Understanding wild meat consumption, trade and sustainability in the Amazon

H. R. El Bizri
PhD 2021

Understanding wild meat consumption, trade and sustainability in the Amazon

HANI ROCHA EL BIZRI

A thesis submitted in partial fulfilment of the requirements of

Manchester Metropolitan University

for the degree of Doctor of Philosophy

Department of Natural Sciences

Manchester Metropolitan University

2021

Abstract

The meat from wild animals, or wild meat, is critical to the survival of rural and Indigenous people worldwide. Typically, these communities live in remote places where access to domestic meats is limited. Unregulated wild meat extraction alongside the increasing demand by urban residents can impact game species populations. In the Amazon, limited information is available on the drivers of wild meat use and trade in rural and urban areas. Knowledge of life-history parameters of Amazonian game species, useful for determining their resilience to hunting, is also lacking. In this thesis I: 1) investigate patterns and drivers of wild meat consumption and trade in the Amazon, and 2) present new data on life-history parameters of a widely hunted species, the lowland paca (*Cuniculus paca*), and advance ways of gathering such data from the wild. In the first part of the thesis, I study the consumption of wild meat by rural and urban households in Amazonas, the largest state in Brazil. I demonstrate that the number of hunters living in rural households determines the rates of consumption and the probability of trading wild meat. I show that flavour of certain species increases their consumption rates, and body mass of the species determines its trade price. I also model the relationship between wild meat use and a selection of important socioeconomic indices in five cities in the Brazilian Amazon. I use the results of this model to scale up to all of 62 main urban settlements in Amazonas. This is the first large-scale estimation of wild meat amounts consumed and traded across the entire Brazilian Amazon. I found that the frequency of wild meat consumption in these cities was positively correlated with the proportion of rural population and with the per capita gross domestic product of the municipality. I estimate 10,691 tonnes of wild meat consumed annually in central Amazonia, 6.49 kg per person per year, and US$21.72 per person or US$35.1 million annual overall in terms of trade. In the second part of my thesis, I investigate the reproductive parameters of the lowland paca from data collected using community-based hunting monitoring and collection of biological materials. I used information gathered over 17 years in a site in Brazil and another in Peru. I found that lowland pacas reproduce seasonally. Moreover, the period of the year when more pregnant females were found overlaps with the period of higher hunting rates, which may likely affect populations of the species. I also found that the species reaches maturity at 4 months of age, at least 3 months earlier than previously reported in the literature. No signs of senescence in the species was detected. I then tested the efficacy of local people in diagnosing pregnancy in hunted female lowland pacas, and used these results to correct hunted specimens' reproductive status data, voluntarily collected by hunters as part of a citizen science project. I show that local people correctly diagnosed pregnancy in 72.5% and 88.2% of tests before and after training, respectively. Monthly pregnancy rates determined by hunters and by researchers were similar. Reported annual pregnancy rates were negatively correlated with the productivity of hunting events, and positively associated with the percentage of immatures in the hunted population. This demonstrates that the voluntary diagnosis of game species' reproductive status by local people is a feasible method to obtain accurate life-history parameters. The information presented in this thesis can help ascertain sustainability of wild meat use in Amazonia.

Acknowledgements

This amazing journey towards obtaining my PhD title would not be possible without the essential support of many people in my life. Firstly, a special thanks goes to my dearest supervisor, Prof Julia E. Fa, who has been an inspiration and reference for my career long before I started my PhD studies. Having received her valuable guidance and encouragements, in addition to getting to know and learn from her personally, was undoubtedly one of the greatest fulfilments of my life. I also would like to thank my co-supervisors Dr Hannah Mossman and Dr Martin Jones for their cordial and full support during the entire process of the production of this PhD thesis. I would like to thank Dr Pedro Mayor for his consistent and essential guidance and partnership through many years; his insights and knowledge have substantially contributed not only to my thesis but to my career as a scientist.

I would like to say thanks to my working partners, Dr João Valsecchi, Dr Richard Bodmer, Dr Mark Bowler, Prof Vincent Nijman, Carlos Frederico, Lisley Gomes, Dr Nicole Ponta, Dr João Vitor Campos-Silva, and many others who contributed in numerous ways to the compelling chapters produced in this thesis. I hope to keep working together with these amazing researchers for much more years ahead in my career. I am also grateful to the National Council for Scientific and Technological Development (CNPq) for providing me with the scholarship (#201475/2017-0) and enabling me to pursue my dream of studying and living in the United Kingdom for four extraordinary years.

I would like to express my gratitude for my wife, Thais Morcatty, my soul mate, who has been by my side in every path, challenge, and personal and professional achievements of my life for more than 10 years. I would also like to thank my precious family, in particular my parents Regina, Samir, and Ian, and siblings Hassan and Zaíra, my grandparents Preciliana and Yolanda, and all my friends. They are the pillars of my life, and their support and esteem have always been invaluable for me to persist and do my best in every step of my life. I am indebted to Dr Felipe Ennes and Prof Jean Boubli who kindly opened their homes to me during my time in Manchester. This work would also be impossible without the fundamental approval and assistance from people of the communities of the Amazon involved in my work. In particular, I would like to thank my friends from the communities Ubim, Boa Esperança and Bom Jesus do Baré of the Amanã Reserve, who have always treated me kindly and received me in their houses as part of their family. I am so grateful for having had the opportunity to live and share experiences side by side with these guardians of the forest. A special thanks to Mr Otílio Feitosa de Araújo (Seu Mimi, *in memoriam*), who more than a friend was my mentor, who taught me the secrets and showed me the beauties of the Amazon. He will be profoundly missed, and this thesis is dedicated to him.

TABLE OF CONTENTS

Chapter 1. General Introduction

1.1 The importance of wild meat for human societies and the impacts on game species

Hunting for wild meat (meat from wild animals, excluding fish) is a widespread practice that occurs in all regions of the world where humans are present. Over 2,000 wild species are used as a source of wild meat across the world (Redmond et al. 2006) and these are essential to ensure the food security of millions of people worldwide. Wild meat is especially critical for the survival of rural and Indigenous communities living in remote regions of tropical forests who usually have little access to domestic meats (Torres et al. 2018). Over 150 million households across Latin America, Asia, and Africa are estimated to regularly consume wild meat (Nielsen et al 2018). For these people, wild meat is one of the most important sources of essential macronutrients and micronutrients, such as protein, fat, iron, zinc, and a series of vitamins (Golden et al. 2011; Sarti et al. 2015; van Vliet et al. 2017). Estimates from the two largest continuous tropical forests on the planet, the Amazon and Congo basins, show that wild meat consumption is responsible for 60% to 80% of daily protein needs for local communities (Nasi et al. 2008; Cawthorn and Hoffman 2015), and approximately 5 to 6 million tonnes of mammal meat - usually the most hunted group in tropical forests - are harvested annually in these areas (Fa et al. 2002; Nasi et al. 2011).

In addition to consuming wild meat, rural and Indigenous Peoples often sell the meat from wild animals as a source of income, both between local communities and in urban markets (Coad et al. 2010; Schulte-Herbrüggen et al. 2013). In the Global South, wild meat is suggested to represent, on average, 2% of households' income; but there can be large variation between sites (Nielsen et al. 2018). For instance, annual income from the sale of wild meat reaches up to 32.8% of total household income on Bioko Island, Equatorial Guinea (Grande-Vega et al. 2013). In North Sulawesi, wildlife meat from forested areas was routinely available for sale in 73% of urban markets surveyed, where 800 tonnes of wild meat were recorded as traded over a year (Latinne et al. 2020). The income obtained by rural or peri-urban hunters from this trade is usually used to purchase other crucial food supplies and goods only available in urban areas, such as cereals, poultry, eggs, clothes and oil (Lindsey et al. 2011; Grande-Vega et al. 2013). Households containing commercial hunters on Bioko Island were wealthier and spent more money on products they did not grow themselves than households that did not sell wild meat (Grande-Vega et al. 2013). In addition, cash obtained from the wild meat trade also provides important protection against economic shocks, such as crop failures or illness. Economic reliance on wild meat and income generation by selling wild meat vary seasonally and are significantly higher during periods in which other sources of food or local income are relatively low (Endo et al. 2016; Nielsen et al. 2018).

Although consumption and trade of wild meat can be essential for numerous peoples throughout the globe, there is increasing evidence that unsustainable hunting is one of the main causes of wildlife population declines worldwide. The growth in human populations, improvements in hunting technologies, and the higher participation of local people into commercial markets of wild meat have escalated exploitation rates of game species (Benítez-López et al. 2017; Brashares et al. 2011; Grande-Vega et al. 2013; Bowler et al. 2020). As a consequence, around 20% of the threatened and near-threatened species listed in the IUCN Red List are directly impacted by hunting; 50% of these are also affected by some kind of trade (Maxwell et al.

2016; Ripple et al. 2016; Scheffers et al. 2019). Hunting is similarly the most frequently reported anthropogenic threat to wildlife in protected areas (Tranquilli et al. 2014; Schulze et al. 2018). Benítez-López et al. (2017) showed that both tropical mammals and birds suffer reductions in their abundance, in the order of 58 to 83% respectively in hunted areas compared to non-hunted areas. In addition, in a review of studies on hunting impacts, Coad et al. (2019) found that on average 50% of game species are unsustainably hunted in tropical forests.

Game species' declines can result in severe ecosystem changes. The loss of ecological functions such as seed dispersal provided by hunted species can promote cascading effects on forest structure and long-term viability, and ultimately on carbon sequestration, and in some cases even influence the weather conditions and aggravate climate change (Brodie and Gibbs 2009; Dirzo et al. 2014; Peres et al. 2016). Furthermore, declines in game species' populations can generate extinctions of interacting species as well as the loss of key ecological services (Terborgh and Estes, 2010; Dirzo et al. 2014; Ripple et al. 2016), such as the provision of food for local communities that depend on this resource (Fa et al. 2003; Fa et al. 2015*a*). For instance, Fa et al. (2015*a*) have shown that decreases in wild meat availability in central Africa were intrinsically related to the occurrence of malnutrition in local children. Therefore, developing plans for the sustainable consumption and trade of wild meat, within safe ecological limits, is one of the most immediate actions needed to protect game species, their ecological services and the livelihoods and health of local people in tropical forests (Ingram et al. 2015). However, although experiences from different tropical forests may enhance the development programmes for sustainable use of wildlife and contribute to better decision-making, in-depth studies in targeted areas are essential to develop context-appropriate programmes.

1.2 Hunting, consumption and trade of wild meat in the Amazon

The Amazon is the largest remnant of tropical forest in the world, with 6.7 million km² distributed across 8 countries in South America (Charity et al. 2016). At least 34 million people live in the Amazon, 12 million (35%) of those within forests, including over 350 different Indigenous Peoples (Charity et al. 2016), who rely largely on wild meat for food (Figure 1). Most of these people live within the 3.6 million km² of protected areas and Indigenous Lands. Rural consumption rates of wild meat in the Amazon corresponds to c. 1.3 million tonnes of meat per year (Nasi et al. 2011), with the per-capita annual consumption estimated at between 22 to 525 g/person/year (Ojasti 1996). Wild meat provides between 8 and 72% of the protein intake for local people (Sarti et al. 2015; Dufour et al. 2016), contributing to local livelihoods and food security that may not be easy to achieve with domestic meat in remote areas.

Although several inner regions in the Amazon remain inaccessible to humans, it is clear that wild meat hunting can adversely affect game species populations in this biome if uncontrolled. Parry and Peres (2015) estimated a large-scale level of depletion of game species populations in the Brazilian Amazon, especially along rivers and near densely populated villages and cities. Peres and Palacios (2007) found that 73% of the 30 game species analyzed in the Brazilian Amazon showed declines in their population numbers, reaching up to 74.8% of reduction in hunted sites compared to less intensively hunted sites. However, there is still a lack of information on consumption rates of wild meat in the more remote areas of the Amazon, primarily because studies are mainly concentrated near universities and research institutes (Silva 2016), and information on the biological and socio-economic drivers of wild meat hunting and consumption in Amazonia is still incipient and ambiguous.

It is clear from most studies that Amazonian hunters usually focus on large-sized species (Bodmer 1995; Jerozolimski and Peres 2003). However, it is still unclear the role that taste preferences (in terms of flavour) may have in the harvest rates of game species, and in shaping wild meat consumption in Amazonian communities. In socio-economic terms, Kirkland et al. (2020) reported that neither market exposure nor village size had a significant effect on harvest rates of wild meat in the rural Peruvian Amazon; in contrast, Nunes et al. (2020) found that village size influenced negatively the hunting efficiency in rural communities, and Chaves et al. (2017, 2020) found that increased market access diminished wild meat consumption in rural areas in the Brazilian Amazon. At the household level, Luz et al. (2015) found no effect of the number of people and guns per household on the hunting rates or hunting efficiency in the Bolivian Amazon, a result supported by Mesquita et al. (2018), who found that neither family size nor number of hunters in the household influenced hunting rates in the eastern Amazon. Torres et al. (2021) also did not find any association between frequency of hunting and wild meat consumption with the number of years of formal education of the male head of the household, monetary income or asset-wealth. By contrast, Nunes et al. (2020) found that family size was negatively correlated with hunting efficiency in western Amazonia. These contradictory results reflect the need for additional data and knowledge on hunting dynamics in Amazonia and, in order to guide better decision-making, a definition of the cultural and socio-economic factors which predict the levels of wild meat consumption.

Figure 1. A hunter from a remote small-sized local community in central Amazonia butchering a lowland tapir (*Tapirus terrestris*) carcasse, which fed the whole community for several days. Credit: Hani R. El Bizri.

Information on the consumption of wild meat in urban centres and the mechanisms of the wild meat trade in cities is also lacking. Until recently, urban wild meat consumption in Amazonia was regarded as negligible (Rushton et al.

2005; Nasi et al. 2011). However, increasing evidence suggests that consumption and trade in urbanized Amazonia is more widespread than previously thought. The most prominent example is Iquitos, the largest city in the Peruvian Amazon and the most well-studied site in terms of urban wild meat consumption in the Amazon. In this city, established open-air markets have been offering access to meat from wild species for more than 45 years (see Castro 1976; Bodmer and Lozano 2001, Mayor et al. 2019).

In a recent wide-scale study in the Brazilian Amazon, wild meat from approximately over 1.7 million turtles and tortoises was estimated as being consumed annually in urban centres in Amazonas state (Chaves et al. 2020). Well-established wild meat markets exist in Abaetuba, Brazilian Amazon (Baía-Júnior et al. 2010), and in the Amazonian tri-frontier (Brazil, Colombia, and Peru), where about 473 tonnes of wild meat were estimated as traded annually (van Vliet et al. 2014). In addition, Parry et al. (2014) found that c. 80% of interviewed households in two cities in southern Brazilian Amazonia regularly consume wild meat, while Chaves et al. (2017) reported that in Tapauá city over 40% of urban households consume wild meat at least once per month. A few other studies have assessed the economic and cultural background of urban wild meat consumers in Amazonia, and have started to unveil the links between rural and urban communities that shape the wild meat trade (Morsello et al. 2015; Chaves et al. 2017; Chaves et al. 2019). These studies showed that the amount of wild meat consumed per capita in urban areas decreased with the size of the city, decreased among generations (children consumed less than adults), and was higher when the head of the household was a migrant from rural areas, but consumption rates declined the longer rural-urban migrants lived in urban areas.

Parry and Peres (2015) showed that the consumption of wild meat in urban centres can have a far-reaching impact on game species, causing depletion halos in hunted animal populations that reach over 100 km from the cities. However, since wild meat harvest, consumption and trade are often excluded from official national trade statistics, volumes traded and consumed in Amazonian cities are not recorded. There is therefore a clear need to improve our understanding of wild meat consumption and trade in urban areas at larger geographical scales so as to improve decision-making for the management of wildlife at the regional and country level. In addition, information about the actors involved in, drivers, and operationalization of this trade within the cities is still absent.

Although access to an adequate living standard, including access to enough food and a fair salary that allow living and supporting the family, is a human right, wild meat consumption and trade in Amazonian countries usually occurs in a legal vacuum since the existing legislation is often inadequate and information and management strategies are unclear (van Vliet et al. 2019; Antunes et al. 2019). The approach most commonly adopted by authorities is to treat hunting, consumption and trade of wild meat as illegal activities that should be suppressed, and therefore most strategies proposed to alleviate hunting pressure in Amazonia is to substitute wild meat with domestic meat (Rushton et al. 2005). However, Nunes et al. (2019) showed that changing consumption of wild meat to beef in Amazonia, for instance, would mean that local people would have to spend around 90% of their wages alongside converting large portions of Amazonian forests into pasture. The negative consequences of this conversion would ultimately have a greater impact on wildlife than by allowing hunting itself. Moreover, changing people’s behaviour in relation to wild meat consumption is still a major challenge. In an experiment in an Amazonian city, Chaves et al. (2019) showed that economic incentives and price reduction of chicken increased the consumption of chicken but were not enough to decrease wild meat consumption. Therefore, valuing local food systems and guaranteeing the sustainability of hunting and trade of wild meat is a better way to legitimize local peoples' rights, make their territories more resilient to adversities and uncertainties, and safeguard both game species and the livelihoods of local people.

Areas occupied and managed by local people in the Amazon are important repositories of useful natural resources for these populations but also protect these landscapes from deforestation, fires and wildlife crimes (Nepstad et al. 2006; Nelson and Chomitz, 2011; Kauano et al. 2017). Despite some progress, protected areas are still under constant threat from policy changes, large-scale development and economic projects, including hydroelectric power plants, mining projects and the expansion of soy and beef supply chains throughout the Amazon (Ferreira et al. 2014; Nepstad et al. 2014). Community-based management is recognized as an effective means to sustainably exploit wildlife whilst ensuring governance of territory and natural resources by local people. A study of over 11,000 population time-series from almost 3,000 species used by humans in Africa and the Americas uncovered that although these populations tend to decline rapidly, there were several evidence of population increases, resulting in species recovery, where harvested species were managed (McRae et al. 2020). Examples of adequately managed species in Amazonian aquatic environments exist, e.g. the community-based management of giant arapaima (*Arapaima gigas*) and freshwater chelonians throughout the Amazon basin (de Freitas et al. 2020). Similar to the aquatic species, co-management approaches can also be applied to terrestrial game species (Campos-Silva et al. 2018). Designing effective community-based management of wild meat in Amazonia will require a deeper understanding of the patterns, drivers and motivations of hunting and an assessment of the sustainability of wild meat consumption and trade in rural and urban areas. For that purpose, robust ecological and life-history data on wildlife species hunted for food is also necessary for the development of models and indicators of sustainability of wildlife exploitation. Such information can be used to build cases for the sustainable harvest of game species, and used as evidence for the implementation and improvement of policies concerning wildlife management in Amazonia.

