interview lasting no more than 50 min. The questionnaire contained 37 questions partitioned into five sections. The sections covered the interviewee's (1) livestock management practice, (2) knowledge and perceptions of wildlife, (3) hunting habits and wild meat consumption, (4) experience of human-carnivore impacts, and (5) socio-demographic characteristics. The order of questions was determined by recommendations in Fink (2009) and Bryman (2012) on design and organization of surveys. The purpose of the questionnaire was to find out what rural smallholders know, including their knowledge of changes in animal abundances, for which we currently have no other sources of information, and to seek their perceptions of human-wildlife interactions, particularly relating to large-felid conservation policies.

A pilot test of a first version of the questionnaire survey was run on two local villagers from the same communities, to identify issues in the questionnaire design, such as the relevance and clarity of one or a set of questions and the real duration of the questionnaire (Fink, 2009). Test interviewees were local ecotourism guides who worked with us in a camera-trap study of jaguar and puma ecology in El Zapotal Conservation Area, and had previous experience of subsistence hunting of local wildlife. The pilot run led to clarifications of several questions, and removal of some questions on livestock management that proved unsuitable or not applicable to this area (e.g., occupation of interviewee, which might compromise anonymity, and livestock sales to national or international markets, which does not happen here).

Ethics Approval and Interview Technique

Ethics approval was obtained from the University of Southampton Ethics and Research Governance Committee (Online ID number: 13836). Before starting the questionnaire, the interviewer read a Participant Information sheet (Supplementary Information 2) to the potential interviewee, containing an assurance of anonymity, and requested agreement to participate in the study. Informed consent to participate was obtained from all

interviewees. This stage was conducted verbally, because most interviewees lacked basic reading and writing skills.

Analysis of Questionnaires

A content analysis of the questionnaire survey was performed on responses to open-ended questions, to identify and classify frequently repeated value judgements (Bryman, 2012; Fink, 2009). A code book was then constructed to codify and manage the classified categories, and the responses to all other questions.

Descriptive statistics were used to illustrate proportions and overall patterns in the codified responses. Univariate analyses described frequency distributions of individual questions. We tested for frequency dependence between categories in five question pairs: (a) livestock losses to large felids vs belief that large felids would attack humans unprovoked; (b) livestock losses by large felids vs community (Nuevo Tesoco, Santa Maria, San Pedro Bacab); (c) belief that large felids would attack humans unprovoked vs community; (d) perceptions of local abundance of carnivores vs herbivores; (e) perceptions of local abundance of game vs non-game species. Tests involving low frequencies for (a)-(c) used the Fisher exact test for 2×2 contingency tables and an equivalent test for 2×3 tables also based on the hypergeometric distribution (Sokal & Rohlf, 1995). Tests for (d)-(e) used chi-square.

Results

A total of 30 smallholders were interviewed from the communities of Nuevo Tesoco (8 men, 2 women), Santa María (8 men, 2 women) and San Pedro Bacab (7 men, 3 women) during 2015 and 2016. Most interviewees were middle-aged with low-level education (Supplementary Information 3: Fig. S2).

Knowledge, Attitudes, and Perceptions of Wildlife

The questionnaire included 37 wildlife species that occur in the northern Yucatán Peninsula (32 mammals, 3 birds, 2 reptiles), of which 36 were recognized as present by at least two interviewees ($\bar{x} = 24 \pm 9$ [s.d.] recognitions per species, $\bar{x} = 28 \pm 4$ [s.d.] species per interviewee; Table 1). Baird's tapir was the only species not recognized as occurring in the area; however, two interviewees recognized its name or image, and said that it had been present in the past. Large felids were considered game species even though hunting of jaguars in Mexico is against the law, and hunting of pumas is regulated (NOM-059-SEMARNAT-2010; SEMARNAT, 2010; Ley General de Vida Silvestre; SEMARNAT, 2018a; Ley General de Equilibrio Ecológico y Protección al Ambiente; SEMARNAT, 2018b).

We pooled wildlife species into groups of herbivores and carnivores to test for differences in their perceived abundances, finding no difference between pooled carnivores and pooled herbivores in allocations by interviewees to high, medium, and low abundances ($\chi^2_2 = 0.15$; $p = 0.93$). Individual species belonging to either group were nevertheless perceived as having high, medium, or low abundance (Table 1), with game species considered to have higher abundances than non-game species ($\chi^2_2 = 28.72$; $p < 0.001$).

