Complex interactions between commercial and noncommercial drivers of illegal trade for a threatened felid

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Abstract

Illegal trade and human-wildlife conflict are two key drivers of biodiversity loss and are recognized as leading threats to large carnivores. Although human-wildlife conflict involving jaguars (*Panthera onca*) has received significant attention in the past, less is known about traditional use or commercial trade in jaguar body parts, including their potential links with retaliatory killing. Understanding the drivers of jaguar killing, trade and consumption is necessary to develop appropriate jaguar conservation strategies, particularly as demand for jaguar products appears to be rising due to Chinese demand. We interviewed 1107 rural households in north-western Bolivia, an area with an active history of human–jaguar conflict, which has also been at the epicentre of recent jaguar trade cases. We collected information on participants' experiences with jaguars, their jaguar killing, trading and consuming behaviours and potential drivers of these behaviours. We found that the relationships between local people and jaguars are complex and are driven largely by traditional practices, opportunism, human–jaguar conflict and market incentives from foreign and domestic demand, in the absence of law awareness and enforcement. Addressing jaguar trade and building human–jaguar coexistence will require a multifaceted approach that considers the multiple drivers of jaguar killing, trade and consumption, from foreign and local demand to human–jaguar conflict.

Introduction

The relationship between humans and wildlife is complex, varying across locations, cultures and taxa, and evolving along with societies' changing values towards nature (Frank and Glikman, 2019). The study of these relationships has been dominated by an anthropocentric focus, which separates humans from the natural world and defines their interactions with wildlife as 'human-wildlife conflict' (HWC), or the 'struggles that emerge when the presence or behaviour of wildlife poses actual or perceived, direct and recurring threat to human interests or needs' (IUCN, 2020). Although the expanding scholarship on human-wildlife interactions continues to emphasize HWC, its definition has evolved over time, acknowledging that many instances of HWC are in fact disagreements between groups of people over wildlife (Peterson

et al., 2010; Redpath et al., 2013; IUCN, 2020). There is also a greater recognition of the various benefits that emerge from the presence of, and interactions with, wildlife, and of the importance of participatory stakeholder involvement for harnessing those benefits, increasing tolerance, and achieving sustainable coexistence with wildlife (Frank and Glikman, 2019; König et al., 2020; Morzillo, de Beurs, and Martin-Mikle, 2014).

Large carnivores are prominent in the study of human-wildlife interactions, particularly in those focussed on conflict. Although many large carnivores have symbolic meanings and practical values for human societies around the world (Alves et al., 2013), their negative impacts on human interests and needs have led to widespread persecution, turning human-wildlife conflict into a leading cause of large carnivore decline (Inskip and Zimmermann, 2009; Ripple et al.,

2014). These negative interactions are accentuated by a wide range of cooccurring, multiscale environmental and social factors (Carter et al., 2017; Lischka et al., 2018; Morzillo, de Beurs, and Martin-Mikle, 2014). Landscape-level habitat degradation can affect wildlife community assemblages and prey availability, which can in turn influence individual large carnivore distribution, behaviour and propensity towards conflict (e.g., Carter et al. 2017; Miller 2015). Societal values towards nature and cultural beliefs can also influence people's tolerance or intolerance of carnivores (e.g., Dickman and Hazzah, 2016), as do carnivore management policies (Linnell and Alleau, 2015; Peterson et al., 2010). Moreover, individual hunters respond to social norms (e.g., Marchini and Macdonald, 2012) and to range of socio-psychological motivators of attitudes and behaviours towards carnivores (e.g., Kansky et al., 2014).

As with other large carnivores, lethal responses to human–jaguar conflict are one of the main threats to jaguars (*Panthera onca*) and have been the subject of considerable research attention (Castaño-Uribe et al., 2016). Experiences of livestock depredation, together with fear of attacks on humans, have led to negative attitudes towards jaguars throughout their range (e.g., Knox et al., 2019; Marchini and Macdonald, 2012). These perceptions are intensified by a lack of knowledge about jaguars (e.g., Engel et al., 2017), inadequate responses by authorities (Conforti and De Azevedo, 2003), group identities and traditions (Harvey, Briggs-Gonzalez, and Mazzotti, 2017), perceived behavioural control (e.g., an actor's perceived ability to conduct a behaviour and the extent to which doing the behaviour is the actor's choice—Ajzen, 2002; Marchini and Macdonald, 2012), and socio-economic characteristics (e.g., Amit and Jacobson, 2017; Carvalho, 2019). Broader economic and landscape factors also influence the likelihood of jaguar depredation on domestic animals and of retaliatory responses (e.g., Cavalcanti et al., 2010).