1.3 Sustainability of hunting: the need for better life-history data on game species

In the last decades, many studies have aimed to assess the sustainability of hunting and the causes of game overexploitation in the tropics. These studies employed numerous sustainability models to examine the vulnerability of wildlife to hunting (e.g., Fa et al. 2005, Fa et al. 2014, Weinbaum et al. 2013). Hunting sustainability models were developed based mostly on fisheries experiences and often depend on life-history, demographic, and harvest data of the target species. Reproductive parameters of game species are key factors in these models because they determine the pace of population increase through the calculation of recruitment rates. These rates are ultimately used to estimate the likelihood of a species being impacted by harvesting by humans, and to set sustainable harvest quotas (i.e., maximum sustainable yield – MSY).

However, there is little information on the reproductive biology of game species, because quantifying reproductive rates in the wild is extremely laborious and costly, in particular for tropical forest species (e.g. Sutherland 2001; Fragoso et al. 2016). For instance, Conde et al. (2019) have shown that only 1.3% of tetrapod species have comprehensive information on birth and death rates. Most hunting sustainability models have therefore ignored or simplified reproductive parameters of game species. Models have primarily employed r_{max} (the intrinsic rate of natural population increase) as a measure of reproductive performance of game species. This index is more usually calculated using Cole's Equation (1954):

$$1 = e^{-rmax} + \mathrm{b}e^{-rmax(\mathrm{a})} - \mathrm{b}e^{rmax\,(\mathrm{w}+1)}$$

where a is the age at first reproduction, w is the age at last reproduction, and b is the annual birthrate of female offspring. The paucity of data has forced researchers to calculate r_{max} using measures of reproductive performance calculated more than 30 years ago mainly using data from captive populations (e.g. Robinson and Redford 1986). Several conditions, such as stress, availability of resources, and the composition of social groups, may differ between wild and captive populations (Goodman 1999; Mayor et al. 2011). Therefore, reproductive rates derived from captive populations may consistently inflate estimates of production and raise estimates of sustainable exploitation (Milner-Gulland and Akçakaya 2001).

The lack of reproductive data has also forced researchers to apply oversimplified models (Fa et al. 2015*b*, van Vliet et al. 2015*a*). For example, the 'Production Model', which relies on r_{max} and accounts for more than 34% of all hunting sustainability assessments conducted so far, has consistently failed to detect unsustainability in situations where it was detected by other models (Weinbaum et al. 2013). Another drawback of using oversimplified models is that they usually rely on static indexes, ignoring complex animal population dynamics, such as age-structure, reproductive seasonality and density-dependent changes of game species' reproductive rates and population structure over time (Sutherland 2001; Weinbaum et al. 2013). Consequently, the sustainability estimations resulting from these models operate under high levels of uncertainty (Levi et al. 2009; Ling and Milner-Gulland 2006; van Vliet et al. 2015*a*; Weinbaum et al. 2013). Even though more complex approaches such as agent-based models (ABMs) are able to incorporate dynamic reproductive aspects of populations, the representation of species' reproductive parameters have been still simplified through the use of classical r_{max} estimates (see for instance Iwamura et al. 2014).

Recent studies have shown that increasing the level of stakeholders' participation and local hunters in particular, in data collection can help fill knowledge gaps on game species' reproductive traits (Mayor et al. 2013, 2017). Mayor et al. (2017) used numerous genitalia samples donated by local hunters to refine estimates of litter size and birth rate, and subsequently to recalculate previous r_{max} values for the top 10 most hunted species in the Peruvian Amazon. Dubost and Henry (2017) used genitalia collected by hunters to uncover seasonality patterns of reproduction of four hunted terrestrial mammals in French Guiana. The use of this approach can therefore be a cost-effective way to obtain more accurate reproductive information for use in hunting sustainability models. Studies can be developed further by training local people to reliably assess and collect the reproductive status of the hunted species by themselves, enabling data collection to occur in places or situations where organ collection, e.g., genitalia, is not possible.

1.4 The lowland paca (*Cuniculus paca*): an appropriate species for understanding sustainable hunting

The need to refine our knowledge of life-history traits is more urgent for heavily hunted species, since these are likely to be the most impacted but also the more important as a source of food and income for humans. Therefore, finding adequate model species is of key importance for the testing of data collection methods and for which management actions can be put in place. A useful model species is the lowland paca (*Cuniculus paca*), a large-sized nocturnal rodent and one of the most hunted game species in the Neotropics (Stafford et al. 2017) (Figure 2). Pacas are highly prized for their meat by local populations (Deustsch and Puglia 1990), their consumption is notably high in the Amazon basin and they are often ranked among the tastiest wild meat by hunters (Bodmer 1995; Valsecchi and Amaral 2009). Pacas are also considered of great nutritional value, with more protein and less fat than beef and sheep meat, and a higher proportion of edible content per individual than other hunted species such as the collared peccary (*Pecari tajacu*), brocket deer (*Mazama americana*) and yellow-footed tortoise (*Chelonoidis denticulata*) (Gálvez et al. 1999).

Van Vliet et al. (2015*b*) have revealed that paca meat is present in more than 50% of all wild-meat-based meals consumed by children in the Colombian Amazon. It was also the most consumed species, accounting for over 50% of all events of wild meat consumption in the Eastern Amazon (Torres et al. 2021). In a large-scale hunting assessment, Read et al. (2010) showed that the paca is the most hunted species by Indigenous communities in the Guyanan Amazon, while Peres (2000) indicated that paca is the second most consumed species in the Brazilian Amazon, with an annual consumption rate of 0.81 pacas per person, corresponding to 730,886 individuals extracted and 11.35% of the total number of mammals harvested yearly. Likewise, paca is also the second most hunted species in the Peruvian Amazon (Bodmer and Lozano 2001), totaling an annual harvest rate of 17,000 individuals. Pacas are also highly traded in wild meat markets, being the top traded animal in the Amazonian tri-frontier (van Vliet et al., 2014) and the second most-traded species in the Iquitos and central Amazonian markets (Mayor et al., 2019; El Bizri et al. 2020). Given its high nutritional value, esteemed flavour, and large consumption and trade rates in the Amazon, this species plays an important role in alleviating poverty and guaranteeing food security for thousands of Amazonian inhabitants.

Figure 2. The lowland paca (*Cuniculus paca*), a large-sized nocturnal rodent and one of the main hunted game species in the Amazon. Credit: Hani R. El Bizri.

Despite the importance of the lowland paca as a source of food and income, the species remains barely studied in the wild, with most life-history parameters originating from captive studies (van Vliet and Nasi 2019). The implementation of effective management programmes to support local people and to protect paca populations is increasingly urgent, hence there is a need for refining life-history parameters for the species. The fact that pacas are extensively harvested and traded means that large amounts of data can be collected through the participation of local actors. The information gathered for the species can assist in user communities generate better ways of managing the hunting of this animal, and become a model species to be applied to other hunted species in Amazonia.

1.5 Thesis structure, aims and objectives

The general aim of this thesis is to investigate patterns of wild meat consumption and trade in the Amazon, and to advance ways of gathering and refining the collection of *in situ* life-history information on game species to form the basis for promoting wild meat sustainability in this biome. For this purpose, I studied the consumption of wild meat in rural and urban areas of the Brazilian Amazon, and investigated life-history parameters of a top-hunted species by using participatory data collection of biological materials and hunting activity in the Brazilian and Peruvian Amazon. This thesis is divided into seven chapters, with **Chapter 1** presenting the general introduction. All data chapters (Chapters 2-6) have already been published in scientific journals, and a version of these publications are included with the PDF version of this thesis.

The objectives of **Chapter 2** were to measure consumption and trade patterns of wild meat, and assess the social and biological factors that may influence consumption rates, trade, and pricing of wild meat by remote rural communities in the Jutaí River basin, in central Amazonia. In this chapter, I present novel results of wild meat use in a very remote region of the Amazon. The study region is around 100 km from the nearest urban center (Jutaí city), a small city with only 17,964 inhabitants. I also unveil the connection and operations of wild meat trade, from rural hunters to the city market.

The objectives of **Chapter 3** were to estimate the amounts of wild meat consumed and traded in urban centres in central Amazonia. For this purpose, I used more than 1,000 interviews with urban residents in five cities to estimate the rates of urban wild meat consumption. I then assessed the effects of socio-economic indices for these cities to predict amounts of wild meat consumed and the revenue generated by wild meat trade in all 62 cities in the central Brazilian Amazon, providing the first large-scale assessment of wild meat consumption in urban areas of the Amazon.

Because of the high representativeness of the lowland paca (*Cuniculus paca*) in the bulk of game species consumed and traded in Amazonia, as indicated in Chapters 2 and 3, and from the literature, it was clear that information on this species' life history is essential to improve management decisions. In the next three chapters I analyse data on the reproductive biology of the lowland paca collected through interviews, participatory hunting monitoring and community-based collection of biological materials in three sites in Amazonia.

The objectives of **Chapter 4** were to assess how environmental factors affect the reproductive seasonality of lowland pacas, and evaluate the possible impacts of seasonal hunting on paca populations. For this purpose, I analyzed the genitalia of pregnant females donated voluntarily by local hunters over 15 years in two sites in Amazonia to first uncover the association between reproductive parameters, fruiting patterns and climate factors. I then described the association between harvest and reproductive rates during different periods of the year.

The objectives of **Chapter 5** were to refine the maturity and senescence of lowland paca females. For this purpose, I analysed the pregnancy status and presence of active cells in ovaries from the same donated genitalia used above, and used this information to refine the r_{max} for the species. These refinements also allowed for the discussion of potential effects of using new values of these parameters in models assessing sustainable harvest rates of wild lowland paca populations.

The objectives of **Chapter 6** were to test the feasibility of a citizen-science collection of data on pregnancy status data of tropical game species by local people. For this purpose, I established the local peoples' capacity to determine the reproductive status of female lowland pacas in three Amazonian sites, before and after a period of training, using interviews with pictures of collected genitalia. I used these results to correct the pregnancy rates estimated for the species from data collected by local people on hunted specimens' reproductive status over a 17-year period (2002-2018) in one study site. With those data, I determined the relationship between pregnancy rates of lowland pacas with hunting indices (capture-per-unit-effort and age-structure) to describe the effects of hunting on the studied game populations.

In the last chapter of the thesis, **Chapter 7**, I summarise the main results and contributions of this thesis, emphasizing the novel aspects of this work for the general understanding and progress towards the sustainable use of wild meat use in Amazonia, and discuss how my work is situated in a wider context of wild meat research in the biome, and some opportunities for future research on this topic.

1.6 References

Antunes, A. P., Rebêlo, G. H., Pezzuti, J. C. B., Vieira, M. A. R. M., Constantino, P. D. A. L., Campos-Silva, J. V., Fonseca, R., Durigan, C. C., Ramos, R. M., Amaral, J. V., Pimenta, N. C., Danzi, T. J. R., Lima, N. A. S., Shepard Jr., G. H. 2019. A conspiracy of silence: Subsistence hunting rights in the Brazilian Amazon. *Land Use Policy* 84:1-11.

Baía-Júnior, P. C., Guimarães, D. A., Le Pendu, Y. 2010. Non-legalized commerce in game meat in the Brazilian Amazon: a case study. *Revista de Biología Tropical* 58:1079-1088.

Benítez-López, A., Alkemade, J. R. M., Schipper, A. M., Ingram, D. J., Verweij, P. A., Eikelboom, J., Huijbregts, M. 2017. The impact of hunting on tropical mammal and bird populations. *Science* 356:180–183.

Bodmer, R. E. 1995. Managing Amazonian wildlife: biological correlates of game choice by detribalized hunters. *Ecological Applications* 5(4):872-877.

Bodmer, R. E., Lozano, E. P. 2001. Rural development and sustainable wildlife use in Peru. *Conservation Biology* 15:1163–1170.

Bowler, M., Beirne, C., Tobler, M. W., Anderson, M., DiPaola, A., Fa, J. E., Gilmore, M. P., Lemos, L. P., Mayor, P., Meier, A., Menie, G. M., Meza, D., Moreno-Gutierrez, D., Pulsen, J. R., Jesus, A. S., Valsecchi, J., El Bizri, H. R. 2020. LED flashlight technology facilitates wild meat extraction across the tropics. *Frontiers in Ecology and the Environment* 18(7):489– 495.

Brashares, J. S., Golden, C. D., Weinbaum, K. Z., Barrett, C. B., Okello, G. V. 2011. Economic and geographic drivers of wildlife consumption in rural Africa. *PNAS* 108:13931–13936.

Brodie, J. F., Gibbs, H. K. 2009. Bushmeat hunting as climate threat. *Science 326*(5951):364-365.

Castro, N., Revilla, J. Neville, M. 1976. Carne de monte como una fuente de proteinas en Iquitos, con referencia especial a monos. *Revista Florestal del Peru* 6:19-32.

Campos-Silva, J. V., Hawes, J. E., Andrade, P. C., Peres, C. A. (2018). Unintended multispecies co-benefits of an Amazonian community-based conservation programme. *Nature Sustainability* 1(11):650-656.

Cawthorn, D. M., Hoffman, L. C. 2015. The bushmeat and food security nexus: a global account of the contributions, conundrums and ethical collisions. *Food Research International* 76:906–925.

Charity, S., Dudley, N., Oliveira, D. and S. Stolton. 2016. *Living Amazon Report 2016: A regional approach to conservation in the Amazon.* WWF Living Amazon Initiative, Brasília and Quito. WWF, Gland, Switzerland.

Chaves, W. A., Wilkie, D. S., Monroe, M. C., Sieving, K. E. 2017. Market access and wild meat consumption in the central Amazon, Brazil. *Biological Conservation* 212:240-248.

Chaves, W. A., Monroe, M. C., Sieving, K. E. 2019. Wild meat trade and consumption in the Central Amazon, Brazil. *Human Ecology 47*(5):733-746.

Chaves, W. A., Valle, D., Tavares, A. S., Morcatty, T. Q., Wilcove, D. S. 2020. Impacts of rural to urban migration, urbanization, and generational change on consumption of wild animals in the Amazon. *Conservation Biology* DOI: 10.1111/cobi.13663.

Coad, L., Fa, J. E., Abernethy, K., van Vliet, N., Santamaria, C., Wilkie, D., El Bizri, H. R., Ingram, D. J., Cawthorn, D. M., Nasi, R. 2019. *Towards a sustainable, participatory and inclusive wild meat sector*. CIFOR, Bogor, Indonesia.

Coad, L., Abernethy, K. A., Balmford, A., Manica, A., Airey, L., Milner-Gulland, E. J. 2010. Distribution and use of income from bushmeat in a rural village, Central Gabon. Conservation Biology 24:1510–1518.

Cole L. 1954. The population consequences of life-history phenomena. *Quarterly Review of Biology* 29:103–137.

Conde, D. A., Staerk, J., Colchero, F., Silva, R., Schöley, J., Baden, H. M., Jouvet, L., Fa, J. E., Syed, H., Jongejans, E., Meiri, S., Gaillard, J. M., Chamberlain, S., Wilcken, J., Jones, O. R., Dahlgreen, J. P., Steiner, U. K., Bland, L. M., Gomez-Mestre, I., Lebreton, J. D., Vargas, J. G., Flesness, N., Canudas-Romo, V., Salguero-Gómez, R., Byers, O., Berg, T. B., Scheuerlein, A., Devillard, S., Schigel, D. S., Ryder, O. A., Possingham, H. P., Baudisch, A., Vaupel, J. W. (2019). Data gaps and opportunities for comparative and conservation biology. *PNAS* 116(19): 9658-9664.

Deutsch, L. A., Puglia, L. R. R. 1990. *Os animais silvestres: proteção, doenças e manejo*. Editora Globo, São Paulo, Brasil.

Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., Collen, B. 2014. Defaunation in the Anthropocene. *Science* 345:401–406.

Dubost, G., Henry, O. 2017. Seasonal reproduction in Neotropical rainforest mammals. *Zoological Studies* 56:e2.

Dufour, D. L., Piperata, B. A., Murrieta, R. S., Wilson, W. M., Williams, D. D. 2016. Amazonian foods and implications for human biology. *Annals of Human Biology* 43(4):330-348.

Endo, W., Peres, C. A., Haugaasen, T. 2016. Flood pulse dynamics affects exploitation of both aquatic and terrestrial prey by Amazonian floodplain settlements. *Biological Conservation 201*:129-136.

Fa, J. E., Peres, C. A., Meeuwig, J. 2002. Bushmeat exploitation in tropical forests: an intercontinental comparison. *Conservation Biology 16*(1):232-237.

Fa, J. E., Currie, D. Meeuwig, J. 2003. Bushmeat and food security in the Congo Basin: linkages between wildlife and people's future. *Environmental Conservation* 30:71–78.

Fa, J. E., Ryan, S. F. Bell, D. J. 2005. Hunting vulnerability, ecological characteristics and harvest rates of bushmeat species in afrotropical forests. *Biological Conservation* 121:167–176.

Fa, J. E., Olivero, J., Real, R., Farfán, M. A., Márquez, A. L., Vargas, J. M., Ziegler, S., Wegmann, M., Brown, D., Margetts, B., Nasi, R. 2015*a*. Disentangling the relative effects of bushmeat availability on human nutrition in Central Africa. *Scientific Reports* 5:8168.

Fa, J. E., Olivero, J., Farfán, M. A., Márquez, A. L., Duarte, J., Nackoney, J., Hall, A., Dupain, J., Seymour, S., Johnson, P. J., Macdonald, D. W., Real, R., Vargas, J. M. 2015*b*. Correlates of bushmeat in markets and depletion of wildlife. *Conservation Biology* 29(3):805-815.

Ferreira, J., Aragão, L. E. O. C., Barlow, J., Barreto, P., Berenguer, E., Bustamante, M., Gardner, T. A., Lees, A. C., Lima, A., Louzada, J., Pardini, R., Parry, L., Peres, C. A., Pompeu, P. S., Tabarelli, M., Zuanon, J. 2014. Brazil's environmental leadership at risk. *Science 346*(6210):706-707.

Fragoso, J. M., Levi, T., Oliveira, L. F., Luzar, J. B., Overman, H., Read, J. M., Silvius, K. M. 2016. Line transect surveys underdetect terrestrial mammals:

implications for the sustainability of subsistence hunting. *PloS One* 11(4): e0152659.

Freitas, C. T., Lopes, P. F. M., Campos-Silva, J. V., Noble, M. M., Dyball, R., Peres, C. A. 2020. Co-management of culturally important species: A tool to promote biodiversity conservation and human well-being. People and Nature 2(1):61-81.