Interviewees' opinions on the presence of wild animals were largely positive towards herbivores, and more frequently negative towards carnivores ($\chi^2_2 = 97.4$; $p < 0.001$; Table 1). These preferences did not depend on their perceptions about local abundances (high, medium, or low; $\chi^2_4 = 0.27$; $p = 0.99$, pooling across species for response frequencies in the three presence, and three opinion categories).

The content analysis identified 96 different value judgements of wildlife species, classified into nine different value types: 'Beautiful (positive aesthetic)', 'Beneficial / not harmful', 'Conservation / ecological value', 'Large-felid prey', 'Not useful / has no value', 'Consumer of domestic or other animals / crops)', 'Predator of people', 'Source of food for people', 'Unpleasant / harmful'. The most frequent value was 'positive aesthetic', followed by 'source of food to people', and 'predator of animals / crops' (Supplementary Information 3: Table S1, Fig. S3). Interviewees perceived that both herbivores and carnivores could damage domestic animals (3 and 12, respectively), crops (10 and 6), or both (1 and 2). Interviewees generally had a positive attitude ('I like it'; Table 1) towards jaguars (70% of interviewees) and pumas (76%), which they most commonly associated with a positive aesthetic ('Beautiful'; 40% for jaguars and 37% for pumas; Supplementary Information 3: Fig. S3).

Interviewees had mixed beliefs on changes in abundances of local populations of wildlife species. Of 345 interviewee × species combinations, 72% ($n = 247$) believed populations were declining, and 28% ($n = 98$) believed populations were increasing. Perceptions of changes in abundance differed between herbivore and carnivore categories, with herbivores declining more than carnivores ($\chi^2_2 = 11.19$; $p < 0.004$), and between game and non-game categories, with game declining more ($\chi^2_2 = 8.74$; $p < 0.013$). Interviewees believed that the main cause of local increases in wildlife populations was the benefits that wildlife derived from taking domestic animals and raiding crops (Table 2). They considered that the main cause of local population declines was human hunting. The third main cause of wildlife declines, after hunting and natural disaster, was thought to be large felid predation, suggesting a perception of shared culpability between human and animal hunters for wildlife declines.

Table 1 Estimation by interviewees of the local abundance of wildlife species, and opinion about their presence in three Maya communities of Northern Yucatán. Each colored bar illustrates the given frequency of response as a proportion of all 30 interviewees. Answers with 'Does not know'/'Did not answer' were not included. Species are classified by type: herbivore and carnivore, and ordered by frequency of answers giving high abundance. Game species are indicated with a star (*). See Supplementary Information 3: Table S1 for scientific names of species

	Common name	Estimation of abundance			Opinion on presence		
		High	Medium	Low	Positive	Negative	Neutral
HERBIVORE	*Plain chachalaca	28	0	1	26	3	1
	*Hispid pocket gopher	26	1	3	24	4	2
	*Collared peccary	26	3	1	30	0	0
	*Ocellated turkey	25	1	3	29	0	0
	Common opossum	20	4	6	6	19	5
	*Eastern cottontail	16	2	12	30	0	0
	*Central American red brocket deer	14	3	10	28	0	0
	*Central American agouti	13	3	13	29	1	0
	*White-tailed deer	11	3	12	26	0	0
	*Yucatan brown brocket deer	10	5	10	26	0	0
	*Geoffroy's spider monkey	9	2	10	18	1	2
	*Creaser's mud turtle	9	3	10	21	0	2
	*Nine-banded armadillo	5	2	21	23	1	6
	*Mexican porcupine	3	2	14	12	7	1
	*Spotted paca	3	1	25	27	0	1
	*Great curassow	2	3	21	25	0	1
	Northern tamandua	2	2	24	18	3	7
	Black howler monkey	0	0	14	11	3	2
	Baird's tapir	0	0	0	0	0	0
CARNIVORE	*White-nosed coati	27	1	1	13	16	1
	*Northern raccoon	21	1	6	13	15	1
	Grey fox	20	2	8	19	9	2
	*Puma	17	4	7	21	6	3
	*Jaguar	15	4	9	23	5	2
	Tayra	14	2	10	8	15	5
	Striped hog-nosed skunk	10	2	16	6	20	1
	Long-tailed weasel	9	1	18	15	8	6
	*Ocelot	8	5	10	20	5	2
	Margay	6	3	15	21	0	6
	Cacomistle	4	0	6	8	2	1
	Kinkajou	4	0	10	8	3	4
	Morelet's crocodile	3	0	10	6	4	2
	Spotted skunk	3	1	5	2	7	0
	Coyote	2	0	10	8	3	1
	Greater grison	1	0	4	2	1	2
	*Jaguarundi	1	1	10	10	2	3
	Neotropical river otter	0	0	2	0	1	1