Less is known about the drivers of nonretaliatory human–jaguar interactions, including jaguar killing for traditional or commercial purposes, even though these have also shaped the relationship between humans and jaguars. Jaguars have played a longstanding role in the cultural life of numerous indigenous societies in Latin America (e.g., Gómez and Payán, 2017) and became an important economic resource for rural communities involved in the supply of the spotted-cat fashion industry throughout the 20th century (Antunes et al., 2016). Although large-scale commercial jaguar trade stopped following their listing on CITES Appendix I, killing and trading continued, with traditional and commercial motivations sometimes outweighing retaliatory ones (Garcia-Alaniz et al., 2010; Jędrzejewski et al., 2017). The past decade has seen an increase in the evidence of jaguar trade, with seizures occurring throughout their range, some of which have been associated with a new demand from people of Asian descent (Morcatty et al., 2020; Verheij, 2019).

Although conflict, domestic use and trade (domestic or foreign) are all important threats to jaguar populations, the relationship between these threats is not well understood. As the evidence of jaguar trade increases, potential links between trade, retaliatory killing and domestic use have been suggested (Reuter et al., 2018) but have so far been overshadowed by a growing concern about the role of foreign markets driving the demand for jaguar products (Lemieux and Bruschi, 2019; Morcatty et al., 2020), a narrative that has caught the attention of the media and which has guided recent jaguar conservation actions. Here, we use the example of human–jaguar interactions in north-western Bolivia, a region with an active history of interactions between humans and jaguars, which has also been at the epicentre of recent jaguar trade cases involving foreign demand (Knox et al., 2019; Nunez and Aliaga-Rossel, 2017), to answer the following question: how do foreign and domestic markets for jaguar products interact to drive jaguar killing, trade and consumption, in the context of complex social, cultural and economic relationships between humans and jaguars?

North-western Bolivia is an ideal location to test the hypothesis that, even in areas where foreign demand and strong market incentives may motivate engagement in jaguar trade, the relationships between local people and jaguars, particularly involving human–jaguar conflict and cultural practices, play an equal or greater role in determining people's behaviours towards jaguars. Based on theoretical and empirical evidence from previous research (Appendix S6), we further hypothesized that actors' socio-economic and socio-psychological characteristics that reduce tolerance to carnivores and that enhance perceived behavioural control and the odds of encountering jaguars would increase engagement with jaguar killing, trade and consumption.

Materials and methods

Household, village and study area sampling methods

We selected four rural study areas neighbouring urban centres in the Departments of Beni, Pando and northern La Paz, north-western Bolivia (Figure 1). These study areas had confirmed jaguar occurrence, reported cases of jaguar killing and trading, strong livestock ranching and hunting livelihoods and Chinese infrastructure investments, all relevant to our hypotheses. This purposive choice of study areas meant that our study, although not being generalizable beyond these areas in terms of specifics, should give a picture of the role of international jaguar trade in the context of locations with long and currently active histories of interactions between humans and jaguars.

Within our four study areas, we randomly sampled villages (study sites) with populations of 250–2000 inhabitants, located < 150 km from urban centres (the cities of Cobija, Riberalta, Rurrenabaque and Trinidad; Appendix S1). We randomly sampled households (our study units) from prenumbered households along all village streets. When the selected household was uninhabited or unwilling to participate, we approached the neighbouring household instead. We interviewed one adult per household, prioritizing the household head, such that households and participants refer to the same study unit. Sampling intensity for villages within study areas and households per village was based on a power analysis
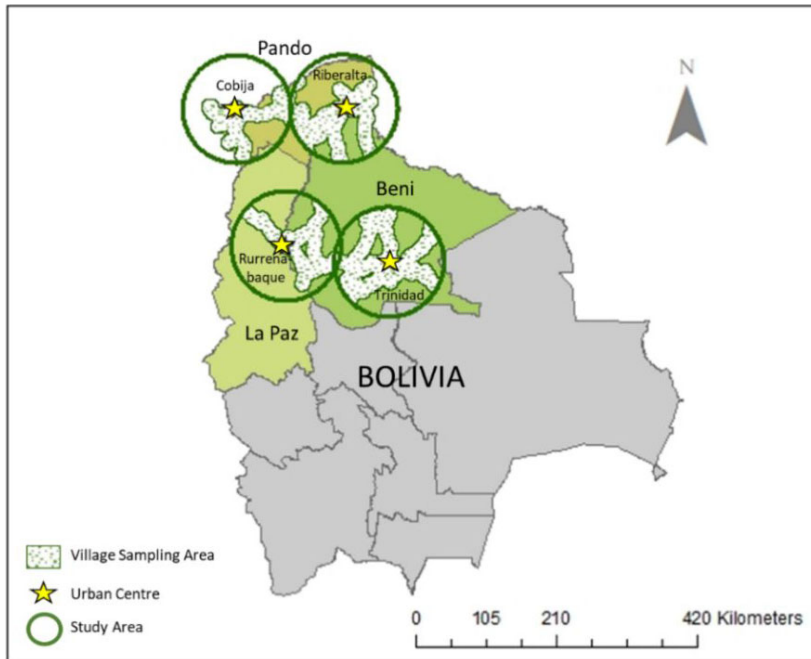
Figure 1 Map of study areas in north-western Bolivia, based on a prioritisation of rural lands around the main urban areas in the Departments of Beni, Pando and northern La Paz