Gálvez, H., Arbaiza, T., Carcelén, F., Lucas, O. 1999. Valor nutritivo de las carnes de sajino (*Tayassu tajacu*), venado colorado (*Mazama americana*), majaz (*Agouti paca*) y motelo (*Geochelone denticulata*). *Revista de Investigaciones Veterinarias del Perú* 10:82-86.

Golden, C. D., Fernald, L. C. H., Brashares, J. S., Rasolofoniaina, B. J. R., Kremen, C. 2011. Benefits of wildlife consumption to child nutrition in a biodiversity hotspot. *PNAS* 108:19653–19656.

Goodman R. 1999. Seasonal reproduction, mammals. In *Encyclopedia of Reproduction*, edited by E. Knobil, J. D. Neill, pp. 341–352. Academic Press, San Diego, USA.

Grande-Vega, M., Carpinetti, B., Duarte, J., Fa, J. E. 2013. Contrasts in livelihoods and protein intake between commercial and subsistence bushmeat hunters in two villages on Bioko Island, Equatorial Guinea. *Conservation Biology 27*(3):576-587.

Ingram, D. J., Coad, L., Collen, B., Kümpel, N. F., Breuer, T., Fa, J. E., Gill, D. J. C., Maisels, F., Schleicher, J., Stokes, E. J., Taylor, G. Scharlemann, J. P. W. 2015. Indicators for wild animal offtake: methods and case study for African mammals and birds. *Ecology and Society* 20(3):40.

Iwamura, T., Lambin, E. F., Silvius, K. M., Luzar, J. B., Fragoso, J. M. 2014. Agent-based modeling of hunting and subsistence agriculture on indigenous lands: understanding interactions between social and ecological systems. *Environmental Modelling & Software* 58:109-127.

Jerozolimski, A., & Peres, C. A. (2003). Bringing home the biggest bacon: a cross-site analysis of the structure of hunter-kill profiles in Neotropical forests. *Biological Conservation* 111(3):415-425.

Kauano, E. E., Silva, J. M., Michalski, F. 2017. Illegal use of natural resources in federal protected areas of the Brazilian Amazon. *PeerJ* 5:e3902.

Kirkland, M., Eisenberg, C., Bicerra, A., Bodmer, R. E., Mayor, P., Axmacher, J. C. 2020. Sustainable wildlife extraction and the impacts of socio-economic change among the Kukama-Kukamilla people of the Pacaya-Samiria National Reserve, Peru. *Oryx* 54(2): 260-269.

Latinne, A., Saputro, S., Kalengkongan, J., Kowel, C. L., Gaghiwu, L., Ransaleleh, T. A., Nangoy, M. J., Wahyuni, I., Kusumaningrum, T., Feferholtz, Y., Li, H., Hagan, Em., Miller, M., Francisco, L., Daszak, P., Olival, K. J., Pamungkas, J. 2020. Characterizing and quantifying the wildlife trade network in Sulawesi, Indonesia. *Global Ecology and Conservation* 21:e00887.

Levi, T., Shepard Jr., G. H., Ohl-Schacherer, J., Peres, C. A., Douglas, W. Y. 2009. Modelling the long-term sustainability of indigenous hunting in Manu National Park, Peru: landscape-scale management implications for Amazonia. *Journal of Applied Ecology* 46(4):804-814.

Lindsey, P. A., Romañach, S. S., Matema, S., Matema, C., Mupamhadzi, I., Muvengwi, J. 2011a. Dynamics and underlying causes of illegal bushmeat trade in Zimbabwe. *Oryx* 45:84–95.

Ling, S., Milner-Gulland, E. J. 2006. Assessment of the sustainability of bushmeat hunting based on dynamic bioeconomic models. *Conservation Biology* 20(4):1294-1299.

Luz, A. C., Guèze, M., Paneque-Gálvez, J., Pino, J., Macía, M. J., Orta-Martínez, M., Reyes-García, V. 2015. How does cultural change affect indigenous peoples' hunting activity? An empirical study among the Tsimane' in the Bolivian Amazon. *Conservation and Society* 13(4):382-394.

Maxwell, S. L., Fuller, R. A., Brooks, T. M., Watson, J. E. M. 2016. The ravages of guns, nets and bulldozers. *Nature* 536:143–145.

Mayor, P., Bodmer, R., López-Plana, C., López-Béjar, M. 2011. Reproductive biology of the wild red brocket deer (*Mazama americana*) female in the Peruvian Amazon. *Animal Reproduction Science* 128:123-128.

Mayor, P., Guimarães, D., López-Plana, C. 2013. Functional morphology of the genital organs in the wild paca (*Cuniculus paca*) female. *Animal Reproduction Science* 140:206-215.

Mayor, P., El Bizri, H. R., Morcatty, T. Q., Moya, K., Solis, S., Bodmer, R. E. 2019. Assessing the minimum sampling effort required to reliably monitor wild meat trade in urban markets. *Frontiers in Ecology and Evolution 7*:180.

Mayor, P., El Bizri, H., Bodmer, R. E., Bowler, M. 2017. Assessment of mammal reproduction for hunting sustainability through community-based sampling of species in the wild. *Conservation Biology* 31(4):912-923.

McRae, L., Freeman, R., Geldmann, J., Moss, G. B., Kjaer-Hansen, L., Burgess, N. D. 2020. A global indicator of utilised wildlife populations: regional trends and the impact of management. *bioRxiv* DOI: 10.1101/2020.11.02.365031v1.

Mesquita, G. P., Rodríguez-Teijeiro, J. D., Barreto, L. N. 2018. Patterns of mammal subsistence hunting in eastern Amazon, Brazil. *Wildlife Society Bulletin* 42(2):272-283.

Miller-Gulland, E. J., Resit-Akçakaya, H. 2001. Sustainability indices for exploited populations under uncertainty. *Trends in Ecology & Evolution* 16:686-692.

Morsello, C., Yagüe, B., Beltreschi, L., van Vliet, N., Adams, C., Schor, T., Quiceno-Mesa, M. P., Cruz, D. 2015. Cultural attitudes are stronger predictors of bushmeat consumption and preference than economic factors among urban Amazonians from Brazil and Colombia. *Ecology and Society* 20(4):21.

Nasi, R., Brown, D., Wilkie, D., Bennett, E., Tutin, C., van Tol, G. Christophersen, T. 2008. *Conservation and use of wildlife-based resources: the bushmeat crisis.* CBD Technical Series No. 33. Secretariat of the Convention on Biological Diversity, Montreal, Canada, and Center for International Forestry Research (CIFOR), Bogor, Indonesia.

Nasi, R., Taber, A. van Vliet, N. 2011. Empty forests, empty stomachs? Bushmeat and livelihoods in the Congo and Amazon Basins. *International Forestry Review* 13: 355–368.

Nelson, A., Chomitz, K. M. 2011. Effectiveness of strict vs. multiple use protected areas in reducing tropical forest fires: a global analysis using matching methods. *PloS One* 6(8):e22722.

Nepstad, D., McGrath, D., Stickler, C., Alencar, A., Azevedo, A., Swette, B., Bezerra, T., DiGiano, M., Shimada, J., Motta, R. S., Armijo, E., Castello, L., Brando, P., Hansen, M. C., McGrath-Horn, M., Carvalho, O., Hess, L. 2014.

Slowing Amazon deforestation through public policy and interventions in beef and soy supply chains. *Science* 344(6188):1118-1123.

Nepstad, D., Schwartzman, S., Bamberger, B., Santilli, M., Ray, D., Schlesinger, Lefebvre, P., Alencar, A., Prinz, E., Fiske, G., Rolla, A. (2006). Inhibition of Amazon deforestation and fire by parks and indigenous lands. *Conservation Biology* 20(1):65-73.

Nielsen, M. R., Meilby, H., Smith-Hall, C., Pouliot, M., Treue, T. 2018. The importance of wild meat in the global south. *Ecological Economics* 146:696-705.

Nunes, A. V., Peres, C. A., Constantino, P. D. A. L., Santos, B. A., Fischer, E. 2019. Irreplaceable socioeconomic value of wild meat extraction to local food security in rural Amazonia. *Biological Conservation* 236:171-179.

Ojasti, J. 1996. *Wildlife utilization in Latin America: current situation and prospects for sustainable management.* FAO, Rome, Italy.

Parry, L., Barlow, J., Pereira, H. 2014. Wildlife harvest and consumption in Amazonia's urbanized wilderness. *Conservation Letters* 7:565-574.

Parry, L., Peres, C. A. 2015. Evaluating the use of local ecological knowledge to monitor hunted tropical-forest wildlife over large spatial scales. *Ecology and Society* 20(3): 15.

Peres, C. A. 2000. Effects of subsistence hunting on vertebrate community structure in Amazonian forests. *Conservation Biology* 14(1):240-253.

Peres, C.A., Palacios, E. 2007. Basin–wide effects of game harvest on vertebrate population densities in Amazonian forests: implications for animal-mediated seed dispersal. *Biotropica* 39:304–315.

Peres, C. A., Emilio, T., Schietti, J., Desmoulière, S. J., Levi, T. 2016. Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. *PNAS*, 113(4):892-897.

Read, J., Fragoso, J., Silvius, K., Luzar, J., Overman, H., Cummings, A., Giery, S., Oliveira, L. 2010. Space, place, and hunting patterns among indigenous peoples of the Guyanese Rupununi region. *Journal of Latin American Geography* 9(3):213-243.

Redmond, I., Aldred, T., Jedamzik, K., Westwood, M. 2006. *Recipes for survival: controlling the bushmeat trade.* Ape Alliance and World Society for the Protection of Animals, London, United Kingdom.

Ripple, W. J., Abernethy, K., Betts, M. G., Chapron, G., Dirzo, R., Galetti, M., Levi, T., Lindsey, P. A., Macdonald, D. W., Machovina, B., Newsome, T. M., Peres, C. A., Wallach, A. D., Wolf, C., Young, H. 2016. Bushmeat hunting and extinction risk to the world's mammals. *Royal Society Open Science* 3:160498.

Robinson, J. G., Redford, K. H. 1986. Intrinsic rate of natural increase in Neotropical forest mammals: relationship to phylogeny and diet. *Oecologia* 68:516-520.

Rushton, J., Viscarra, R., Viscarra, C., Basset, F., Baptista, R., Brown, D. 2005. *How important is bushmeat consumption in South America: Now and in the future*. ODI Wildlife Policy Briefing, Number 11, ODI, United Kingdom.

Sarti, F. M., Adams, C., Morsello, C., van Vliet, N., Schor, T., Yagüe, B., Tellez, L. 2015. Beyond protein intake: bushmeat as source of micronutrients in the Amazon. *Ecology and Society* 20: 22.

Scheffers, B. R., Oliveira, B. F., Lamb, I., Edwards, D. P. (2019). Global wildlife trade across the tree of life. *Science* 366(6461):71-76.

Schulte-Herbrüggen, B., Cowlishaw, G., Homewood, K., Rowcliffe, J.M. 2013. The importance of bushmeat in the livelihoods of West African cash-crop farmers living in a faunally-depleted landscape. *PLoS One* 8:e72807.

Schulze, K., Knights, K., Coad, L., Geldmann, J., Leverington, F., Eassom, A., Marr, M., Butchart, S. H. M., Hockings, M., Burgess, N. D. 2018. An assessment of threats to terrestrial protected areas. *Conservation Letters* 11:e12435.

Silva, A. L. V. 2016. *Distribuição espacial dos estudos de caça de mamíferos na Amazônia* (MSc dissertation). Universidade Federal do Amapá. 87p.

Stafford, C. A., Preziosi, R. F., Sellers, W. I. 2017. A pan-neotropical analysis of hunting preferences. *Biodiversity and conservation* 26:1877-1897.

Sutherland, W. J. 2001. Sustainable exploitation: a review of principles and methods. *Wildlife Biology* 7(3): 131–140.

Terborgh, J., Estes, J. 2010. *Trophic cascades: predators, prey, and the changing dynamics of nature.* Island Press, Washington D. C., USA.

Torres, P. C., Morsello, C., Parry, L., Pardini, R. Forest cover and social relations are more important than economic factors in driving hunting and bushmeat consumption in post-frontier Amazonia. *Biological Conservation* 253:108823.

Torres, P. C., Morsello, C., Parry, L., Barlow, J., Ferreira, J., Gardner, T., Pardini, R. 2018. Landscape correlates of bushmeat consumption and hunting in a post-frontier Amazonian region. *Environmental Conservation* 45(4):315-323.

Tranquilli, S., Abedi-Lartey, M., Abernethy, K., Amsini, F., Asamoah, A., Balangtaa, C., Blake, S., Bouanga, E., Breuer, T., Brncic, T. M., Campbell, G., Chancellor, R., Chapman, C. A., Davenport, T. R. B., Dunn, A., Dupain, J., Ekobo, A., Eno-Nku, M., Etoga, G., Furuichi, T., Gatti, S., Ghiurghi, A., Hashimoto, C., Hart, J. A., Head, J., Hega, M., Herbinger, I., Hicks, T. C., Holbech, L. H., Huijbregts, B., Kühl, H. S., Imong, I., Yeno, S. L. D., Linder, J., Marshall, P., Lero, P. M., Morgan, D., Mubalama, L., N'Goran, P. K., Nicholas, A., Nixon, S., Normand, E., Nziguyimpa, L., NzoohDongmo, Z., Ofori-Amanfo, R., Ogunjemite, B. G., Petre, C. A., Rainey, H. J., Regnaut, S., Robinson, O., Rundus, A., Sanz, C. M., Okon, D. T., Todd, A., Warren, Y., Sommer, V. 2014. Protected areas in tropical Africa: assessing threats and conservation activities. *PLoS One* 9:e114154.

Valsecchi, J., Amaral, P. V. 2009. Perfil da caça e dos caçadores na Reserva de Desenvolvimento Sustentável Amanã Amazonas – Brasil. *Uakari* 5:33-48.

van Vliet, N., Mesa, M. P. Q., Cruz-Antia, D., Aquino, L. J. N., Moreno, J., Nasi, R. 2014. The uncovered volumes of bushmeat commercialized in the Amazonian trifrontier between Colombia, Peru and Brazil. *Ethnobiology and Conservation* 3.

van Vliet, N., Fa, J., Nasi, R. 2015*a*. Managing hunting under uncertainty: from one-off ecological indicators to resilience approaches in assessing the sustainability of bushmeat hunting. *Ecology and Society* 20(3):7.

van Vliet, N., Quiceno-Mesa, M., Cruz-Antia, D., Tellez, L., Martins, C., Haiden, E., Oliveira, M., Adams, C., Morsello, C., Valencia, L., Bonilla, T., Yagüe, B., Nasi, R. 2015*b*. From fish and bushmeat to chicken nuggets: the nutrition transition in a continuum from rural to urban settings in the Tri Frontier Amazon region. *Ethnobiology and Conservation* 4:6.

van Vliet, N., Moreno, J., Gómez, J., Zhou, W., Fa, J. E., Golden, C., Alves, R. R. N., Nasi, R. 2017. Bushmeat and human health: assessing the evidence in tropical and sub-tropical forests. *Ethnobiology and Conservation* 6(3):1-45.

van Vliet, N., Antunes, A. P., Constantino, P. D. A. L., Gómez, J., Santos-Fita, D., Sartoretto, E. 2019. Frameworks regulating hunting for meat in tropical countries leave the sector in the limbo. *Frontiers in Ecology and Evolution* 7:280.

van Vliet, N., Nasi, R. 2019. What do we know about the life-history traits of widely hunted tropical mammals? *Oryx* 53(4):670-676.

Weinbaum, K. Z., Brashares, J. S., Golden, C. D., Getz, W. M. 2013. Searching for sustainability: are assessments of wildlife harvests behind the times? *Ecology Letters* 16:99-111.

Chapter 2. Social and biological correlates of wild meat consumption and trade by rural communities in the Jutaí River basin, central Amazonia

Published in *Journal of Ethnobiology*

El Bizri, H. R., Morcatty, T. Q., Ferreira, J. C., Mayor, P., Neto, C. F. V., Valsecchi, J., Nijman, V., & Fa, J. E. (2020). Social and biological correlates of wild meat consumption and trade by rural communities in the Jutaí River basin, central Amazonia. *Journal of Ethnobiology*, *40*(2), 183-201.

DOI: 10.2993/0278-0771-40.2.183

2.1 Abstract

Wild animals are an important source of food and income throughout the Amazon basin, particularly for forest-dependent communities living in the more remote regions. Through interviews in 51 households within 16 communities in the Jutaí River Extractive Reserve, Amazonas, Brazil, we determined animal taxa consumed and frequency of wild meat consumption, as well as patterns of wild meat trade. We then investigated the influence of social and biological factors on wild meat consumption and trade. People declared consuming wild meat on an average of 3.2 ± 2.8 days/month/household, amounting to 198.85 kg/month consumed by all sampled households. The vast majority of respondents got wild meat by hunting themselves or it was given to them by their neighbors. The most consumed taxa were paca (*Cuniculus paca*) and collared peccary (*Pecari tajacu*). Approximately two-thirds of respondents declared selling wild meat; meat destined for urban markets was more expensive and was primarily sold from houses of relatives living in the city. Wild meat consumption was determined by taste preferences, while prices were related to the body mass of the taxa concerned. Frequency of wild meat consumption and the probability of selling wild meat were positively associated with the number of hunters in the household. We highlight the importance of wild meat for remote communities and importantly, the prominent links these communities have with urban markets. These findings are useful in developing strategies to ensure the sustainable use of wildlife in the Amazon.

2.2. Introduction

In tropical forested regions throughout the world, increasing human populations, better access to previously unhunted areas, and improvements in hunting technologies have intensified pressures on wildlife and habitats (Coad et al. 2019). In addition, the integration of local people into the wider market economy in the recent decades has driven the switching of hunting for home consumption to trading and fulfilling city markets' demands for wild meat, exacerbating wildlife harvest in the tropics (Ripple et al. 2016; Benítez-López et al. 2017). In this context, understanding the livelihood, economic, and cultural values of wild meat (here considered as any wild vertebrate animal used for food, excluding fish) and the drivers of hunting and trade in tropical forests is fundamental to develop strategies for the conservation of game species and to guarantee food sovereignty of local people (Coad et al. 2019).

In the Amazon basin—a region that encompasses c. 4,982,000 km² of tropical forests shared by eight countries in South America—wild meat represents important sources of food and income for many forest peoples (Sarti et al. 2015), especially where meat from domestic animals is scarce or expensive (Nunes et al. 2019*a*). Together with manioc (*Manihot esculenta*) flour and fish, wild meat comprises one of the main components of the diet of rural and Indigenous communities in the Amazon (Adams et al. 2009). In the Brazilian Amazon alone, according to Peres (2000), as many as 23.5 million game vertebrates are hunted for subsistence yearly by rural and Indigenous communities.