Livestock Management

Properties owned by interviewees were small (< 100 ha), and mostly no larger than 0.2 ha ($n = 9$ of 12 properties). Householders kept chickens, domestic pigs, goats, sheep, and cattle, mostly for home consumption of meat, eggs, and milk, and in lower proportion to sell within their communities. Cows, sheep, pigs and goats also functioned as insurance against financial or food hardship (Table 3). Animals were kept in backyards or inside fenced cowsheds/chicken coops, which were surrounded by wooden ($n = 6$), barbwire ($n = 3$), chicken wire and concrete fences ($n = 1$). Only one interviewee reported keeping animals in an open pasture. Interviewees not owning plots of land also had no animals.

Hunting Practices

Of the 26 interviewees (87%) reporting knowledge of hunting by people in their community, a large proportion estimated that less than 10% of adult males hunt (69%, $n = 18$); a minor proportion estimated that more than 10% of adult males hunt (16%, $n = 4$), with the rest declaring no knowledge. Of those reporting hunting, 92% ($n = 24$) said that it occurs mainly on people's own plots of private land, and the remaining 8% ($n = 2$) said that it takes place everywhere in the forest. More than half of these interviewees reported decreases over the last 10 years in hunting events (58%, $n = 15$) and in participants (69%, $n = 18$), whereas a minor proportion declared no changes (hunting events 35%, $n = 9$,

Table 2 Reasons for local decrease or increase of all wildlife species included in our survey in three Maya communities of Northern Yucatán. Each colored bar illustrates the given frequency of response as proportion of all 345 interviewee × species combinations

	Reason for change	n
DECREASE	People kill/eat it	78
	Natural disaster	67
	Large cats kill/eat it	43
	Lack of habitat	29
	Lack of natural prey/food	11
	Natural decrease	11
	Predators kill/eat it	8
INCREASE	Eats crops/livestock/domestic animals	30
	Natural increase	22
	Enough natural prey/food	15
	People don't kill/eat it	14
	Enough/suitable habitat	13
	Lack of predators	3
	Introduced by humans	1

and participants 27%, $n=7$), or increases (hunting events 8%, $n=2$, and participants 4%, $n=1$). There was consensus on the disbursement of the wild meat. For hunting events involving many people, the meat had to be distributed amongst participants (62%; $n=16$); when hunting alone, distribution became a family decision (38%, $n=10$).

The main purpose of hunting in these communities was to supplement dietary protein, and to a lesser extent to sell the wild meat, or to protect crops from predators (Table 4). The species most frequently reported as hunted were deer, collared peccary, medium-sized carnivores (white-nosed coati and Northern raccoon), large birds (ocellated turkey, greater curassow and plain chachalaca), nine-banded armadillo and Central American agouti. The species most favored for consumption were Yucatán brown brocket deer, collared peccary, Central American red brocket deer and white-tailed deer. White-nosed coati was the single most hunted species for crop protection (Table 4).

Table 3 Livestock owned by local ranchers and purpose of ownership in three Maya communities of Northern Yucatán. Each colored bar illustrates the given frequency of response as a proportion of all 30 interviewees.

Livestock	For eating	For sale	As insurance
Chicken	16	1	0
Sheep	4	3	1
Pigs	4	2	1
Cows	3	3	0
Goats	2	1	0
Turkeys	1	0	0

Human-large Felid Impacts

A small proportion of all interviewees reported previous killing of a jaguar on their property (10%, $n=3$, ca. 20–30 years ago), and none of a puma. More than half of all 30 interviewees believed that jaguars and pumas do not attack humans unless provoked (59%, $n=17$ of 29 answers); a lesser proportion feared unprovoked attack (38%, $n=11$), with only one reporting no knowledge. This perception depended neither on livestock ownership ($\chi^2_1 = 0.006$; $p=0.94$) nor on experience of livestock losses to large felids ($\chi^2_1 = 0.65$; $p=0.42$). We found detectable differences between the three communities in whether they thought that large felids would attack humans without provocation (hypergeometric exact 2-tailed $p=0.022$, $n=28$), matching their differences in whether or not they had experienced livestock losses to large felids (hypergeometric exact 2-tailed $p=0.001$, $n=30$).