and was proportional to the population size of each study area and village (Appendix S1). Although we considered all households, sampled sites (villages) and study areas as a single population, our statistical analyses reflect the nested structure of our observations through random effects. We discuss differences between study areas in Arias et al., (2020).

Questionnaire and survey

Our semistructured survey instrument comprised 32 open and closed questions (Appendix S2), divided into the following sections: (1) socio-economic characteristics; (2) perceptions of jaguars, their population sizes and the risks of attacks on humans; (3) attitudes towards jaguars and jaguar killing and knowledge of killing methods; (4) experiences with jaguars, including attacks on humans and domestic animal depredation; (5) jaguar body parts uses and prices; (6) awareness of jaguar protection laws; and (7) awareness of, and interactions with, traders. These sections corresponded to our predictor variables. Additionally, we asked participants whether in the past 5 years they had been personally involved in jaguar killing, trading (selling) and consuming (owning and buying) behaviours, and whether in the same period they had been requested by others to kill jaguars, or whether they had themselves asked others to kill jaguars. We asked these sensitive questions directly and using the Ballot Box Method (BBM, Arias et al., 2020a), with the goal of reducing social desirability bias in participants' responses (Appendix S3). An analysis of the performance of the BBM can be found in Arias et al., (2020) and Appendix S3. To capture the intentions of those who had not directly engaged in these behaviours, we asked

Figure 2 Word cloud of most common words concerning perceptions towards jaguars, meant as a preliminary visualisation rather than an empirical analysis. 'Fear' was the most common word, mentioned by 29% of our sample (*n* = 1107), followed by 'dangerous' (15%). Though less frequent, common positive words included 'pretty' (5%) and 'beautiful' (2%), common neutral words included 'fierce' and 'wild', each representing 4% of the sample.

participants what they would do in a hypothetical scenario of encountering a jaguar. These actual and hypothetical behaviours corresponded to our response variables.

Table 1 Actor typologies behind jaguar killing, trading and consuming behaviours, based on (Arias, Hinsley, and Milner-Gulland, 2020b)

Type	Category	Description	Percentage (n = 1107)
Not involved	Not involved	Does not engage in jaguar killing, owning, purchasing, selling or recruiting.	42.8%
Noncommercial	Possessor	Owns jaguar body parts without purchasing or killing (e.g., gifts, inheritance).	17.2%
	Killer	Kills jaguars but does not extract body parts (e.g., retaliation, self-defence killing).	6.2%
	Killing possessor	Kills jaguars and keeps the body parts for personal use (e.g., subsistence, cultural, retaliatory).	1.8%
	Indirect killer	Asks others to kill a jaguar for reasons other than trade or use (e.g., retaliation, fear).	2.4%
Commercial	Killing trader	Buys and sells jaguar body parts from others, while also killing jaguars.	9.0%
	Consumer	Buys jaguar body parts for personal use (e.g., cultural, medicinal).	7.3%
	Trader	Buys and sells jaguars body parts from others.	5.6%
	Killing consumer	Kills jaguars and buys the body parts for personal use (e.g., decoration, trophy).	1.5%
Messengers	Attempted recruit	Has been asked by others to kill a jaguar, but has not undertaken the action.	4.5%
	Messenger	Has been asked by others to kill a jaguar, and has asked others to do so, without undertaking the action.	1.5%

Note: These are not exhaustive categories, but cover all the main types of interactions in our dataset.