As well as consuming wild meat, hunters also sell part of their quarry to nearby communities or in urban centers to complement their income and to enable them to purchase urban goods such as salt, oil, and clothes (Antunes et al. 2019; Morcatty and Valsecchi 2015). The trade in wild meat in Amazonia occurs within and between rural communities and in urban areas (van Vliet et al. 2015*a*,*b*; Chaves et al. 2019). Rural communities and urban centers are connected especially by 1) the typical multi-sited household organization, i.e., a network among relatives that connects different localities, with community-based or commercial boats carrying people and goods between localities (Padoch et al. 2008; Chaves et al. 2019); and 2) the riverine trader, or "patron," who acts as an intermediary in commercial relationships, traveling between urban centers and rural communities selling industrialized products and buying forest products, such as manioc flour, fish, and wild meat (Lima 2009). Although households in rural communities regularly exchange fish and wild meat as part of a local reciprocity system (Lima 2009), recent studies show that trade in wild meat also occurs within and between communities (Morcatty and Valsecchi 2015).

Differences in market connectivity, type of habitat, as well as the cultural background of communities, are known to influence patterns of wild meat consumption and trade (Chaves et al. 2019; Morcatty and Valsecchi 2015; van Vliet and Nasi 2008). However, there is still a lack of knowledge of potential drivers of wild meat use in more isolated Amazonian communities. For instance, people's willingness to engage in conservation and land use management depends on their place attachment and how they identify with their surroundings (Walker and Ryan 2008). These bonds are strongly influenced by people's time of residence in an area (Hernández et al. 2007). Although to our knowledge never tested for wildlife exploitation, hunting pressure and frequency of trade in Amazonian communities may differ between long-standing inhabitants and newcomers.

Cooperation among hunters is likely to increase hunting yields (Alvard and Nolin 2002); however, it is unclear whether a larger number of related hunters within a household can increase hunting and trade rates. Additionally, although abundance and body mass influence the species hunters pursue (Peres 2000), there is little data available on how taste preferences affect hunting choice and consumption of game species.

Determining patterns and correlates of wild meat consumption and trade among remote Amazonian communities will allow a more accurate understanding of the use of wildlife resources in the region, and to foster more effective strategies for the sustainable use of Amazonian fauna (Levi et al. 2009). In this study, we measured consumption and trade patterns of wild meat within remote rural communities in the Jutaí River basin, in central Amazonia. We also assessed the social and biological factors that may influence the consumption rates, trade, and pricing of wild meat by these communities.

2.3 Materials and Methods

2.3.1 Study area and cultural context

This study was conducted in the Jutaí River Extractive Reserve, in the Jutaí River basin, between the Jutaí and Riozinho Rivers (Figure 1). The Jutaí River Extractive Reserve is 2755 km², mainly covered by upland forests, although other vegetation types occur to a lesser extent (e.g., white-water and black-water flooded forests). Annual precipitation in the reserve averages 883 mm per month in the rainy season (December–March) and 665 mm per month in the dry season (June–September). A total of 1221 riverine people, distributed among 223 families within 24 communities (11 on the Jutaí River and 13 on the Riozinho River), live in the Jutaí River Extractive Reserve (ICMBio 2011). The city of Jutaí, with 17,964 inhabitants, is the closest urban center from the Jutaí River Extractive Reserve, 75– 200 km (92.2 ± 54.7 km) from the sampled communities by river.

Extractive reserves are a category of protected areas defined by Brazilian environmental law (Law No. 9985/2000) as a "sustainable use conservation unit," meaning that local populations living within it are allowed to use natural resources. In the past, extractive families lived scattered along Amazon rivers working in rubber tapping. During the 1970s, the Catholic Church brought together extractive families into organized communities (Lima and Peralta 2017). With the support of the progressive branch of the regional Catholic Church, community dwellers in the Jutaí River created the Jutaí River Extractive Reserve in 2002. Inhabitants of the Jutaí River Extractive Reserve call themselves *extrativistas* (extractive people), meaning that they are non-Indigenous people, descendants of Amazonia's colonial history (Lima 2009). They are better referred to as "agro-extractive," given their engagement in agriculture, fishing, hunting, logging, and other extractive activities (Fraser et al. 2018).

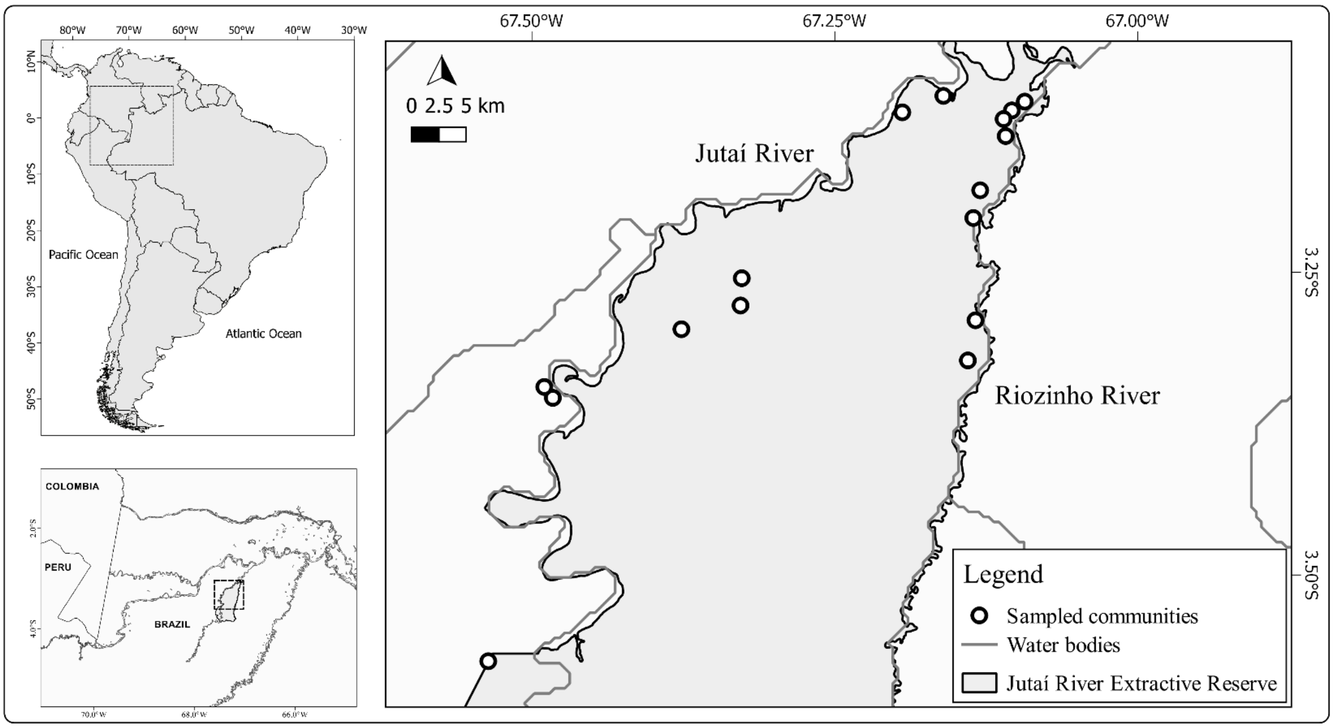


Figure 1. A map showing the location of the Jutaí River Extractive Reserve, central Amazonia, and the 16 sampled communities settled on the Jutaí and Riozinho Rivers.

2.3.2 Data collection

We interviewed household heads of a total of 51 different families in 16 Jutaí River Extractive Reserve communities from June 9–19, 2014. Within each community, we selected households in which the head was available for interview (i.e., not occupied with other activities). We were able to interview at least one household from each community (average: 3.2 ± 2.8 households/community).

We used a standardized, semi-structured questionnaire to ask interviewees the following questions: 1) background information: age of the interviewee, number of residents in the household, number of hunters in the household, whether the household head was born in the community (yes/no, hereafter origin), and residency time in the community (in years); and 2) wild meat consumption and trade patterns: frequency of eating wild meat (in days per month), how wild meat is obtained (i.e., hunting, buying, earning as a gift, or exchanged with other products), the most consumed (open question) and the three most preferred (in terms of meat flavor) taxa, whether wild meat is sold by the household (yes/no), and if sold, where (city or their own/neighboring communities) and what taxa are sold, the sale unit (i.e., entire specimen or in kg), and price it sells for.

Participants were familiarized with our consultation process, as well as the aims of the study prior to the interview. We held a joint meeting with all available residents in each community at the time of the visit, during which we presented the aims of our visit and interviews. We also clarified that respondents were free to participate in the study and to leave the study at any time, and that they were free to refrain from responding to questions they were uncomfortable to answer. All visited households agreed to participate. Interviewees were provided with an Informed Consent Form detailing the project aims and guaranteeing that their identities would remain anonymous. The data collection protocol was approved by the Committee on Research Ethics of the Mamirauá Sustainable Development Institute (Protocol #001-2011).

2.3.3 Data analysis

We used descriptive statistics to describe the frequency of consumption of wild meat, the means by which wild meat is obtained, most consumed and preferred taxa, and the number of people selling wild meat along with prices. The global threat status of the consumed taxa was classified according to the International Union for Conservation of Nature (IUCN) Red List threat categories (IUCN 2019). If local names provided by informants did not allow us to unequivocally catalog the species, we used genus or family.

The amount of wild meat consumed monthly per household was estimated using the following formula (see El Bizri et al. 2020):

$$B = 0.18\ F_c * N_{people}$$

where B is the wild meat biomass consumed; 0.18 is a working value of grams of wild meat consumed per person, per day on which wild meat was eaten (obtained from a study of 13 Indigenous communities [Ojasti 1996]); F_c is the declared monthly frequency of wild meat consumption in the household; and N_{people} is the number of people living in the household. The overall monthly biomass consumed in the 51 households was calculated by summing the values for all informants. For those informants who did not declare their frequency of consumption (n = 8 or 15.7% of the total number of informants), we applied the average F_c for all informants. We estimated the amount of meat consumed of each taxon by using the percentage citations of the taxon of the overall biomass (B). The number of individuals consumed was estimated by dividing the biomass consumed of each taxon by the body mass of eviscerated specimens for the taxon (see García et al. 2004; El Bizri et al. 2020).

We used Generalized Additive Models for Location, Scale, and Shape (GAMLSS) to test the effects of social and biological factors on consumption and trade patterns of wild meat. Firstly, we tested whether the frequency of consumption and the probability of selling wild meat varied with the residence time in the community (calculated as percentage of the number of years the interviewees declared they had lived in the community divided by their age), and the number of people and hunters in the household. We then assessed whether the percentage citations of consumed taxa were related to the percentage citations of preferred taxa, as well as the effect of the size of the taxa (body mass) on percentage citations. In addition, we built a model to test whether the price per taxon is related to their body mass and to the locality where sold (whether urban centers or within/among communities), using taxa as a random effect due to differences in the number of citations among them. Body mass of all mentioned taxa was obtained from García et al. (2004) and from Robinson and Redford (1986). Prices per taxon were calculated in USD/kg; when the sale unit was the entire specimen, we divided the price by the eviscerated body mass of the species or taxon (García et al. 2004). We adjusted for inflation and converted the selling price for each taxon by employing the exchange rate for June 15, 2014 to convert Brazilian reals (R$) into US dollars (R$ 2.24 = 1.00 USD), based on the General Price Index for Brazil estimated by the Getúlio Vargas Foundation (http://www14.fgv.br/fgvdados20/default.aspx).

To build the models, we tested combinations of predictor variables in linear or non-linear relationships using different distribution families. Firstly, we checked for collinearity among variables. Since the number of people was positively correlated with the number of hunters in the household (Spearman R = 0.66), these variables were never included in the same models, but tested separately. Final models were selected based on the Akaike Information Criterion (AIC), considering all models with good support as those with ΔAIC values smaller than two in relation to the model with the smallest AIC. In cases when more than one model was best fitted, we selected the model with the smallest number of parameters (simplest model).

We used R 3.3.3 software and *gamlss* R-package for generalized additive models, and GGally R-package for the collinearity test. For the variables' effects, we assumed significance when $p < 0.05$.

2.4 Results

2.4.1 Wild meat consumption patterns

Households were occupied by seven people on average, and the number of hunters in households ranged from none to six people (Table 1). The majority of the respondents were born outside of the sampled communities. All interviewees confirmed that they ate wild meat, with the vast majority of respondents getting wild meat by hunting themselves or receiving it from their neighbors (Table 1). Buying wild meat or exchanging it for other products occurred less frequently (Table 1). Those who exchanged products for wild meat did so for sugar, kitchen oil, soap, petrol, flour, or bananas.

People declared consuming wild meat on an average of 3.2 ± 2.8 days/month/household, resulting in a total of 198.85 kg of wild meat consumed per month by all surveyed households. The declared frequency of wild meat consumption was positively correlated with the number of hunters within the household (Table 2; Figure 2). However, there was no relationship between the number of persons occupying the household or with the percentage time of residency in the community and the frequency of wild meat consumption (Table 2; Figure 2). This suggests that the origin of the family (whether born in the community or not) does not influence wild meat consumption, and that the number of hunters in the household is more important to define wild meat consumption rates than the amount of people in a family depending on these hunters for food provision.

Table 1. Details on the households interviewed and their patterns of consumption and trade of wild meat in the Jutaí River basin.

Characterization of households and patterns of trade and consumption of wild meat	**Average**	**SD**
N of inhabitants	7.0	3.5
N of hunters	1.4	1.0
Frequency of wild meat consumption (days/month)	3.2	2.8
Amount of wild meat consumed (kg/month)	3.9	3.8
	N of respondents	**% of respondents**
Origin of the respondents		
Born in the sampled community	11	21.6
Born out of the sampled community	38	74.5
Not declared	2	3.9
Origin of the wild meat consumed		
Hunted	38	86.4
Received from neighbors	34	77.3
Bought from neighbors	23	52.3
Exchanged for products	12	27.3
Destination of the wild meat sold		
Jutaí city	20	69.0
Neighbors or nearby communities	7	24.1
Both Jutaí city and rural communities	2	6.9

Table 2. Details of the best-fit generalized additive models for location, scale and shape (GAMLSS) for the frequency of consumption of wild meat, percentage of consumption per taxon, probability of selling wild meat and prices applied according to a number of social and biological predictor variables on the Jutaí River basin, central Amazonia. Smoothers were fitted using cubic splines (*cs*) and p-splines (*pb*). ΔAIC null is the difference between the AIC of the selected model and the AIC of the null model. Families of distribution: EXP = Exponential; ZAGA = Zero-adjusted Gamma; BI = Binomial; BCTo = Box-Cox-t original. *Statistically significant variables.

Best-fit model		**Estimate**	***P*-value**	**Family of distribution**	**Link function**	**AIC (ΔAIC null)**
Response variables	**Predictor variables**					
Frequency of wild meat consumption	(Intercept) + *cs*(Number of hunters in the household)	0.5427 0.3780	0.0520 0.0237*	EXP	Log	167.40 (5.15)
Percentage of consumption per taxon	(Intercept) + Percentage of preference per taxon	1.07035 0.10151	0.00498* 0.02590*	ZAGA	Log	115.95 (3.7)
Probability of selling wild meat	(Intercept) + Number of hunters in the household	-1.1980 1.6870	0.1643 0.0261*	BI	Logit	49.71 (6.56)
Price per taxon	(Intercept) + Destination + *pb*(Body mass) + *random*(Taxa)	1.6337 -0.2326 -0.0027 -	<0.0001* <0.0001* <0.0001* -	BCTo	Log	662.33 (307.08)

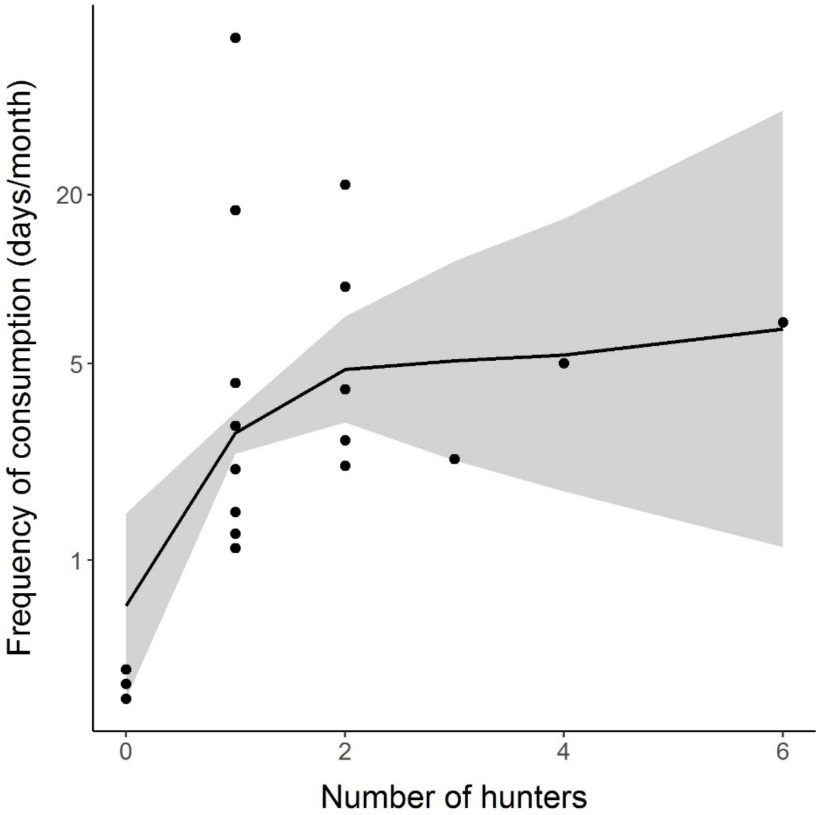


Figure 2. Relationship between the frequency of consumption of wild meat and the number of hunters living in the household on the Jutaí River. Gray shaded area represents the 95% confidence interval. The points are normalized residuals plotted on a log-transformed (ln) y-axis.

2.4.2 Most consumed and preferred taxa

Sixteen taxa were mentioned by interviewees in a total of 140 citations of the most consumed wild meat. Mammals were the most cited group, followed by birds and chelonians (Table 3). Six taxa, namely paca (*Cuniculus paca*), collared peccary (*Pecari tajacu*), Razor-billed Curassow (*Mitu tuberosum*), Juruá red howler monkey (*Alouatta juara*), white-lipped peccary (*Tayassu pecari*), and tapir (*Tapirus terrestris*) represented 78.6% of all citations. Overall, an estimated 47 individuals of all taxa were consumed monthly by the 51 households, the most common being curassows and paca. Among the cited taxa for which it was possible to identify the species (n = 14), at a global level, six (42.9% of the taxa) are currently threatened with extinction (Table 3).