Eight interviewees reported having experienced livestock predation by large felids, including nine attacks by jaguars and three by pumas. Evidence used to identify predator species included tooth marks on the killed animal, predator footprints, camera-trap photographs, or witnessing the event. Three interviewees reported more than one attack, with gaps of 5 and 8 years between predation events. The domestic species most frequently taken by large felids was sheep ($n=64$ individuals taken); only one incident involved cattle, with the loss of three calves. Amongst the 8 interviewees who reported livestock predation incidents by large felids, 4 believed attacks have increased in the past 10 years, whereas two believed they have declined, and one believed attacks have remained the same.

In response to livestock attacks, four interviewees declared that they had moved their livestock to a safer site. One had sought direct assistance from local NGO Pronatura. The NGO provided aid by setting up camera-traps and noise deterrents for large felids, as well as indirect aid to the community at large by facilitating access to information about the Livestock Insurance Fund. One interviewee who had yet to modify their husbandry practice following an attack, declared willingness to make adjustments by building paddocks. The two interviewees who had modified their husbandry practices following an attack, by keeping animals inside chicken coops and fenced pastures, declared willingness to make further adjustments, likewise by building paddocks.

The 30 interviewees ($n=35$ answers) believed that their best options for reducing large-felid impacts on their economies were: (1) to seek livestock payments from the Livestock Insurance Fund (37%, $n=13$); (2) for government to provide subsidies for paddock fencing and payments for protection against jaguars on their properties (31%, $n=11$); (3) to obtain advice on available practices to mitigate livestock losses to large felids (14%, $n=5$); (4) better fulfilment of

Table 4 Purpose of hunting wildlife species in three Maya communities of Northern Yucatán. Each colored bar illustrates the given frequency of response as a proportion of all 30 interviewees. See Supplementary Information 3: Table S1 for scientific names of species

Wildlife species	For eating	For sale	To protect crops
Yucatan brown brocket deer	20	3	1
Collared peccary	20	2	1
Central American red brocket deer	17	3	1
White-tailed deer	16	2	1
Ocellated turkey	7	1	1
White-nosed coati	3	0	4
Northern raccoon	0	0	2
Plain chachalaca	0	0	2
Great curassow	1	0	1
Nine-banded armadillo	1	0	0
Central American agouti	1	0	0

the law by the authorities (6%, $n=2$); and (5) game gardening ('breed natural prey or livestock and give them to the jaguars'; 3%, $n=1$). Most interviewees believed current law helped to reduce large-felid impacts (70%, $n=21$ interviewees), whereas smaller proportions believed it did not help (14%, $n=4$) or did not know/did not answer (16%, $n=5$). Nine out of 30 interviewees indicated they supported lethal control on large felids in response to livestock predation, ten people opposed it, nine had mixed opinions, and two people did not know/preferred not to say. After the formal interview, one interviewee mentioned they believed it was their right to eliminate the predator when they needed to protect themselves from depredation on their animals. They were aware that this is against the law (NOM-059-SEMARNAT-2010; SEMARNAT, 2010; Ley General de Vida Silvestre; SEMARNAT, 2018a; Ley General de Equilibrio Ecológico y Protección al Ambiente; SEMARNAT, 2018b). Also, two interviewees complained that the Livestock Insurance Fund was slow to make payments or withheld payments, and one reported that government officials were untruthful about the conditions for obtaining payments. Two interviewees reported that attacks on livestock by large felids made them feel afraid or angry.

Discussion

Our case study of rural communities of the northern Yucatán Peninsula aimed to contribute to understanding of what people living in isolated forest communities know and feel about their wildlife, their livestock management practices, how they practice hunting, and their experiences of human-wildlife impacts. Our work was motivated by a recognition that biodiversity in the region has been studied largely from western hypothesis-testing perspectives, which can handicap conservation actions when it fails to consider the complexities of indigenous knowledge and resource use (Díaz et al., 2018; Etkin, 2002). A principal measure of success in mitigating negative human-wildlife impacts is attitude change (Hodgson et al., 2020). A full understanding of the context-specific and often idiosyncratic nature of attitudes, however, will require synthesis across numerous case studies.