We conducted the surveys from June to August 2019, following two weeks of piloting in villages of similar characteristics. The pilot study used a preliminary version of the same questionnaire as the full survey but differed in that it tested different indirect questioning techniques (Appendix S3). The interviews took 20–40 min to complete and were carried out by a team of four Bolivian and one foreign researchers with experience investigating human–jaguar interactions. The study was approved by the Central University Research Ethics Committee of Oxford University (Reference: R63986/RE001) and the Bolivian Ministry of Environment and Water (Reference: MMAYA/VMABCCGDF/DGBAP/MEG No. 0251/2019).

Data analysis

For binary, multilevel categorical and Likert-type questions, we analysed the percentage of participants in our sample that mentioned each response category (Appendix S4). Where relevant, we converted open and continuous questions into categorical variables (perceptions about, and interactions with, jaguars and jaguar abundance). We used a word cloud as a preliminary visualisation of jaguar perceptions (Figure 2) using NVivo software (QSR International Pty Ltd. Version 12 Pro, 2018). We first identified all possible combinations of jaguar killing, trading and consuming behaviours (*n* = 64) and then developed a typology of actors by grouping these combinations (Table 1), based on the characteristics of illegal jaguar traders described in Arias, Hinsley, and Milner-Gulland, (2020b).

To restrict the number of predictors of jaguar killing, trading and consuming behaviours, we hypothesized the direction of the effect that each potential predictor would have on behaviour, based on the literature and our understanding of the data (Appendix S5). We selected predictors that had stronger support in the literature and which represented potentially important relationships to the behaviours. These were gender, livelihood, income, age, education, perceived jaguar abundance, perceived risk of an attack on humans, opinion towards jaguar killing, experience of attacks on humans or livestock,

awareness of jaguars' legal status, awareness of jaguar traders and of prices. We conducted multivariate imputation for missing values in the predictors when these represented less than 5% of the sample, otherwise missing values were analysed as a level in a categorical variable, using the package 'mice' (van Buuren and Groothuis-Oudshoorn, 2011). Our response variables (jaguar killing and trading actions) were based on the responses to the BBM. Missing values in the response variables caused by missing BBM responses were imputed using the responses to direct questioning from the same respondent. Predictor categories that represented less than 5% of the sample were collapsed with the next most relevant category. All categorical and continuous dependent and independent variables were tested for association applying Cramer's V (for categorical variables) and point-biserial correlation (for continuous and categorical variables) through the packages 'DescTools' in R (Signorell, 2021) and 'ltm' (Rizopoulos, 2006), in R version 3.6.2 (R Core Team, 2019). Medium and low levels of association (<0.5) were found, ruling out collinearity. For each lethal (killing, being asked to kill, asking others to kill and hypothetical killing), commercial (selling and hypothetical selling), consumer (buying, owning and hypothetical owning), and tolerant behaviour, we ran logistic mixed effects generalized linear models, implemented through the package lme4 in R (Bates et al., 2015), with study area and village as nested random effects, and estimated 'Wald' confidence intervals (Figure 3, Appendix S6). Estimates are presented for each specific behaviour and no grouping of behaviours was undertaken.

Results

Sample characteristics

We interviewed 1107 people in 36 villages of our four study areas (see Appendix S4 for complete descriptive results). Village distance from the main urban centres ranged from 11 to 150 km, averaging 70 km, and from two to 196 km from protected areas, averaging 80 km. Over half of our participants were women (55%), and the most common economic

activity was hunting and fishing (44.4%). Education and income levels were predominantly low.

Local people's relationships with jaguars

Participants held predominantly negative perceptions towards jaguars (75%), as shown by their choice of words to describe jaguars (Figure 2). In alignment with their negative perceptions, more than half of participants (52.4%) preferred a decrease in jaguar populations. Jaguar abundances were mostly perceived as being low and decreasing, as described by 34% and 47% of participants, respectively. The acceptability of jaguar killing was high, being the preferred outcome for more than half of participants (52.1%).

Interactions with jaguars were common in our study areas. Three percent of participants reported being attacked by a jaguar, or knew of attacks involving their relatives (7.9%) within the past 10 years. Similarly, 24.8% had experienced livestock depredation incidents involving jaguars in the same period. Other interactions included seeing a live jaguar in the wild (57%), seeing a dead jaguar that had been killed by a third party (38%) and other indirect experiences (5%).