However, in terms of individuals consumed, threatened taxa represented only 9.8% (n = 4.4 individuals).

As many as 17 different species were cited 117 times as preferred species by the interviewees. Mammals were the most representative group, followed by chelonians, and then birds (Table 3). The top five most preferred taxa were the yellow-spotted river turtle (*Podocnemis unifilis*), curassows, white-lipped peccary, tapir, and paca, together comprising 75.2% of all citations. The percentage number of citations for consumption of each taxon was positively correlated with the percentage number of citations for preference (Table 2; Figure 3). We found no significant effect of species' body mass on the percentage consumed.

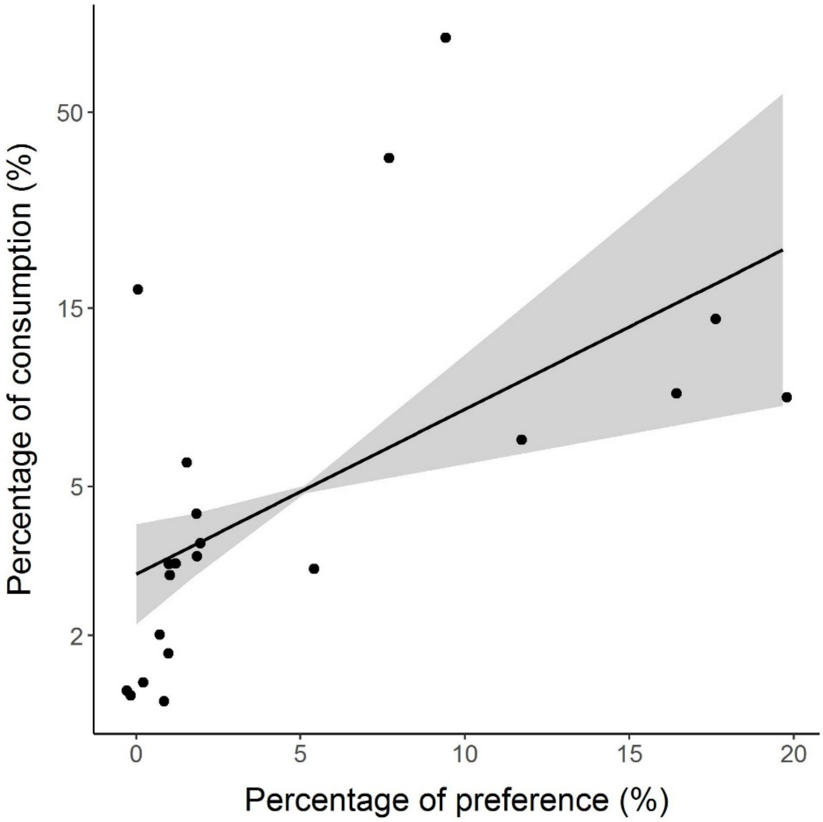


Figure 3. Relationship between the percentages of wild meat consumption per species according to the percentage of preference of meat flavor of the species on the Jutaí River. Gray shaded area represents the 95% confidence interval. The points are normalized residuals plotted on a log-transformed (ln) y-axis.

Table 3. Details of game taxa cited by 51 households of 16 local communities within the Jutaí River Extractive Reserve, central Amazonia, with their gross body mass, net body mass after evisceration, conservation status, percentage of citations as consumed and preferred, and wild meat biomass and number of individuals estimated to be consumed monthly. Taxa names are ordered according to the number of consumption citations.

Táxon	Gross body mass (kg)	Net body mass (kg)	Conservation status (IUCN 2019)	N of consumption citations (%)	N of preference citations (%)	Biomass consumed (kg/month)	Individuals consumed (ind/month)
Lowland paca (*Cuniculus paca*)	8	6	LC	35 (25.0)	11 (9.4)	49.71	8.29
Collared peccary (*Pecari tajacu*)	25	13	LC	25 (17.9)	9 (7.7)	35.51	2.73
Razor-bulled curassow (*Mitu tuberosum*)	3	2.2	LC	20 (14.3)	21 (17.9)	28.41	12.91
Red howler monkey (*Alouatta juara*)	6	4	LC	11 (7.9)	0 (0)	15.62	3.91
White-lipped peccary (*Tayassu pecari*)	35	20	VU	10 (7.1)	19 (16.2)	14.20	0.71
South American tapir (*Tapirus terrestris*)	140	90	VU	9 (6.4)	14 (12.0)	12.78	0.14
Black agouti (*Dasyprocta fuliginosa*)	5	2	LC	7 (5.0)	2 (1.7)	9.94	4.97
Muscovy duck (*Cairina moschata*)	3	2	LC	6 (4.3)	2 (1.7)	8.52	4.26
Yellow-spotted river turtle (*Podocnemis unifilis*)	8	3.5	VU	5 (3.6)	23 (19.7)	7.10	2.03
Brocket deer (*Mazama* spp.)	18.5	12.5	-	4 (2.9)	6 (5.1)	5.68	0.45
Spix's guan (*Penelope jacquacu*)	2	1.2	LC	2 (1.4)	1 (0.9)	2.84	2.37
Silvery woolly monkey (*Lagothrix poeppigii*)	11	8	VU	2 (1.4)	1 (0.9)	2.84	0.36
Maguari stork (*Ciconia maguari*)	4	2	LC	1 (0.7)	0 (0)	1.42	0.71
Six-tubercled river turtle (*Podocnemis sextuberculata*)	3	1.5	VU	1 (0.7)	0 (0)	1.42	0.95
Black-faced black spider monkey (*Ateles chamek*)	9	6.5	VU	1 (0.7)	1 (0.9)	1.42	0.22
Tinamous (Family Tinamidae)	1	0.6	-	1 (0.7)	0 (0)	1.42	2.37
South American Giant river turtle (*Podocnemis expansa*)	40	18	LC/CD	0 (0)	2 (1.7)	0.00	0.00
Bald uakari (*Cacajao calvus*)	3.2	2	VU	0 (0)	1 (0.9)	0.00	0.00
Amazonian manatee (*Trichechus inunguis*)	400	256	VU	0 (0)	2 (1.7)	0.00	0.00
Yellow-footed tortoise (*Chelonoidis denticulatus*)	8	3	VU	0 (0)	1 (0.9)	0.00	0.00
Big-headed Amazon river turtle (*Peltocephalus dumerilianus*)	17	6.8	VU	0 (0)	1 (0.9)	0.00	0.00
Total	-	-	-	140 (100)	117 (100)	198.85	47.37

2.4.3 Trade in wild meat

Regarding the trade of wild meat, from the 48 interviewees that responded to these questions, 30 (62.5%) declared selling wild meat. The trade in wild meat on the Jutaí River basin occurs between neighbors or nearby communities and in the Jutaí city, but most people declared selling exclusively in the city (Table 1). For those selling in the city, most declared selling in only one single place within the city (n = 11), five interviewees declared selling wild meat in two places, five others in three places, and one in four places. Localities where wild meat was sold in urban centers were in most cases houses of relatives in the city (n = 14), followed by direct trade at the Jutaí city quay (n = 9), to intermediaries (n = 7), delivered directly to peoples' houses who pre-order wild meat (n = 7), or directly to consumers in local fairs (n = 3). Similar to the results for the frequency of wild meat consumption, the probability of selling wild meat increased with the number of hunters in the household; households with more than three hunters had ~100% of probability of selling wild meat (Figure 4). However, this probability was not related to the number of people in the household nor with the time of residency in the community.

Wild meat was sold at an average price of 5.6 ± 4.2 USD/kg (6.0 ± 4.4 USD/kg in cities and 4.6 ± 3.5 USD/kg in the communities). Fifteen taxa were recorded as sold; the number of taxa sold in the city being greater than in the communities (14 [n = 134 citations] vs. 10 [n = 69 citations] taxa) (Table 4). The yellow-spotted river turtle was the most cited species sold in the city, while the tapir was the most cited species traded between neighbors and with nearby communities. The most expensive taxa were the yellow-spotted river turtle and the curassow, independent of their sale destination (Table 4). Price per kg was higher in the city than in the communities, and a U-shaped trend pattern described the relationship between prices and gross body mass of the sold taxa (Table 2; Figure 5).

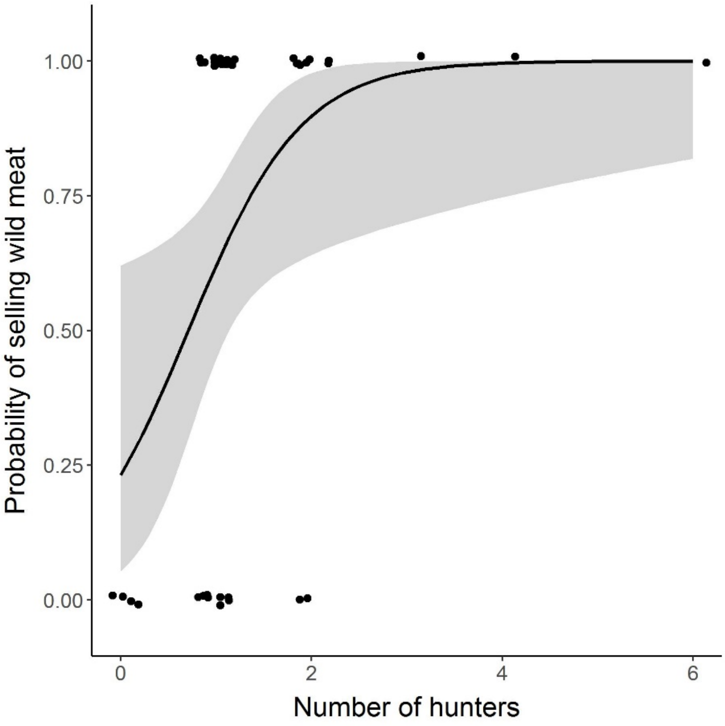


Figure 4. Probability of people selling wild meat on the Jutaí River according to the number of hunters living in the household. Gray shaded area represents the 95% confidence interval.

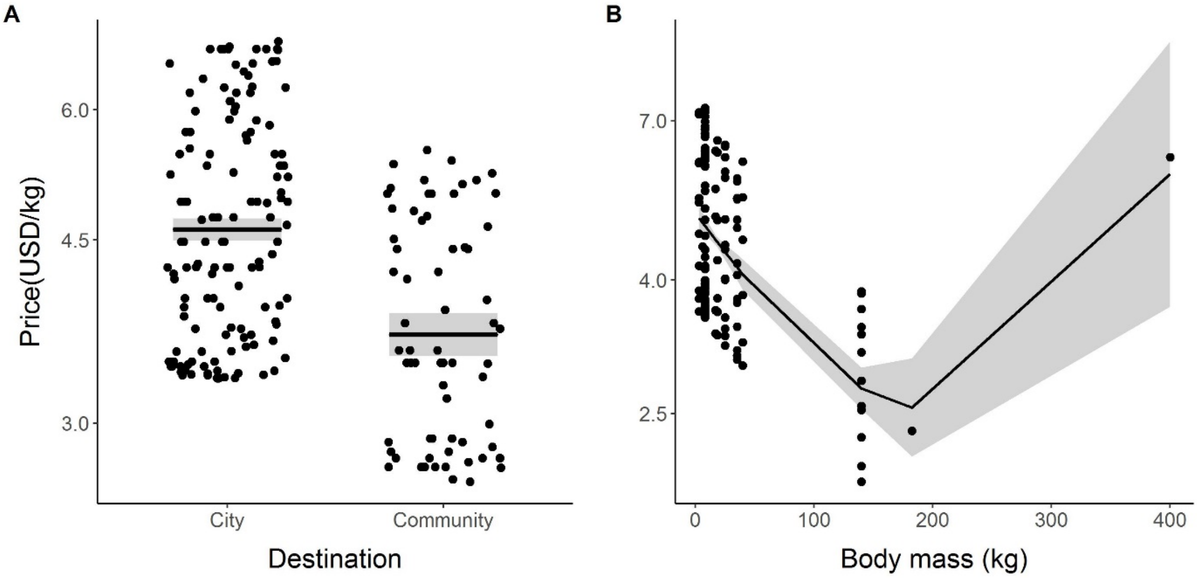


Figure 5. Price of wild meat (in USD/kg) on the Jutaí River according to (A) destination of the product (whether bounded to urban markets or traded within and between rural communities) and (B) body mass of the species. Gray shaded area represents the 95% confidence interval. The points are normalized residuals plotted on a log-transformed (ln) y-axis.

Table 4. Details of game species cited as sold and the prices applied in the city and within/between rural communities on the Jutaí River basin, central Amazonia. Taxa names are ordered according to the total number of citations as sold.

Taxa	**N of citations as sold in the city (%)**	**N of citations as sold in the communities (%)**	**Price in the city (USD/kg ± SD)**	**Price in the communities (USD/kg ± SD)**
Lowland paca (*Cuniculus paca*)	29 (21.6)	10 (14.5)	2.77 (0.63)	2.85 (1.32)
Yellow-spotted river turtle (*Podocnemis unifilis*)	30 (22.4)	6 (8.7)	13.84 (4.84)	9.14 (2.73)
White-lipped peccary (*Tayassu pecari*)	20 (14.9)	15 (21.7)	3.58 (0.68)	2.84 (0.61)
South American tapir (*Tapirus terrestris*)	14 (10.4)	18 (26.1)	3.54 (0.55)	2.77 (0.45)
Collared peccary (*Pecari tajacu*)	11 (8.2)	10 (14.5)	3.35 (0.67)	2.57 (0.66)
Brocket deer (*Mazama* spp.)	3 (2.2)	4 (5.8)	2.9 (1.02)	2.68 (0.48)
Yellow-footed tortoise (*Chelonoidis denticulatus*)	5 (3.7)	1 (1.4)	5.21 (1.66)	3.72 (0)
Razor-billed curassow (*Mitu tuberosum*)	4 (3.0)	2 (2.9)	14.79 (4.21)	12.83 (0.79)
South American Giant river turtle (*Podocnemis expansa*)	6 (4.5)	0 (0)	11.57 (4.41)	-
Big-headed Amazon river turtle (*Peltocephalus dumerilianus*)	3 (2.2)	2 (2.9)	4.71 (1.24)	4.1 (1.16)
Six-tubercled river turtle (*Podocnemis sextuberculata*)	5 (3.7)	0 (0)	4.85 (3.41)	-
Caimans (Family Alligatoridae)	2 (1.5)	0 (0)	1.12 (0)	-
Black agouti (*Dasyprocta fuliginosa*)	0 (0)	1 (1.4)	-	2.23 (0)
Red howler monkey (*Allouata juara*)	1 (0.7)	0 (0)	3.28 (0)	-
Amazonian manatee (*Trichechus inunguis*)	1 (0.7)	0 (0)	8.93 (0)	-
Total/Average	134 (100)	69 (100)	6.03 ± 4.40	4.57 ± 3.53

2.5 Discussion

Our results show that the use of wild meat as food and income in the Jutaí River basin is widespread, and most wild meat was obtained directly by hunters in the families. Amazonian communities further away from urban markets are known to consume larger amounts of wild meat than those having access to other meats in closer city markets (Chaves et al. 2017). Given that the communities in the Jutaí River basin are around 92 km from the nearest urban center, where markets selling domestic meats are found, and are not culturally used to raise domestic animals, access to urban goods, especially domestic meats, is limited. Although we did not quantify this, according to informal reports, inhabitants of the Jutaí River basin travel to the city only once every two to three months. Thus, reliance on timber and non-timber forest products is the norm. In addition, the lack of access to reliable electricity supply still does not permit Jutaí River basin inhabitants to refrigerate domestic meat or perishable foods for long periods.

A high proportion of respondents received wild meat as gifts from neighbors. This is not unusual in many rural and traditional societies, reinforcing social bonds and improving food security among closely related people and relatives (see Gurven 2004). In Amazonian communities, there is a term called *vizinhar* that means sharing products with the neighbors, which is frequently used as reference for sharing wild meat (Lima 2009). The rules about *vizinhar*, such as which part or amount of the animal should be donated and to whom they should be donated, vary widely among societies (Almeida et al. 2002). For example, in Riozinho da Liberdade Extractive Reserve, in the Brazilian Amazon, half of all hunted wild meat was given to other village members (Nunes et al. 2019*b*). In the Ipaú-Anilzinho Extractive Reserve, also in the Brazilian Amazon, the killed animal is divided among the hunters that participated in the hunting event, but the hunter who shot it has preference over certain parts (Figueiredo and Barros 2016).

Wild meat was traded within and between our study communities. Buying wild meat from neighbors eliminates long periods spent hunting, time that can be dedicated to other income-generating activities, e.g., farming and fishing. In addition, when some communities purchase wild meat from others, it may actually alleviate pressure on game populations in their hunting zones. For wild meat traders, selling the product locally also requires lower investment in transport and meat preservation. Comparative information on the trade of wild meat within and between rural communities in the Amazon and other parts of the tropics is still scarce. However, some studies indicate that the amounts of wild meat sold inside communities can vary significantly. For instance, Coad et al. (2010) estimated that 18.5% of the overall wild meat offtake in a community in Gabon was sold within it. In another example, Morcatty and Valsecchi (2015) found that 31.4% of tortoises hunted in a community in Amazonia were sold within or between neighboring communities.

Van Vliet et al. (2015a) showed that some Amazonian urban hunters may supply urban markets with wild meat directly, but our study revealed that more than half of the interviewees living in rural areas of the Jutaí River basin sold wild meat exclusively to urban centers. This corroborates data from the Peruvian Amazon, which show that 6.5% of the total harvest in rural areas is sold in cities (Bodmer and Lozano 2001). In Amazonian cities, wild meat is commonly traded within local fairs but can also be sold from the hunters' or intermediaries' houses, in the streets, and at docks (Chaves et al. 2019; El Bizri et al. 2020). We showed the importance of hunters having links with people living in the city, since most interviewees declared that wild meat was sold from relatives' houses. This may be a means of avoiding detection and prosecution for selling wild meat. In other cities, strategies for selling wild meat differ in response to law enforcement and surveillance intensity by the authorities. For instance, in the Amazon tri-frontier region between Colombia-Brazil-Peru, hunters already use cell phones to inform their clients about the availability of wild meat and sell the product directly to their consumers, thus avoiding potential controls (van Vliet et al. 2015*b*). These strategies are so far effective, since information on wild meat trade in cities in Brazilian Amazonia indicates a lucrative wild meat market that, despite being forbidden by law in the country (Law No. 5197/1967), is worth over 35 million USD annually (El Bizri et al. 2020).