Traditional ecological knowledge held by indigenous communities has the potential to complement scientific knowledge, and can assist the conservation of biodiversity, especially outside protected areas (Zhang et al., 2020). Our questionnaire survey revealed a wide knowledge of local wildlife species amongst people involved in subsistence hunting. Of all 37 species included in our list that could potentially be distributed in this area, only Baird's tapir was considered absent by all interviewees, and it may in fact have been extirpated from the wider region including this area of Tizimín (which in Maya means 'tapir'; IUCN SSC Tapir Specialist Group, 2016). Interviewees enjoyed living with their wildlife species, including large felids, even though they had a generally more negative perception of carnivores than herbivores. This appreciation of nature's contributions was evidenced by their generally positive attitudes and appreciation of aesthetics in relation to wildlife.

Subsistence hunting has been practiced throughout the Yucatán Peninsula since pre-Hispanic times (Montiel et al., 2000). Besides providing low-income households with substantial animal protein, hunting is a cultural activity, present in myths and religious ceremonies. The beliefs and knowledge of rural communities have shaped the ways they perceive nature, influencing how they use and manage their natural resources (Barrera-Bassols & Toledo, 2005). Rural communities in the southern Yucatán Peninsula and Southern Mexico are knowledgeable about biological and behavioral aspects of their local wildlife species, especially mammals and birds linked to agricultural practices, gardening and hunting, which informs the objectives, strategies and techniques of their hunting trips (Aguilera, 1985; Santos-Fita et al., 2012).

In the communities we studied, subsistence hunting was practiced mainly to eat wild meat, and in minor proportion to control pests of crops. Our results also found a cultural aspect to local hunting, evidenced in group hunts when hunters decided how to disburse the wild meat. These communities used a broad number of wildlife species as game, but relied on a relatively small set of medium and large-sized species as their main source of protein. Our results were similar to previous findings in other rural communities from the Central and Southern Yucatán Peninsula (Santos-Fita et al., 2012). The principal game species in the communities studied were ungulates: red and brown brocket deer, white-tailed deer, and collared peccary. Our observations also follow a regional pattern, with similar hunting preferences found in other Maya communities throughout the Yucatán Peninsula (Hernández, 2009; Montiel et al., 2000; Oliva et al., 2014; Quijano-Hernández & Calmé, 2002; Ramírez & Naranjo, 2005; Rodríguez et al., 2012). These hunting preferences impose a heavy mortality on a small number of prey species, which have additionally been found to constitute the preferred prey of large felids in nearby private reserves of El Edén Ecological Reserve and El Zapotal Conservation Area (Piña-Covarrubias, 2019). Since these species remain an important source of animal protein for Maya communities, their conservation is of particular social-ecological concern (Mandujano & Rico-Gray, 1991; Naranjo et al., 2004).

If large felids compete with humans for a limiting supply of wild ungulates, a reduced prey base for these top predators caused by human hunting may trigger livestock predation by the felids, and aggravate human-wildlife impacts in the area (Escamilla et al., 2000). In the Belizean Yucatán Peninsula, Foster et al. (2014) estimated a national annual harvest by hunters of 4 kilotons of the six wild mammal species that predominate in large-felid diet. This offtake was considered likely to be unsustainable for the felids. Mitigation of negative impacts on people from livestock depredation must address the issue of forest conversion to agriculture, which exacerbates hunting pressure by people and predators (Foster et al., 2014). Our results point to an ongoing need for demographic studies to determine the viability of prey populations that are targeted both by people and carnivores in the region, and robust estimates of productivity of wild-meat species and the carnivores that hunt them, to inform assessments of sustainability and hunting legislation. Interviewees reported local declines in ungulate prey, as previously found in other communities in the Yucatán Peninsula (Oliva et al., 2014). They believed that hunting by humans and by large felids are amongst the main reasons for declines, which suggests a perception of competition with jaguars and pumas for the same prey. This perceived belief in competition is further evidence of the depth of understanding these people have of their local wildlife, despite lacking the technology to monitor it systematically.

Even though one third of the interviewees believed large felids could attack humans without being provoked (e.g., hunting for food), none recounted any actual attack. To our knowledge, there are no records of deaths to humans by large felids in Mexico, in contrast to the widely reported attacks by cougars in the USA (Mattson et al., 2011). Communities may use lethal control against large felids in response to perceptions of threat as well as the threat itself (Marchini & Macdonald, 2012). Thus, we see a need for further assessment of risk perception, and its underlying causes (e.g., fear, motivations, internal/external barriers: Ajzen, 1985; Marchini & Macdonald, 2012), before promoting strategies of tolerance to wild predators (Naughton-Treves et al., 2003; van Eeden et al., 2017).