Awareness of market opportunities and costs

According to the 67% of participants who were aware of the existence of jaguar traders in and around their communities, the most common trader group was Bolivian nationals (including local radio broadcasters requesting jaguar body parts, 44.4%), followed by traders of Asian descent (including Asian students saying they needed jaguar body parts for research, 21.3%), Caucasian-looking foreigners (14.5%) and foreigners from neighbouring countries (6%). Awareness about the prices of jaguar body parts was also common amongst participants (27.4%).

The jaguar is listed as a 'vulnerable' species under Bolivian legislation, which makes it illegal to kill or trade jaguars and their body parts (Ayala and Wallace, 2009). However, 85.3% of participants were either unaware or confused about the illegality of killing jaguars. Similarly, the majority of participants (64%) were unaware of any authorities responsible for handling jaguar-related issues, and few (12.2%) had heard of penalties of enforcement related to killing or trading jaguars.

Prevalence of jaguar killing, trading and consuming behaviours

The most prevalent jaguar killing, trading or consuming behaviour was possessing jaguar body parts or live animals (42.1%), followed by killing (18.6%), selling (14.6%) and buying (13.1%) jaguar body parts. Additionally, some participants (24.3%) had been recruited to kill jaguars, or had asked somebody else to do so (15.5%). Although 51.9% of participants said they would react passively to a hypothetical jaguar encounter, other common reactions included

wanting to kill jaguars to either sell or keep the body parts (48.1%).

The largest percentage of participants (27.6%) engaged in behaviours that can be classified as noncommercial because they involve no financial transactions, including possessing jaguar body parts or live animals ('possessors'; those who own jaguar body parts without purchasing them or without having personally killed a jaguar, Arias et al., 2020), those killing for noncommercial reasons or both (Table 1). The majority of possessors (73%) were aware of the presence of jaguar traders in or around their communities but chose to keep the jaguar body parts for themselves regardless. Those who act commercially represented 23.4% of our sample (Table 1). Meanwhile, messengers or recruiters who received or passed on requests to kill jaguars without undertaking any other actions represented 6% of our sample.

Although a larger percentage of participants was involved in noncommercial than commercial purposes, of the people who had killed jaguars (18.6%), more than half (56.4% of 116) had probably killed a jaguar for commercial reasons, as they had also sold jaguar body parts (Table 1). Nine percent of our sample (n = 99) were traders who also killed jaguars. These may be key players because they participate throughout the jaguar trade chain. Killing traders were predominantly male (72% of 99) bushmeat hunters and fishers (75%). Thirty-six percent of them had experienced jaguar depredation events, 78% of them were aware of traders of multiple nationalities in their area, and 70% of them had received a specific request to kill a jaguar (of which only 3%, or three individuals, had received requests from Asian traders). All killing traders reported that jaguars are killed by shooting, and 75% of them mentioned the use of targeted methods such as baiting, trapping, sound luring or poisoning.