One important finding in our study was that the more hunters there were in a household, the higher the household frequency of consumption and amount of wild meat sold was. Cooperation among hunters, often close relatives (e.g., Alvard 2003), led to higher hunting success and return rates (e.g., Hitchcock et al. 1996; Alvard and Nolin 2002). In particular, more hunters in the household also means that large-sized species, such as peccaries and tapirs, which usually require several hunters, can be hunted. In addition, more hunters in a household may mean that the likelihood that at least one household member has ties to outside markets increases. It will likely also lead to increased skills and knowledge sharing about hunting, including those related to pathways and mechanisms for the sale of wild meat, enabling the persistence of the wild meat trade as a culturally acceptable practice in the region.

Since percentage citations of consumed taxa was related to the citations of favored taxa, this suggests that local perceptions on species' flavor is likely to play a crucial role in determining diet breadth in the Jutaí River basin (e.g., Renoux and de Thoisy 2016). For some groups, such as chelonians, however, they may be consumed less frequently despite being highly preferred. Chelonians are highly valued, appearing among the top hunted species throughout the Amazon (Peres 2000; Chaves et al. 2019; El Bizri et al. 2020), but their capture is highly seasonal and most of the yield is frequently traded instead of consumed (Pantoja-Lima et al. 2014; Morcatty and Valsecchi 2015). In addition, Amazonian freshwater turtles have historically been used since the eighteenth century as a food resource and to produce oil for cooking and lighting (Casal et al. 2013), leading to a severe decline in their populations (Smith 1979; Johns 1987). Therefore, the disproportionate percentage of citations of chelonians as consumed (only 4.3%), in comparison to the percentage citations of preference (23.1%), in this study may also reflect depletion in chelonian populations in the Jutaí River basin.

The relationship between price and taxa body mass was very similar to that found by El Bizri et al. (2020) for species sold in urban markets, reflecting that, when pricing species, hunters take into account a balance between prey profitability and yield (Rowcliffe et al. 2004). Smaller species are generally more abundant and easier to capture but are sold at a higher price per kilo because they yield less meat. Conversely, large-bodied species, such as the manatee (*Trichechus inunguis*), although more profitable in terms of meat obtained, are less abundant and difficult to capture, explaining the U-shaped curve in this relationship. Wild meat was less expensive when sold within rural communities than in urban centers. The same difference in prices between urban and rural sectors was observed by Morcatty and Valsecchi (2015) for the trade in yellow-footed tortoise (*Chelonoidis denticulatus*) meat in central Amazonia. However, the observed prices increased only by 24% from rural communities to urban centers, which probably reflects an additional amount to cover travel costs. Considering that urban inhabitants generally have a higher income and greater purchasing power than inhabitants from rural and weakly-monetized communities, the small difference in price might indicate that the wild meat in the Jutaí city is not a luxury item, i.e., only accessed by the wealthier class, as suggested for African cities (e.g., Fa et al. 2009).

Our results show that wild meat still plays a crucial role in societies that are considerably isolated from urban centers on the Jutaí River basin in central Amazonia, being used to guarantee both the subsistence and the economy of local people. A number of social and biological factors seems to be related to the consumption and trade of wild meat in the region, especially the number of hunters in the household, taste preferences, and species' body mass, and should be considered for designing any conservation strategy. Therefore, once we understand the livelihood, economic, and cultural value of wild meat consumption, it is possible to develop management programs that consider local peoples' needs and enhance the sustainable use of wild species.

Rushton et al. (2005) argued that, in rural areas of South America, wild meat could potentially be substituted by domestic meat, especially in Brazil, where there are high rates of livestock production, ultimately reducing the impacts of hunting. However, a complete transition from eating wild meat to exclusively eating beef in Amazonia would require the spending of around 90% of the total wages of local people and the conversion of large portions of Amazonian forests into pasture (Nunes et al. 2019*a*). Game species represent culturally important elements for Amazonian people, meaning that the depletion of their populations would affect not just their food security but erode the traditional knowledge and practices related to these animals (Tavares de Freitas et al. 2019). Therefore, considering the high level of isolation and dependence on wild meat of communities living in the Jutaí River basin, strategies for sustainably managing wildlife for consumption seems to be a better option than substituting wild meat for domestic meat. The largest-scale wildlife conservation program in the Brazilian Amazon is currently focused on river turtles, and for 30 years, this community-based program has been protecting river turtles' nesting beaches, guaranteeing an increase in the recruitment rate and subsequent population growth for the most historically depleted species, without banning egg consumption by local people (Eisemberg et al. 2019). Since 2007, Jutaí River Extractive Reserve is part of this program, supported by the governmental environmental agency, where the inhabitants released more than 10,000 freshwater turtle hatchlings in 2010 alone, helping to recover these species while guaranteeing the sustenance of local people (ICMBio 2011).

In terms of wild meat trade, a long history of extractive production to the market, under a debt-peonage system called *aviamento*, shaped the patterns of natural resource management and commerce in the Amazon (Almeida 2002; Lima 2009). After the decline of the Amazon rubber production, the domestic and international trade in animal hides replaced it (Antunes et al. 2016). However, during the 1960s, with the advent of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), trade has been more tightly regulated. More recently, the boom and growth of urban agglomerations and intensive migration from rural areas to urban centers increased the demand for wildlife products in Amazonian cities.

There is a consensus that commercial hunting for trade is more impactful to animal populations than subsistence hunting (Coad et al. 2019), but the current prohibition on wildlife commerce in the Amazon has been driving the establishment of hidden markets that hampers control. In urban areas, the replacement of the wild meat with domestic meat at a more affordable price is usually recommended (Rushton et al. 2005), but this strategy has been shown to be ineffective. For instance, a previous experiment conducted in an Amazonian city showed that access to discount coupons to buy chicken had not dissuaded people from consuming wild meat (Chaves et al. 2017). Instead, social marketing with information campaigns and community engagement on activities related to the reduction of wild meat consumption were more effective strategies (Chaves et al. 2017). We argue that this could be applied in the city of Jutaí and other Amazonian cities to reduce the demand for wild meat.

Experiences of wildlife management prove that community-based efforts, if appropriately implemented, provide an effective way to manage natural resources, especially where law enforcement is ineffective (Tavares de Freitas et al. 2019). Our results showed that households with three or more hunters were guaranteed to sell wild meat, so trade is an important source of income for those families. Therefore, regulating wild meat trade and bringing it into the formal economy instead of banning it could improve rural livelihoods, while maintaining the cultural importance of hunting for local people. A major example of this is the community-based management of the giant arapaima fish (*Arapaima gigas*) in the Amazon, which allowed the sustainable commercial exploitation of the species along with the recovery of its previously overharvested populations (Tavares de Freitas et al. 2019). Our results showed that most of the species consumed and traded by local people in the Jutaí River basin are not listed as threatened with extinction on the IUCN Red List. Therefore, this system could be applied for hunted game species that are more resilient, which are also generally more demanded by urban people, such as the paca (*Cuniculus paca*) and the collared peccary (*Pecari tajacu*) (El Bizri et al. 2020). A key first step would be revising national hunting laws in Brazil, since hunting and trade of wild meat still occupies an uncertain status in the legal framework of the country, even for traditional Amazonian populations depending on these activities to live (Antunes et al. 2019). By doing so, game species conservation with the maintenance of their ecosystem services could be aligned with the provision of food and income for local people in the Amazon.

2.6 Acknowledgments

We thank all local people from the Jutaí River Extractive Reserve for participating in this study and for kindly hosting us during our trip to the reserve. This work was supported by the grant agreement for Instituto de Desenvolvimento Sustentável Mamirauá of the Gordon and Betty Moore Foundation (number 5344) and the National Council for Scientific and Technological Development (CNPq) (grant numbers 300005/2013-0, 452908/2016-7, 201475/2017-0, 300346/2013-1 and 312729/2015-4). T. Q. Morcatty is supported by the WCS Graduate Scholarship Program, a program of the Wildlife Conservation Society and the Christensen Conservation Leaders Scholarship, and by the Wildlife Conservation Network Scholarship Program through the Sidney Byers Scholarship award.

2.7 References

Adams, C., Murrieta, R., Siqueira, A., Neves, W., Sanches, R. 2009. Bread of the land: The invisibility of manioc in the Amazon. In *Amazon peasant societies in a changing environment: political ecology, invisibility and modernity in the rainforest*, edited by C. Adams, R. Murrieta, W. A. Neves, and M. Harris, pp. 281–305. Springer, Dordrecht, Netherlands.

Almeida, M. W. B. 2002. The politics of Amazonian conservation: The struggles of rubber tappers. *The Journal of Latin American Anthropology* 7:170–219.

Almeida, M. W. B., Lima, E. C., Aquino, T. V., Iglesias, M. P. 2002. Parte IV: as atividades: caça. In *A enciclopédia da floresta. O alto Juruá: práticas e conhecimentos das populações*, edited by M. C. Cunha and M. W. B. Almeida, pp. 311–335. Companhia das Letras, São Paulo, Brazil.

Alvard, M. S. 2003. Kinship, lineage, and an evolutionary perspective on cooperative hunting groups in Indonesia. *Human Nature* 14:129–163.

Alvard, M. S., Nolin, D. A. 2002. Rousseau's whale hunt? Coordination among big-game hunters. *Current Anthropology* 43:533–559.

Antunes, A. P., Fewster, R. M., Venticinque, E. M., Peres, C. A., Levi, T., Rohe, F., Shepard Jr., G. H. 2016. Empty forest or empty rivers? A century of commercial hunting in Amazonia. *Science Advances* 2:e1600936.

Antunes, A. P., Rebêlo, G. H., Pezzuti, J. C. B., de Mattos Vieira, M. A. R., Constantino, P. D. A. L., Campos-Silva, J. V., Fonseca, R., Durigan, C. C., Ramos, R. M., Valsecchi, J., Pimenta, N. C., Ranzi, T. J. D., Lima, N. A. S., Shepard Jr., G. H. 2019. A conspiracy of silence: subsistence hunting rights in the Brazilian Amazon. *Land Use Policy* 84:1–11.

Benítez-López, A., Alkemade, R., Schipper, A. M., Ingram, D. J., Verweij, P. A., Eikelboom, J. A. J., Huijbregts, M. A. J. 2017. The impact of hunting on tropical mammal and bird populations. *Science* 356:180–183.

Bodmer, R. E., Lozano, E. P. 2001. Rural development and sustainable wildlife use in Peru. *Conservation Biology* 15:1163–1170.

Casal, A. C., Fornelino, M. M., Restrepo, M. F. G., Torres, M.A. C., Velasco, F. G. 2013. Uso histórico y actual de las tortugas charapa (*Podocnemis expansa*) y terecay (*Podocnemis unifilis*) en la Orinoquia y la Amazonia. *Biota Colombiana* 14:45–64.

Chaves, W. A., Wilkie, D. S., Monroe, M. C., Sieving, K. E. 2017. Market access and wild meat consumption in the central Amazon, Brazil. *Biological Conservation* 212:240–248.

Chaves, W. A., Monroe, M. C., Sieving, K. E. 2019. Wild meat trade and consumption in the central Amazon, Brazil. *Human Ecology* 47:733–746.

Coad, L., Abernethy, K., Balmford, A., Manica, A., Airey, L., Milner-Gulland, E. J. 2010. Distribution and use of income from bushmeat in a rural village, Central Gabon. *Conservation Biology* 24:1510–1518.

Coad, L., Fa, J. E., Abernethy, K., van Vliet, N., Santamaria, C., Wilkie, D., El Bizri, H., Ingram, D., Cawthorn, D.-M., Nasi., R. 2019. *Towards a sustainable, participatory and inclusive wild meat sector*. CIFOR, Bogor, Indonesia.

Eisemberg, C. C., Vogt, R. C., Balestra, R. A. M., Reynolds, S. J., Christian, K. A. 2019. Don't put all your eggs in one basket–lessons learned from the largest-scale and longest-term wildlife conservation program in the Amazon basin. *Biological Conservation* 238:108182.

El Bizri, H. R., Morcatty, T. Q., Valsecchi, J., Mayor, P., Ribeiro, J. E., Vasconcelos Neto, C. F., Oliveira, J. S., Furtado, K. M., Ferreira, U. C., Miranda, C. F., Silva, C. H., Lopes, V. L., Lopes, G. P., Florindo, C. C., Chagas, R. C., Nijman, V., Fa, J. E. 2020. Urban wild meat consumption and trade in central Amazonia. *Conservation Biology* 34:438–448.

Fa, J. E., Albrechtsen, L., Johnson, P. J., Macdonald, D. W. 2009. Linkages between household wealth, bushmeat and other animal protein consumption are not invariant: Evidence from Rio Muni, Equatorial Guinea. *Animal Conservation* 12:599–610.

Figueiredo, R. A. A., Barros, F. B. 2016. Caçar, preparar e comer o ‘bicho do mato’: Práticas alimentares entre os quilombolas na Reserva Extrativista Ipaú-Anilzinho (Pará). *Boletim do Museu Paraense Emílio Goeldi. Ciências Humanas* 11:691–713.

Fraser, J. A., Cardoso, T., Steward, A., Parry, L. 2018. Amazonian peasant livelihood differentiation as mutuality-market dialectics. *The Journal of Peasant Studies* 45:1382–1409.

García, J. B., Acosta, N. B., Olivares, L. V. 2004. Técnicas de preservación y factor de conversión de fauna silvestre en la región Loreto, Perú. In *Memorias del VI congreso internacional sobre el manejo de fauna silvestre en la Amazonía y Latinoamérica*, edited by R. Bodmer, pp. 427–433. Universidad Nacional de la Amazonía Peruana; Durrell Institute of Conservation and Ecology; and Wildlife Conservation Society, Iquitos, Peru.

Gurven, M. 2004. To give and to give not: The behavioral ecology of human food transfers. *Behavioral and Brain Sciences* 27:543–559.

Hernández, B., Hidalgo, M. C., Salazar-Laplace, M. E., Hess, S. 2007. Place attachment and place identity in natives and non-natives. *Journal of Environmental Psychology* 27:310–319.

Hitchcock, R. K., Yellen, J. E., Gelburd, D. J., Osborn, A. J., Crowell, A. L. 1996. Subsistence hunting and resource management among the Ju/'Hoansi of Northwestern Botswana. *African Study Monographs* 17:153–220.

ICMBio (Instituto Chico Mendes de Conservação da Biodiversidade). 2011. Plano de Manejo da Reserva Extrativista do Rio Jutaí. Tefé/AM. [online] URL: http://www.icmbio.gov.br/portal/unidadesdeconservacao/biomas-brasileiros/amazonia/unidades-de-conservacao-amazonia/512-resex-rio-jutai. Accessed on November 17, 2019.

IUCN. 2019. The IUCN Red List of Threatened Species. Version 2019-2. [online] URL: http://www.iucnredlist.org. Accessed on November 17, 2019.

Johns, A. D. 1987. Continuing problems for Amazon river turtles. *Oryx* 21:25–28.

Levi, T., Shepard Jr, G. H., Ohl-Schacherer, J., Peres, C. A., Douglas, W. Y. 2009. Modelling the long-term sustainability of indigenous hunting in Manu National Park, Peru: Landscape-scale management implications for Amazonia. *Journal of Applied Ecology* 46:804–814.

Lima, D. M. 2009. The domestic economy in Mamirauá, Tefé, Amazonas State. In *Amazon peasant societies in a changing environment: political ecology, invisibility and modernity in the rainforest,* edited by C. Adams, R. Murrieta, W. A. Neves, and M. Harris, pp. 131–156. Springer, Dordrecht, Netherlands.

Lima, D. M., Peralta, N. 2017. Developing sustainability in the Brazilian Amazon: Twenty years of history in the Mamirauá and Amanã Reserves. *Journal of Latin American Studies* 49:799–827.

Morcatty, T., Valsecchi, J. 2015. Social, biological, and environmental drivers of the hunting and trade of the endangered yellow-footed tortoise in the Amazon. *Ecology and Society* 20.

Nunes, A. V., Peres, C. A., Constantino, P. D. A. L., Santos, B. A., Fischer, E. 2019a. Irreplaceable socioeconomic value of wild meat extraction to local food security in rural Amazonia. *Biological Conservation* 236:171–179.

Nunes, A. V., Guariento, R. D., Santos, B. A., Fischer, E. 2019b. Wild meat sharing among non-indigenous people in the southwestern Amazon. *Behavioral Ecology and Sociobiology* 73:26.

Ojasti, J. 1996. *Wildlife utilization in Latin America: current situation and prospects for sustainable management*. FAO Conservation Guide 25. Food and Agriculture Organization, Rome, Italy.

Padoch, C., Brondizio, E., Costa, S., Pinedo-Vasquez, M., Sears, R. R., Siqueira, A. 2008. Urban forest and rural cities: multi-sited households, consumption patterns, and forest resources in Amazonia. *Ecology and Society* 13:2.

Pantoja-Lima, J., Aride, P. H., de Oliveira, A. T., Félix-Silva, D., Pezzuti, J. C., Rebêlo, G. H. 2014. Chain of commercialization of *Podocnemis* spp. turtles (Testudines: Podocnemididae) in the Purus River, Amazon Basin, Brazil: Current status and perspectives. *Journal of Ethnobiology and Ethnomedicine* 10:8.

Peres, C. A. 2000. Effects of subsistence hunting on vertebrate community structure in Amazonian forests. *Conservation Biology* 14:240–253.

Renoux, F., de Thoisy, B. 2016. Hunting management: the need to adjust predictive models to field observations. *Ethnobiology and Conservation* 5:1–13.

Ripple, W. J., Abernethy, K., Betts, M. G., Chapron, G., Dirzo, R., Galetti, M., Levi, T., Lindsey, P. A., Macdonald, D. W., Machovina, B., Newsome, T. M., Peres, C. A., Wallach, A. D., Wolf, C., Young, H. 2016. Bushmeat hunting and extinction risk to the world's mammals. *Royal Society Open Science* 3:160498.

Robinson, J. G., Redford, K. H. 1986. Body size, diet, and population density of Neotropical forest mammals. *The American Naturalist* 128:665–680.

Rowcliffe, J. M., de Merode, E., Cowlishaw, G. 2004. Do wildlife laws work? Species protection and the application of a prey choice model to poaching decisions. *Proceedings of the Royal Society of London B: Biological Sciences* 271:2631–2636.

Rushton, J., Viscarra, R., Viscarra, C., Basset, F., Baptista, R., Brown, D. 2005. *How important is bushmeat consumption in South America: Now and in the future*. ODI Wildlife Policy Briefing, Number 11, ODI, United Kingdom.

Sarti, F. M., Adams, C., Morsello, C., van Vliet, N., Schor, T., Yagüe, B., Tellez, L., Quiceno-Mesa, M., Cruz, D. 2015. Beyond protein intake: bushmeat as source of micronutrients in the Amazon. *Ecology and Society* 20:22.