The implementation within the last 10 years of the Mexican government's Livestock Insurance Fund has not had a measurable impact on mitigating livestock depredation by large felids. This is not surprising, since it only pays the value of lost livestock, and does not fund mitigation to prevent future losses. Most interviewees nevertheless believed it to be the best option for minimizing human-felid impacts in their communities. Compensation schemes by themselves have previously not sufficed to improve tolerance toward predators amongst local livestock owners (Marino et al., 2016). They are considered more likely to succeed when tied to community participation and good livestock husbandry practices (Can et al., 2014; Madden, 2004). Our surveyed communities were applying a mixture of strategies to facilitate reduction of human-wildlife impacts, with assistance from local NGO Pronatura. Several interviewees had made, or showed willingness to make, changes to their husbandry practices, by keeping their animals inside fenced paddocks, relocating them to areas closer to the community, or by using noise deterrents for predators. These types of mitigation were self-funded, and assisted by Pronatura with provision of noise deterrents and camera-traps.

Local NGOs such as Pronatura play a valuable part in adaptation to large-felid impacts in rural communities by providing technical assistance for improving access to compensation schemes. However, it remains uncertain whether current government subsidies and NGO assistance aimed at improving the resilience of ranchers to wildlife impacts can also suffice to incentivize self-regulation of game hunting. A shift towards sustainable subsistence hunting will require nudging rural communities towards altering their hunting practices within the context of their motivations for hunting, and supported by effective regulation of offtake for the mutual benefit of prey populations and their users (Santos-Fita, et al., 2012). Government incentives should be established to encourage wildlife users to design, implement and enforce their own hunting rules. Stakeholders might expect external governance of their wildlife use (as happens in other nearby Maya

communities: Oliva et al., 2014). The current law should clarify what subsistence hunters can and cannot do (e.g., Ley General de Vida Silvestre; SEMARNAT, 2018a), and how they can influence the conservation of their local wildlife (Santos-Fita et al., 2012).

This study faced many constraints, which restrict its scope of inference to a case study of the northern Yucatán Peninsula. Firstly, limited access to communities and their inhabitants resulted in a small sample size of interviewees. In the communities where we worked, it was common for many people to share the same household, reducing the pool of independent interviewees. Additionally, local men migrate temporarily to seek jobs in nearby cities (Mérida and Cancún), which further constrained sample size. Secondly, our limited access to the women of a household, who were often occupied by childcare or housework, resulted in a male bias in our survey with potential to bias responses. In a study in the Bolivian Amazon, Knox et al. (2019) found that women had more negative attitudes toward jaguars than men. Thirdly, we could only work with communities where local NGO Pronatura had already established a link. Although the role of Pronatura as a 'gatekeeper' in selecting informants could have biased our hoice of interviewees (Singh & Wassenar, 2016), their presence enabled us to access recruiters and interviewees, and ensure the safety of the interviewers. We recommend further surveys, where safety and access allows, comparing the communities we studied with nearby communities that have not yet received any technical assistance from NGOs (e.g., San Angel, Solferino or Chiquilá).

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Authors' Contributions Evelyn Piña-Covarrubias and Cuauhtémoc Chávez initiated the idea for the study. Evelyn Piña-Covarrubias and C Patrick Doncaster developed the aims, objectives, and methods. Evelyn Piña-Covarrubias designed the questionnaire, managed the evaluation of ethics in accordance with the University of Southampton policy, performed the surveys, analyzed the results, and led the writing of the manuscript. All authors contributed to writing the paper, and gave final approval for publication.

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Data Availability The datasets that support the findings of this study are not openly available to protect the confidentiality and personal information of respondents.

Declarations

Ethical Approval and Consent to Participate Data collection in this study followed the ethical guidelines required for conducting research at the University of Southampton Ethics and Research Governance Committee (Online ID number: 13836). Before starting the questionnaire, the interviewer read a Participant Information sheet (Supplementary Information 2) to the potential interviewee, containing an assurance of anonymity, and requested agreement to participate in the study. Informed consent to participate was obtained from all interviewees. This stage was conducted verbally because most interviewees lacked basic reading and writing skills.

Human and Animal Ethics Not applicable.

Consent for Publication The results obtained are published with the consent of the participating communities.

Competing Interests The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

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