Drivers of jaguar killing, trading and consuming

We found several similarities and also important differences in the drivers of behaviours pertaining to jaguar killing, trading and consuming (Figure 3). Of the socio-economic variables, men were more likely to engage in killing (OR 2.36, CI [1.50, 3.70]) and selling (OR 1.83, CI [1.12, 2.97]) behaviours and were also more likely to be asked to kill a jaguar (OR 1.76, CI [1.19, 2.61]), and to have the intention to kill (OR 2.66, CI [1.72, 4.14]), sell (OR 2.11, CI [1.38, 3.21]) or possess (OR 2.74, CI [1.55, 4.85]) jaguar body parts (Appendix S6). Bushmeat hunting and fishing livelihoods increased the odds of killing (OR 2.11, CI [1.43, 3.12], and of related behaviours such as being asked or asking to kill) and selling (OR 1.89, CI [1.22, 2.92]), but significantly reduced the odds of buying jaguar body parts (OR 0.58, CI [0.37, 0.92]. This suggests that bushmeat hunters and fishers act as suppliers of jaguar body parts in our study areas. Agricultural and livestock ranching livelihoods led to higher odds of killing (OR 1.61, CI [1.03, 2.51]) but were not strong predictors of any commercial jaguar uses. Ranchers were also more inclined to want to possess jaguar
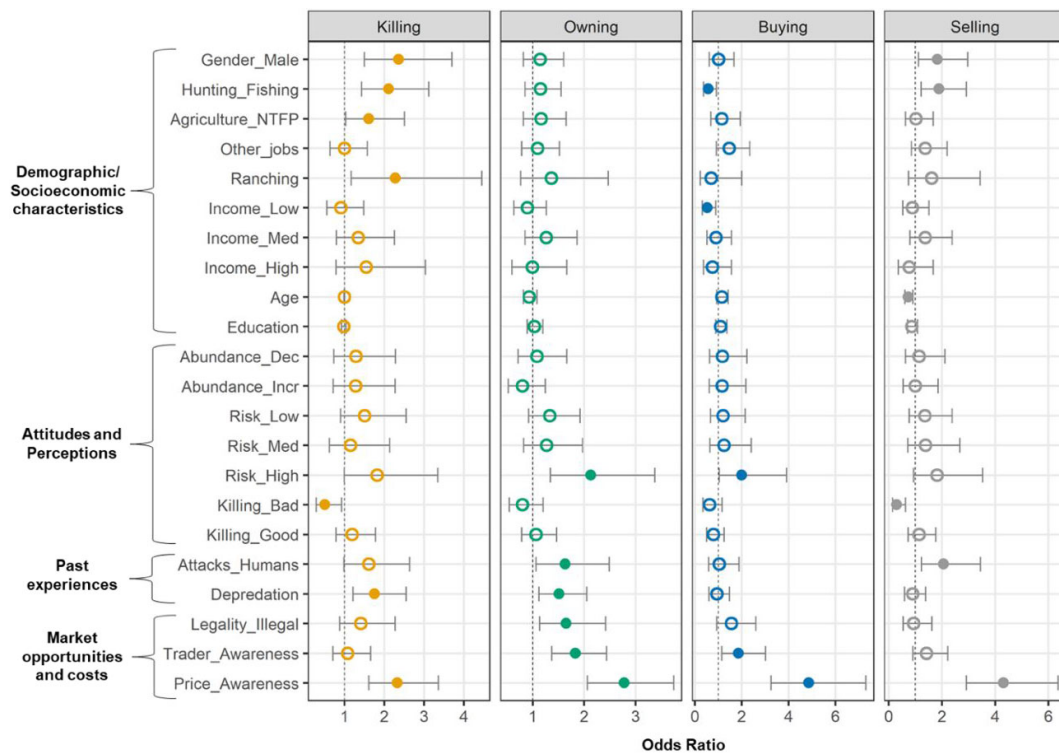
Figure 3 Odds ratios and 95% confidence intervals of predictors of jaguar killing, owning, buying and selling behaviours. Values above or below one indicate whether predictors are associated with higher or lower odds of each behaviour, respectively. Solid circles represent statistical significance ($p < 0.05$)

body parts (OR 2.24, CI [1.06, 4.70]) and less likely to react passively to a hypothetical encounter with a jaguar (OR 0.47, CI [0.24, 0.91]). Low incomes led to a reduced likelihood of purchasing (OR 0.54, CI [0.32, 0.90]) and to an increased interest in selling (OR 1.58, CI [1.02, 2.46]) jaguar body parts, but income did not significantly affect any other behaviours, and neither did education levels (Figure 3). Age had a significant negative relationship with selling (OR 0.74, CI [0.60, 0.92]) and with both recruiting behaviours (being asked, OR 0.75, CI [0.63, 0.89], or asking to kill, OR 0.76, CI [0.62, 0.94]), which suggests that younger participants were more likely to be suppliers of jaguar body parts.

Socio-psychological factors like perceptions and attitudes towards jaguars were generally not strong predictors of any of these behaviours, with a few exceptions (Figure 3). For example, the perception that there are high risks of jaguar attacks on humans was associated with higher odds of owning (OR 2.13, CI [1.34, 3.38]) and buying (OR 2.01, CI [1.04, 3.92]) jaguar body parts. Participants who perceived the killing of jaguars as wrong were also less likely to kill a jaguar and sell jaguar body parts (OR 0.30, CI [0.14, 0.62]) and more likely to have tolerant behaviours towards jaguars (OR 1.66, CI [1.11, 2.47], Figure 3).

Of the predictors pertaining to past experiences with jaguars, participants who had been previously attacked by jaguars (themselves or their families) were significantly more likely to have sold (OR 2.06, CI [1.23, 3.45]) or possessed

(OR 1.63, CI [1.06, 2.49]) jaguar body parts than those who had not (Figure 3). Similarly, those who experienced jaguar depredation events were significantly more likely to have killed (OR 1.76, CI [1.22, 2.55]) and possessed (OR 1.51, CI [1.12, 2.05]) jaguar body parts and less likely to have reacted passively (OR 0.71, CI [0.51, 0.99]) to jaguar encounters. However, the fact that they were not significantly more likely to engage in trading behaviours suggests that not all retaliatory jaguar killing leads to trade.