Smith, N. J. 1979. Aquatic turtles of Amazonia: an endangered resource. *Biological Conservation* 16:165–176.

Tavares de Freitas, C., Macedo Lopes, P. F., Campos-Silva, J. V., Noble, M. M., Dyball, R., Peres, C. A. 2019. Co-management of culturally important species: a tool to promote biodiversity conservation and human well-being. *People and Nature* 2:61–81.

van Vliet, N., Nasi, R. 2008. Hunting for livelihood in Northeast Gabon: patterns, evolution, and sustainability. *Ecology and Society* 13:33.

van Vliet, N., Cruz, D., Quiceno-Mesa, M. P., Neves de Aquino, L. J., Moreno, J., Ribeiro, R., Fa, J. E. 2015a. Ride, shoot, and call: wildlife use among contemporary urban hunters in Três Fronteiras, Brazilian Amazon. *Ecology and Society* 20:8.

van Vliet, N., Quiceno, M. P., Cruz, D., Neves de Aquino, L. J., Yagüe, B., Schor, T., Hernandez, S., Nasi, R. 2015b. Bushmeat networks link the forest to urban areas in the trifrontier Region between Brazil, Colombia, and Peru. *Ecology and Society* 20:21.

Walker, A. J., Ryan, R. L. 2008. Place attachment and landscape preservation in rural New England: a Maine case study. *Landscape and Urban Planning* 86:141–152.

Chapter 3. Urban wild meat consumption and trade in central Amazonia

Published in *Conservation Biology*

El Bizri, H. R., Morcatty, T. Q., Valsecchi, J., Mayor, P., Ribeiro, J. E., Vasconcelos Neto, C. F., Oliveira, J. S., Furtado, K. M., Ferreira, U. C., Miranda, C. F. S., Silva, C. H., Lopes, V. L., Lopes, G. P., Florindo, C. C. F., Chagas, R. C., Nijman, V., & Fa, J. E. (2020). Urban wild meat consumption and trade in central Amazonia. *Conservation Biology*, *34*(2), 438-448. DOI: 10.1111/cobi.13420.

3.1 Abstract

The switch from hunting wild meat for home consumption to supplying more lucrative city markets in Amazonia can adversely affect some game species. Despite this, information on the amounts of wild meat eaten in Amazonian cities is still limited. We estimated wild meat consumption rates in 5 cities in the State of Amazonas in Brazil through 1,046 door-to-door household interviews conducted from 2004 to 2012. With these data, we modeled the relationship between wild meat use and a selection of socioeconomic indices. We then scaled up our model to determine the amounts of wild meat likely to be consumed annually in the 62 urban centers in central Amazonia. A total of 80.3% of all interviewees reported consuming wild meat during an average of 29.3 (CI 11.6) days per year. Most wild meat was reported as bought in local markets (80.1%) or hunted by a family member (14.9%). Twenty-one taxa were cited as consumed, mostly mammals (71.6%), followed by reptiles (23.2%) and

then birds (5.2%). The declared frequency of wild meat consumption was positively correlated with the proportion of rural population as well as with the per capita gross domestic product of the municipality (administrative divisions) where the cities were seated. We estimated that as much as 10,691 t of wild meat might be consumed annually in the 62 urban centers within central Amazonia, the equivalent of 6.49 kg per person per year. In monetary terms, this amounts to US$21.72 per person per year or US$35.1 million overall, the latter figure is comparable to fish and timber production in the region. Given this magnitude of wild meat trade in central Amazonia, it is fundamental to integrate this activity into the formal economy and actively develop policies that allow the trade of more resilient taxa and restrict trade in species sensitive to hunting.

3.2 Introduction

Wild meat contributes to the diet of millions of people worldwide, making up 20-70% of all protein intake, particularly in isolated tropical forest regions, where domestic meat is scarce (Coad et al. 2019). Increased urbanization within the tropics has resulted in a greater demand for wild meat from cities and large towns; these population centers are supplied from the rural areas where wildlife occur. Thus, many rural peoples have shifted from being strictly traditional subsistence hunters to selling wild meat in cities (e.g., Dounias 2016). Whilst the sale of wild meat provides an important income source for many, uncontrolled trade to large urban markets is a conservation problem in many tropical countries (Nasi et al. 2011).

Until recently, the only published references to urban wild meat consumption in the Amazon were from studies in 1 city, Iquitos, in Peru (Bodmer and Lozano 2001). Based on this, urban wild meat consumption in

Amazonia was regarded for some time as negligible (Rushton et al. 2005; Nasi et al. 2011). However, recent studies suggest there are significant city markets in the region where a large number of wild animals are sold for human consumption. For example, well-established wild-meat markets exist in Abaetuba, Brazilian Amazon (Baía-Júnior et al. 2010), and in 2 prefrontier cities in southern Brazilian Amazonia, where around 80% of interviewed households regularly consumed wild meat (Parry et al. 2014). About 473 t of wild meat were estimated as traded annually in cities in the Amazonian trifrontier (Brazil, Colombia, and Peru) (van Vliet et al. 2014).

Because most of these studies are descriptive, restricted to relatively short sampling periods, and on a local scale, there is still a need to determine the levels of wild meat use and the volumes traded in Amazonian cities in much larger areas. Although factors affecting wild meat consumption and trade in African cities are relatively well known (Fa et al. 2009), these are still largely undescribed for Amazonia. A few studies have been conducted on how the economic and cultural background of consumers in Amazonian cities can affect how much wild meat is eaten (Morsello et al. 2015; Chaves et al. 2017); however, studies that can predict the volume of wild meat consumed in urban centers at a regional level are still absent.

We estimated wild meat consumption rates in five cities in the State of Amazonas in Brazil. From these data, we developed statistical models to determine the relationship between wild meat use and a number of socioeconomic indices obtained from government sources and scaled up our model to estimate the amounts of wild meat likely to be consumed annually in urban centers throughout central Amazonia, an area representing about one-third of the entire Amazon biome. We also calculated the monetary value of the wild meat trade in this region. The results of our study can be useful to understand the extent of urban demand for wild meat in the Amazon as a whole and generate insights that may inform conservation efforts and policies to ensure the sustainable use of wildlife.

3.3 Methods

3.3.1 Study sites

This study was conducted in Amazonas state, the largest state by area in Brazil (1,571,000 km²). The state is almost entirely covered by moist broadleaf forest and encompasses about 29% of the Amazon Basin.

Brazilian states are divided into administrative municipalities that contain natural areas and urban and rural human settlements. Each municipality has a city that is the seat of the area's administration; these seat cities are not specified in law according to a minimum population size, area, or facilities. Amazonas state contains 62 municipalities with around 3.4 million inhabitants, of which around 2.7 million (79.4%) live in cities (IBGE 2018).

Because most cities in the state are far apart, accessible after long hours of travel by boat or plane, we chose those closest to our main research base in Tefé. Among these more accessible cities, we selected those within municipalities that would be representative of the range of socioeconomic variables we wanted to consider: rural and urban human population, human development index (HDI), and gross domestic product (GDP). We sampled households in the seat cities of five municipalities: Alvarães (14,080 inhabitants) and Tefé (61,399 inhabitants), at the confluence of the Tefé and Solimões Rivers; Coari (75,909 inhabitants), between the Urucu and Solimões Rivers; Maraã (17,364 inhabitants) on the lower Japurá River; and Fonte Boa (22,659 inhabitants) on the Solimões River (Table 1; Figure 1). The economy of these municipalities is based around small-scale industries and farming (IBGE 2018).

3.3.2 Data collection

Data on wild meat consumption and trade were obtained through household surveys conducted from April 2004 to May 2012 (Table 1). Depending on the time available for research in each city, we randomly selected at least 50% of neighborhoods within which we had a minimum of 2 interviews per neighborhood (Table 1). We asked heads of households (women and men) the following questions: is wild meat consumed in the house (*yes* or *no* response), how often is wild meat consumed (number of days per week, month, or year), which species are eaten, how is the consumed wild meat obtained (hunting, buying, or as a gift), if purchased, where is it purchased, and what price is paid for each species and what is the selling unit (e.g., kilograms, entire animal or half the animal specimen).

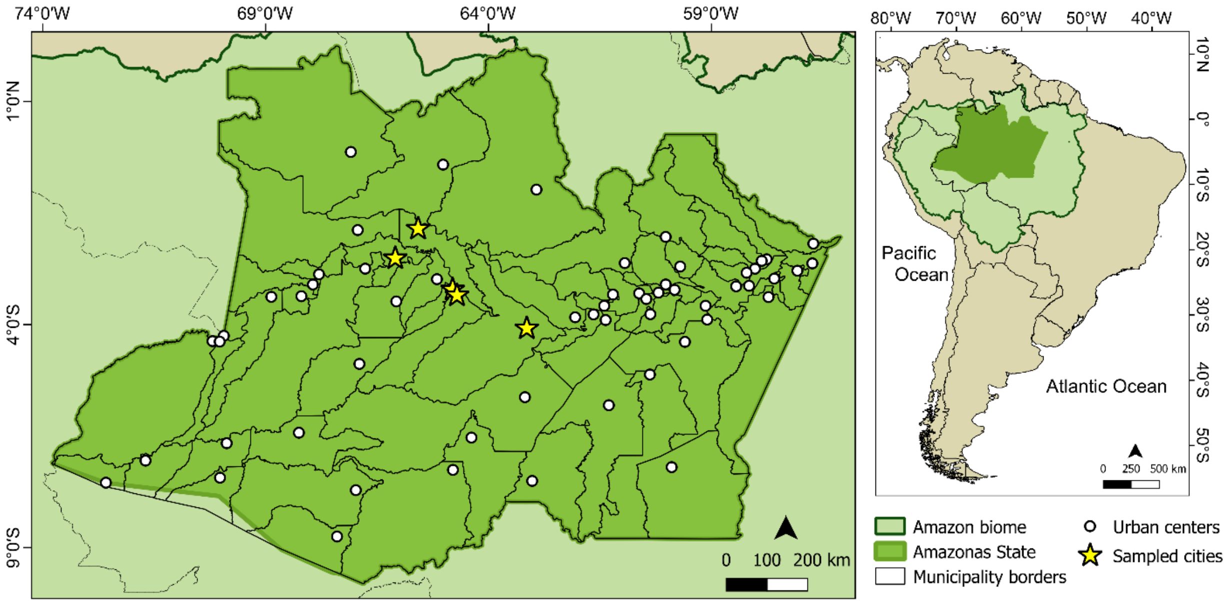


Figure 1. A map portraying the location of the sampled cities within central Amazonia (state of Amazonas).

Although urban consumption and trade of wildlife is forbidden by law in Brazil (Law 5.197/1967) (Antunes et al. 2019), local wildlife management authorities tend to persecute hunters and traders, not consumers. Therefore, consumers do not perceive they are acting illegally and do not fear persecution. Given this, we did not use indirect questioning methods; rather, we applied direct questioning, as used in previous studies of wild meat consumption in the region (e.g., Parry et al. 2014; van Vliet et al. 2015; Chaves et al. 2017). Participants were made comfortable with our interview process by informing them of the study aims prior to the interview. Respondents were free to participate in the study and were informed that we would not disclose their identity. Of a total 1085 visited households, 96.4% (1,046 households) agreed to be interviewed, an indication that most people felt comfortable participating (Table 1). We followed the Guidelines for Applying Free, Prior and Informed Consent in Buppert and McKeehan (2013).

Table 1. Details of cities in Amazonas state where surveys on wild meat consumption were conducted. *Based on the last survey carried out in 2010 by the Brazilian government (IBGE 2018).

City	Coordinates	Area (km^2)	Total inhabitants, urban inhabitants	Population density (ind/km^2)*	Temporal range of interviews	Households interviewed (%)	No. of neighborhoods (no. interviewed)
Alvarães	03º 13' 15" S, 64º 48' 15" W	5,923.46	14,080 (7,878; 55.95)	2.38	Jul - Aug 2007	153 (11.2)	5 (5)
Coari	04º 05' 06" S, 63º 08' 29" W	116,572.71	75,909, (49,638; 65.4)	1.31	Oct 2011 – May 2012	60 (0.6)	15 (8)
Fonte Boa	02º 30' 50" S, 66º 05' 30" W	116,572.71	22,659 (15,039; 66.37)	1.86	Nov 2011	20 (0.7)	10 (6)
Maraã	01º 51' 22" S, 65º 34' 52" W	116,572.71	17,364 (8,759; 50.44)	1.03	Oct 2011	22 (1.6)	8 (8)
Tefé	03º 21' 15" S, 64º 42' 41" W	116,572.71	61,399 (50,072; 81.55)	2.59	Apr – Nov 2004 Aug 2005 – Mar 2006	791 (7.9)	20 (17)
Total	-	116,572.71	191,411	-	-	1,046	58 (44)

3.3.3 Data analyses

The overall amount of wild meat consumed (*B*) in each city was estimated using the following formula:

$$B = F_c * P_c * D_c$$

where F_c is the mean frequency of consumption reported by the interviewees expressed as the number of days wild meat was consumed per person per year and P_c the total potential consumers in the city based on the percentage of informants declaring that they consumed wild meat in our survey multiplied by the number of urban inhabitants. Because actual daily amounts of wild meat consumed by Amazonian urban dwellers is not currently available, we used 0.18 kg/person/day (CI 0.07) (obtained from a study of 13 indigenous communities [Ojasti 1996]) as an average amount of wild meat consumed per person per day (D_c).

For each city, we estimated the amount of meat consumed of each taxon by using the percentage of times the taxon was mentioned (hereafter referred to as citations) from the overall amount of wild meat consumed (*B*). We estimated the number of individuals consumed per taxon per year by dividing the estimated biomass consumed of each taxon by the body mass of eviscerated specimens of the species (García et al. 2004).

All taxa were classified according to the International Union for Conservation of Nature (IUCN) Red List threat categories (vulnerable; endangered; critically endangered) (IUCN 2018). If the local names provided by informants did not allow an unequivocal classification to species, we used genus or family.

We calculated the average selling price for each taxon by adjusting for the inflation rate for the different years during which each city was sampled based on the General Price Index for Brazil estimated by the Getúlio Vargas Foundation. We used the exchange rate for 1 June 2018 to convert Brazilian reais (R$) into US dollars (R$3.85 = US$1.00). Hereafter all monetary units are U.S. dollars.

We built generalized additive models for location, scale, and shape (GAMLSS) to assess drivers of the three response variables: frequency of consumption (reported number of days of wild meat consumption per year), taxa citations, and price per kilogram. As predictor variables, we used socioeconomic indices compiled by the Brazilian Government for each municipality (IBGE 2018): total population (number of inhabitants), percent rural population (rural population/total population), HDI, and the per capita GDP in dollars per individual. Data from 2010 was used as reference for the first three variables because no information was available for the specific years when our interview data were collected. Per capita GDP values were available for each sampling year. We considered the gross body mass (non-eviscerated weight in kilograms) and habitat type (terrestrial, arboreal, and aquatic) for each taxon as biological drivers for the models in relation to the taxa citations and price per kilogram. We also included taxa as a random factor due to differences in the number of citations among cities and the price per kilogram as a predictor variable for the taxa citations. Gross body mass of all mentioned species was obtained from García et al. (2004) and Robinson and Redford (1986). To avoid overestimating the number of people consuming wild meat due to low sample sizes in some cities, we calculated the potential number of consumers (P_c) by using the same variables of the municipalities as predictors in a logistic regression (Appendix S1).

To build the models, we tested combinations of predictor variables in linear and nonlinear forms with different distribution families. We checked for collinearity among variables. Because the percentage of rural population was negatively correlated with the total population (r^2=0.99) and HDI (r^2=0.94), these variables were never included in the same models and were tested separately. Final models were selected based on the Akaike information criteria (AIC); all models with good support were those with ΔAIC values <2 in relation to the model with the smallest AIC. In cases when more than one model was a best fit, we selected the model with the smaller number of parameters.

Based on our best-fit models and variables, we used the function gamlss.predict to predict the current frequency of wild meat consumption, the amount of consumed wild meat (corrected by the percentage of consumers among urban dwellers), and the monetary value generated by wild meat for the entire central Amazonia region, and calculated these parameters for all 62 cities in the Amazonas state with the most updated values for the predictor variables available from the government statistics. We used R version 3.3.3 (http://www.R-project.org/) and the gamlss R-package for generalized linear and additive mixed models and predictions and GGally R-package for the collinearity test. For the variables effects, we assumed significance when p <0.05.

3.4 Results

Sampled municipalities were representative of the 62 municipalities in the state of Amazonas. Average per capita GDP ($2,835.34 [SD 2,540.01]) and average percentage rural population (36.06% [SD 11.88]) in our five sampled municipalities were not statistically different from the averages for the remaining

57 municipalities (average GDP $2,463.56 [SD 1396.36], t = 0.53, df = 60, p = 0.65; rural population $44.95 [SD 14.30], t = 1.45, df = 60, p = 0.15).

3.4.1 Consumption and procurement of wild meat

All interviewees in Maraã (20/20) and Fonte Boa (22/22), 90.8% (139/153) in Alvarães, 85.0% in Coari (51/60), and 76.9% (608/791) in Tefé declared consuming wild meat; overall average was 80.3% (Table 2). Respondents declared consuming wild meat during 29.3 (CI 11.6) days per year (Table 2). An average of 80.1% of interviewees reported buying wild meat, and 14.9% of consumers reported hunting wildlife (Table 3). The estimated mean annual wild meat biomass consumed per capita was 4.60 kg/person/y (SD 1.87), a total of 500,497.56 kg (CI 203 - 254.42).

Table 2. Details on the estimated consumption of wild meat in 5 cities in central Amazonia.

City	No. that consumed wild meat (%)		No. of potential consumers (%)[a]	Average frequency of consumption (CI) (days person^{-1} year^{-1})	Overall wild meat consumption (CI range) (kg year^{-1})[b]	Per capita urban wild meat consumption (CI range) (kg person^{-1} year^{-1})
	yes	no				
Alvarães	139 (90.8)	14 (8.2)	7,258.81 (92.1)	32.83 (11.07)	41,887 (24,876 - 58,897)	5.32 (3.16 - 7.48)
Coari	51 (85.0)	9 (15.0)	43,715.73 (88.1)	29.33 (5.70)	225,546 (133,951 - 317,141)	4.54 (2.70 - 6.39)
Fonte Boa	20 (100.0)	0 (0)	13,167.44 (87.6)	24.77 (12.58)	57,383 (34,079 - 80,686)	3.82 (2.27 - 5.37)
Maraã	22 (100.0)	0 (0)	8,223.41 (93.9)	42.67 (26.04)	61,713 (36,651 - 86,775)	7.05 (4.18 - 9.91)
Tefé	608 (76.9)	183 (23.1)	38,545.36 (77.0)	16.81 (2.51)	113,969 (67,686 - 160,252)	2.28 (1.35 - 3.20)
Total	840 (80.3)	206 (19.7)	110,910.75	29.28 (11.58)	500,498 (297,243 - 703,752)	4.60 (2.73 - 6.47)

[a] Calculated with logistic regressions to obtain the likely percentage of people consuming wild meat within the entire population of each city (see Appendix S1). [b] Calculated by summing average wild meat amount.