Variables related to market costs and opportunities were important predictors of our behaviours of interest. Awareness of the presence of jaguar traders in and around participants' communities was significantly associated with buying (OR 1.86, CI [1.15, 3.01]) and owning (OR 1.83, CI [1.37, 2.44]) jaguar body parts and it stimulated messenger or recruiting behaviours (being asked to kill, OR 1.99, CI [1.36, 2.92], asking others to kill, OR 1.71, CI [1.12, 2.63]). However, the fact that it was not associated with a higher likelihood of lethal or trade behaviours suggests that awareness of the opportunity for trade is not in itself enough to lead to trade in our study areas. On the other hand, awareness of the price of jaguar body parts was strongly and significantly associated with all jaguar killing (OR 2.33, CI [1.61, 3.36]), trading (OR 4.31, CI [2.92, 6.36]) and consuming (OR 4.87, CI [3.25, 7.30]) behaviours. Awareness of the illegality of engaging in any of our behaviours of interest did not affect participants' reported actions, except that those who were aware of illegality were more likely to own jaguar body

parts (OR 1.65, CI [1.13, 2.42]) and also more likely to tolerate jaguars (OR 0.43, CI [0.27, 0.68]) if encountered.

Discussion

Previous studies have suggested that human–jaguar conflict caused by livestock depredation by jaguars may be an underlying cause of jaguar trade because farmers and ranchers who resort to lethal control may have an added incentive to sell the parts as compensation for their losses (Jędrzejewski et al., 2017; Reuter et al., 2018). The link between commercial and retaliatory killing has also been proposed for other felids (Everatt, Kokes, and Lopez Pereira, 2019; Li and Lu, 2014). The high value of felid body parts in domestic and foreign markets, and their simultaneous status as threats to livestock and humans, mean that these two drivers of felid killing are often intertwined (Jędrzejewski et al., 2017). Commercial trade can act as both a by-product of retaliatory killing and an incentive for it, but the pathways of causality can be difficult to untangle. In separating the different behaviours related to jaguar trade (killing, trade and consumption), we began to unfold this relationship. We found that even though ranching livelihoods and livestock depredation by jaguars strongly explained jaguar killing, and about a third of killing traders had killed jaguars in the context of retaliation, both ranching and conflict were not strong predictors of commercial behaviours in our sites. This means that conflict is just one aspect of jaguar trade, rather than its underlying cause. We call for a more integrated investigation of the links between felid trade and conflict, considering that their interrelatedness may vary across species and geographies, influencing the effectiveness of conservation efforts to reduce anthropogenic felid mortality.

We show that commercial behaviours are likely to be more strongly driven by a combination of opportunism and market incentives than human–jaguar conflict. Whether they kill jaguars intentionally or opportunistically, bushmeat hunters and fishers were strongly associated with trade in jaguar body parts in our study sites. Bushmeat hunters, in particular, possess the necessary skills, experience, capacity and equipment (e.g., shotguns) that enable them to kill jaguars. As providers and protectors in local communities, they are also likely to count with the social acceptability and legitimacy to kill wildlife that is perceived as dangerous or damaging (Carvalho, 2019). Given their knowledge of, and time spent in, jaguar habitat, bushmeat hunters have increased opportunities of encountering jaguars, having prime access to a resource, which may otherwise be restricted. Although a large portion of the trade may be rooted in chance encounters between bushmeat hunters and jaguars (opportunism), we also found signs that market incentives might be leading to targeted hunting of jaguars. Not only were bushmeat hunters and other killing traders more likely to be aware of the presence of jaguar traders (both foreign and local) in their villages, and to know the prices of jaguar body parts, but many of them had been specifically recruited to kill jaguars, and mentioned the use of targeted jaguar hunting methods such as baits and traps. These behaviours took place in the

absence of law awareness, as shown in our survey, but also due to deficiencies in law enforcement, coinciding with Knox et al., (2019). This combination of actor and opportunity-based drivers coincides with the Routine Activity Theory (Eliason, 2012), which explains that crimes are likely to occur when capable and motivated offenders (e.g., bushmeat hunters incentivized by the market) meet suitable targets (e.g., jaguars) in the absence of guardianship factors (e.g., ineffective enforcement, Carter et al., 2017). Thus, our study sites appear to have the optimal conditions for jaguar killing and trading to thrive if these drivers are not addressed.

The dominant role of noncommercial behaviours in our study areas emphasizes the domestic, cultural and traditional side of jaguar trade. Most jaguar body parts have traditional uses, which may be related to decorative, medicinal, cultural or nutritional purposes (Garcia-Alaniz et al., 2010; Arias, Hinsley, and Milner-Gulland, 2020b). This broad range of longstanding values position jaguars as 'cultural keystone species' (Garibaldi and Turner, 2004). This cultural relationship with jaguars, manifested through the use of jaguar body parts, also means that a large portion of the demand for jaguar body parts is domestic. In particular, the large amount (17.2%) of possessors in our sample, many of whom were simultaneously aware of the existence of a market for jaguar body parts, shows that the desire to keep jaguar body parts may sometimes outweigh the need or interest to sell. This is in contrast to studies that have characterized jaguar trade as Chinese-driven based on seizure data (e.g., Morcatty et al., 2020; Nunez and Aliaga-Rossel, 2017). Although these seizures remain a concern, and may indicate an emerging trend of externally driven commodification and export of jaguars, this discrepancy reiterates the importance of considering multiple evidence sources and of investigating these behaviours on the ground.

Our findings highlight topics that deserve further research and conservation attention to address jaguar killing, trade and consumption. Given the preponderance of noncommercial behaviours, investigating contemporary jaguar uses from both an anthropological and an ecological perspective is necessary. Traditional uses threaten hundreds of species worldwide (de Vasconcellos Pegas, Grignon, and Morrison, 2015), but they can also play an important role in species protection by incentivizing sustainable and long-lasting use of wildlife resources (Dickman and Hazzah, 2016). As traditional jaguar uses are currently illegal for nonindigenous communities in Bolivia (Ministerio de Ambiente y Agua, 2020), which include most of our participants, achieving conservation gains may require opening a more inclusive dialogue about the cultural importance and conservation implications of these behaviours. Because most human-wildlife conflict has roots in human-human conflict, such as the establishment of illegitimate or unrealistic prohibitions (Peterson et al., 2010), failing to account for these traditional jaguar uses, can hinder the path towards human–jaguar coexistence by alienating local communities (Duffy et al., 2016).

Given that jaguar trade was closely linked to wildlife hunting more generally, working with local communities is also necessary to reduce their reliance on wildlife hunting

and trading. Increasing the benefits and financial gains from conserving wildlife in contrast to those from engaging in illegal wildlife trade are potential ways forward (Cooney et al., 2017). It is also worth highlighting that, although most participants held negative perceptions and attitudes towards jaguars, positive attitudes (e.g., believing that killing jaguars is wrong) led to reduced engagement with jaguar killing and trading, and increased tolerance to jaguars. This suggests that shifting attitudes through awareness and education, taking advantage of the already strong cultural and symbolic meaning of jaguars in these communities, may be an effective way to address these behaviours, as shown by other studies (e.g., Engel et al., 2017; Marchini and Macdonald, 2020). However, the simultaneous existence of commercial and non-commercial interests behind the jaguar trade, and of domestic and foreign markets, means that further efforts should also focus on understanding market dynamics. Determining whether the system is supply or demand driven is necessary, and requires exploring the temporal variation in the price and quantity of the traded parts, in hunting effort, in trader networks, and in the condition of jaguar populations (McNamara et al., 2016). While increasing awareness and enforcement of laws may go a long way (given that many of our participants were unaware about jaguar protections), it may not be enough to stop jaguar killing and trading due to strong market incentives, a high prevalence of human–jaguar conflict, financial need, and the potential ties between trade and corruption (Challender and MacMillan, 2014; Morcatty et al., 2020). Future research would also benefit from adopting a socio-ecological systems approach, as suggested by Carter et al., (2017) and Lischka et al., (2018), to explore the role of the wider social and institutional context (such as social norms, as considered by Knox et al., 2019), as well as of jaguar behaviour, ecology and landscape dynamics.

To conclude, our findings suggest that jaguar killing, trading and consuming behaviours are related but also separate actions, which are often carried out by different individuals and influenced by different underlying drivers, including human–jaguar conflict, opportunism, market incentives and culture. We highlight that these drivers, and their interactions, must be considered together to more effectively understand and address jaguar trade, and to enable coexistence with jaguars over the long term.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Study site, village and participant sampling methods

Appendix S2. Survey Guide (ENGLISH).

Appendix S3. Ballot Box Method and Direct Questioning.

Appendix S4. Descriptive results.

Appendix S5. Hypothesized effects of predictors on jaguar trade-related behaviours.

Appendix S6. Model results for all behaviours and intentions.