3.4.2 Taxa consumed

Twenty-one taxa were mentioned as eaten by respondents. As many as 40% (6 of 15) of the taxa identified to species are threatened with extinction (Appendix S2). Among the 2,067 citations, mammals were the predominant group (n=1,480, 71.6%), followed by reptiles (n=479, 23.2%) and birds (n=108, 5.2%). In terms of biomass, the white-lipped peccary (*Tayassu pecari*) (37,955.30 kg), the tapir (*Tapirus terrestris*) (23,362.72 kg), the lowland paca (*Cuniculus paca*) (21,303.39 kg), and the yellow-spotted river turtle (*P. unifilis*) (10,840.29 kg) were the most representative, making up together 67% of the total (Figure 2). A total of 95,772 (CI 38,893) animals were estimated as consumed annually; four species, *P. sextuberculata*, *P. unifilis*, agouti (*Dasyprocta fuliginosa*), and *C. paca*, represented 76.6% of this total (Appendix S2).

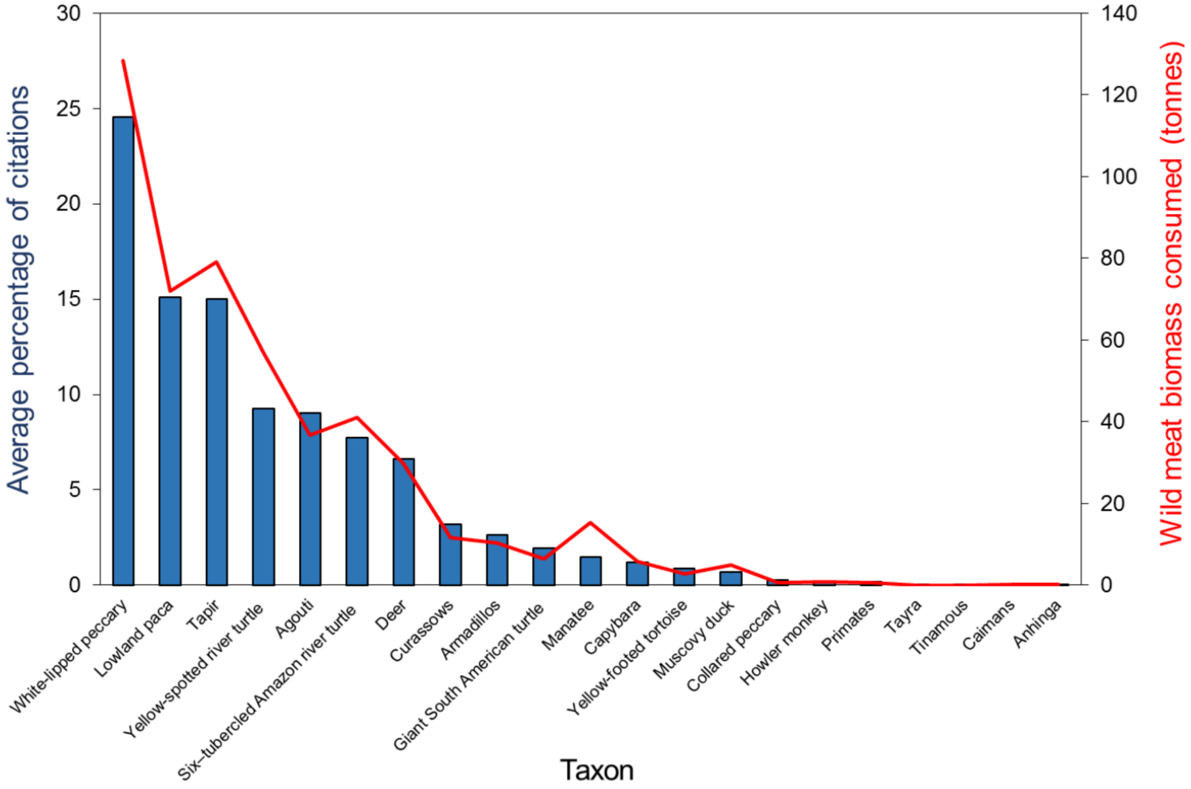


Figure 2. Average percentage of citations (bars) and overall wild meat biomass estimated as consumed (line) per taxon in 5 cities in central Amazonia. Scientific names are in Appendix S2.

3.4.3 Traded biomass

Of the total biomass estimated as consumed, 403,311 kg (80.6%) were estimated as purchased in urban markets. People declared they usually bought wild meat in only 1 place (n=605, 94.4%), although some informants declared buying in two (n=27, 4.2%) or three different places (n=9, 1.4%). Informants reported that wild meat is mainly obtained at local fairs (n=313, 46.1%), followed by hawkers (n=208, 30.2%), private residences (n=69, 9.2%), directly in rural communities (n=63, 9.3%), and from riverboats (n=33, 5.2%).

Table 3. Declared means by which urban consumers obtained wild meat in 5 cities in central Amazonia.

City	No. buying (%)	No. hunting (%)	No. buying or hunting (%)	No. receiving gifts (%)	Total
Alvarães	100 (75.8)	18 (13.6)	14 (10.6)	0 (0.0)	132
Coari	42 (82.4)	4 (7.8)	3 (5.9)	2 (3.9)	51
Fonte Boa	16 (80.0)	4 (20.0)	0 (0.0)	0 (0.0)	20
Maraã	19 (86.4)	2 (9.1)	1 (4.5)	0 (0.0)	22
Tefé	463 (75.9)	146 (23.9)	0 (0.0)	1 (0.2)	610
Total (average %)	640 (80.1)	174 (14.9)	18 (4.2)	3 (0.8)	834

Information on prices was reported by informants for 17 taxa: mean price was \$3.82/kg (SD 1.60). The sale of these taxa was estimated to generate \$1,522,412/year (CI 240,919). The commercialization of four taxa alone, two chelonians (*P. unifilis* and *P. sextuberculata*) and two mammals (*T. pecari* and *T. terrestris*), were responsible for 68.9% of this amount. Curassows (mean price \$8.39/kg) and the three freshwater turtles (mean prices \$7.67/kg for *P.*

unifilis: \$6.49/kg for *P. sextuberculata*; \$6.01/kg for *P. expansa*) were the most expensive taxa (Appendix S3).

3.4.4 Drivers of and overall wild meat consumption in central Amazonia

The reported frequency of wild meat consumption per person increased significantly relative to the percent rural population in the municipality (2.504e-02 [SE 5.597e-03], t=4.4, p <0.001) (Figure 3a) and as per capita GDP increased (1.393e-04 [SE: 1.573e-08], t=8855.1, p<0.001) (Figure 3b). The gross body mass positively influenced the taxa citations (0.077 [SE 0.007], t=10.0, p< 0.001) (Figure 3c). Prices per kilogram presented a nonlinear relationship with the taxa's gross body mass (-0.001 [SE 0.0001], t=-10.7, p< 0.001) (Figure 3d) and increased as the percentage of rural population in the municipality increased (0.005 [SE 0.0005], t=8.7, p< 0.001) (Figure 3e).

Using the models obtained from these relationships, we estimated that 10,691,103 kg (CI 4,342,101) of wild meat was consumed annually in the 62 cities (2,755,756 urban inhabitants) within central Amazonia. This translates to a mean annual per capita consumption of 6.49 kg/person/year (CI 2.64) and amounts to a total monetary value of \$35,112,904/year (CI 14,260,811) (average of \$21.58 /person/year [CI 8.76]). The cities with the largest estimated amounts of wild meat consumed per year were along the western part of the state, and few were located in the central part of the Amazon River basin. The cities with a greater estimated per capita wild meat consumption were located along the northwestern portion of the state (Figure 4).

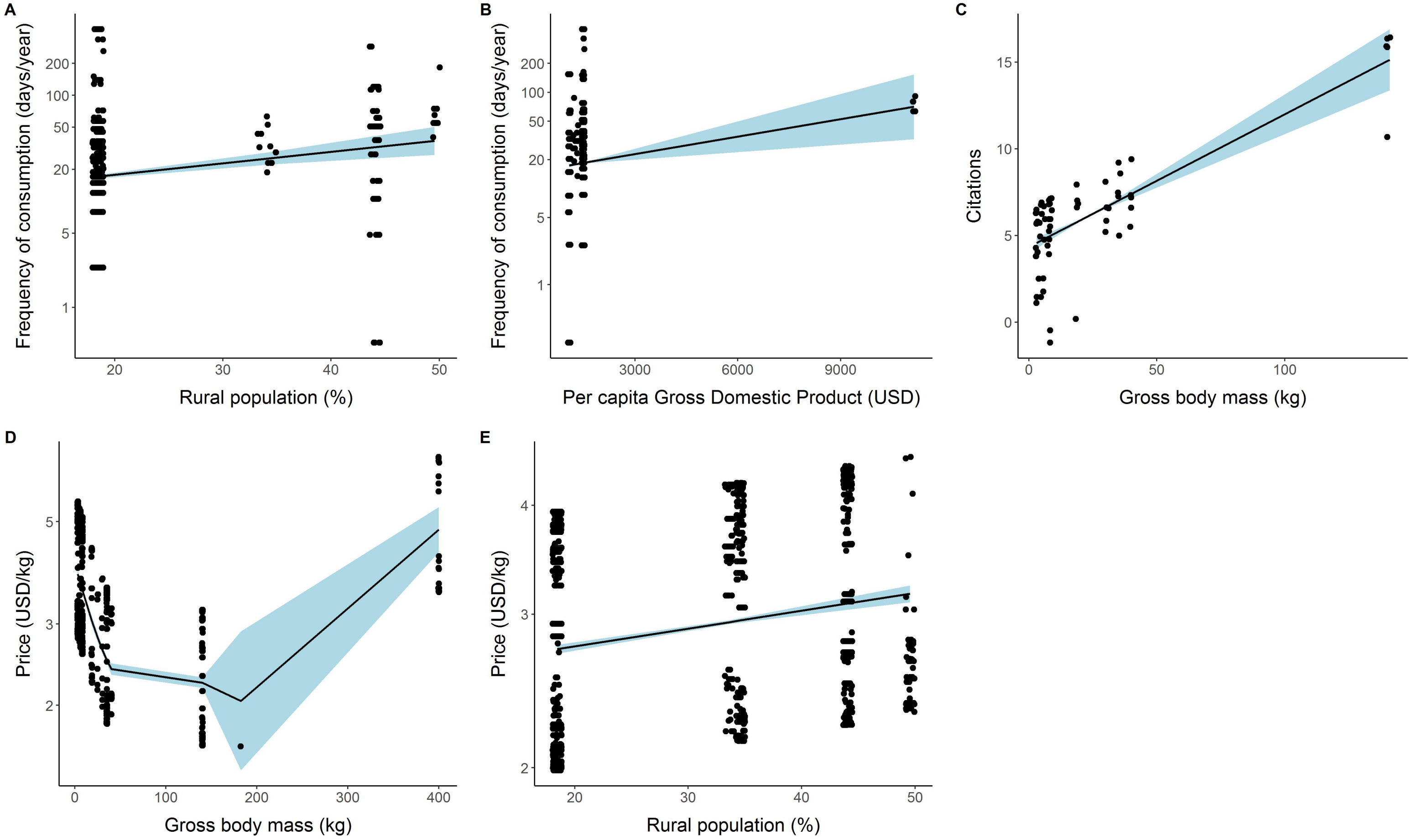


Figure 3. Relationships between (a) percentage of rural population and (b) per capita gross domestic product of the municipalities with the declared frequency of consumption of wild meat: between (c) gross body mass with the percentage of citations of each taxon and between (d) gross body mass and (e) percentage of rural population of the municipalities with the price of each taxon in 5 cities of central Amazonia. Only taxa cited in at least 3 cities were considered for the model (c). Blue shading, 95% CI; The points are normalized residuals, which are plotted on a log-transformed (ln) y-axis in graphs *a*, *b*, *d*, and *e*. Model details, such as families of distribution, link functions, and p values, are in Appendix S4.

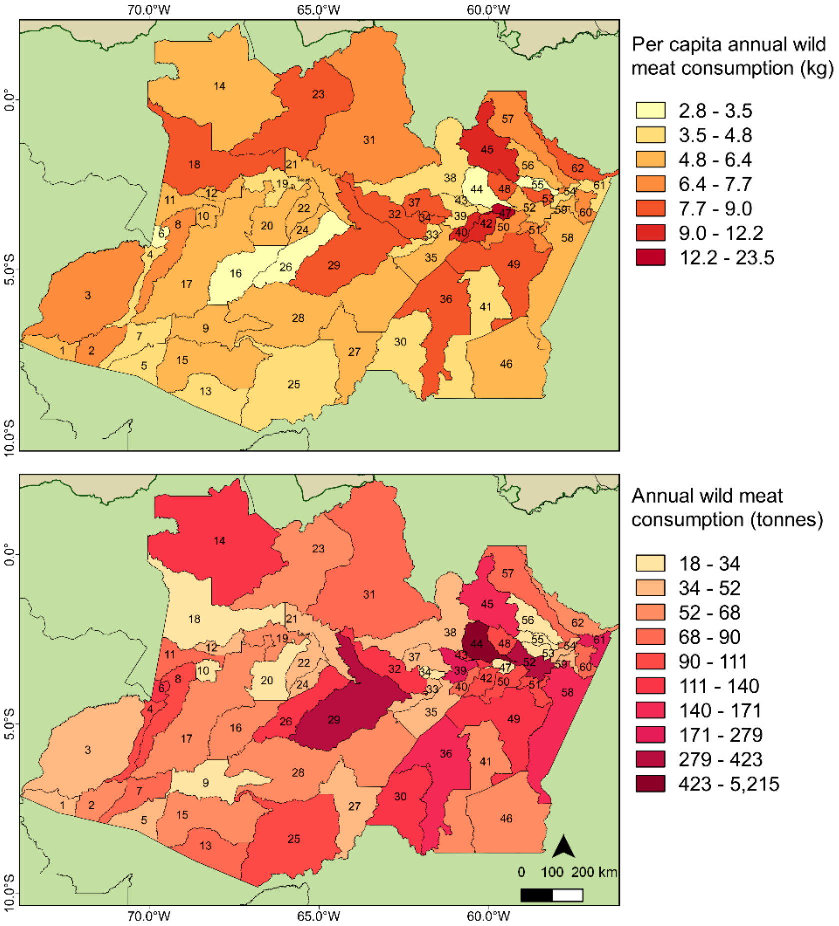


Figure 4. Two maps portraying the predicted per capita wild meat consumption (top) and annual amount of wild meat consumption (bottom) in the cities of 62 municipalities in central Amazonia. The municipalities surveyed for modeling were Alvarães (24), Coari (29), Fonte Boa (19), Maraã (21), and Tefé (26).

3.5 Discussion

A very large proportion of interviewees in our study reported eating wild meat, corresponding to one day of wild meat eaten for every 12.47 days consuming domestic meat in a year. These results correspond with Parry et al.'s (2014) study in the southern Brazilian Amazon, which shows that as many as 80% of the inhabitants consumed wild meat at least once per year.

Data on daily wild meat consumption in Amazonian urban centers are largely unavailable. The average per capita wild meat consumption we used to estimate overall consumption volumes is necessarily a working value only, but it is heuristically useful for estimating the amount of meat consumed in wild meat-based meals and for extrapolating to the entire study region. There is no doubt that more precise information on amounts consumed per individual or household in urban centers is required, and we suggest this should be a priority for future work.

We acknowledge that some respondents could have underreported how much wild meat they consumed. Because we did not apply indirect questioning techniques to determine the level of underreporting, our consumption estimates must be treated as a minimum. We also believe underreporting rates were probably similar among cities because sampled cities are culturally similar and under the same enforcement regimes.

Data collection for the different cities was spread out over seven years and data for some socioeconomic indices were not available for the same years of data collection. This may have affected our results because consumption rates and socioeconomic indices may have varied over time. In addition, the most recent values of socioeconomic statistics were not obtained at the same time by the government (last available GDP values are from 2016, whereas last census of population was conducted in 2010). However, temporal changes in the two variables (rural population, per capita GDP) we used varied differently. The GDP changed substantially over the short-term (i.e., some studied municipalities’ GDPs more than doubled from 2010 to 2016), whereas the proportion of rural population changed by only -1.0% on average from 2000 to 2010 (IBGE 2001). Despite these shortcomings, our estimation of 3.49 kg/person/year for Tabatinga, a city in the Brazil-Colombia-Peru frontier, was very similar to the 3.40 kg/person/year van Vliet et al. (2015) derived from direct observations at for the same site. In addition, our predicted per capita frequency of wild meat consumption for Tapauá (39.1 days/year) was also comparable to estimates of Chaves et al. (2017) (38.4 days/year) in the same city. We argue that, despite the limitation posed by the lack of some governmental statistics, these observations support the robustness of our model (Supporting Information).

Our results clearly showed that urban wild meat markets are well established in Amazonas state. In all surveyed cities, most interviewed urban dwellers reported buying wild meat, and most of them declared purchasing meat from the same salesmen, vendors in local fairs and hawkers, an indication of constancy in supply. Parry et al. (2014) show that the poorest urban households hunt to obtain wild meat, whereas wealthier residents buy wild meat. This is because hunting is the cheaper option for poorer people in cities, but also because the lack of formal employment, which is more common among this group, allows them to spend more time in this activity. Although we have not systematically collected data on this, some informants who declared hunting wild meat for consumption in our study informally declared selling part of their quarry. In the Amazonian cities of Benjamin Constant and Atalaia do Norte in Brazil, urban hunters profit from the sale of up to 97% of their game to closed markets (van Vliet et al. 2015). The low number of urban people declaring hunting wild meat shows that rural hunters supply city markets. Hunters from rural areas in Amazonia are mainly subsistence hunters, but may sell part of their hunting yields, likely to obtain money to buy urban goods, such as clothes and foods (Antunes et al. 2019). For instance, in the Peruvian Amazon, Bodmer and Lozano (2001) found that rural hunters sell around 7% of mammals hunted, whereas Morcatty and Valsecchi (2015) found that around 21% of yellow-footed tortoises (*Chelonoidis denticulatus*) harvested by rural hunters in Amazonia were traded in urban wild-meat markets.

The main groups (mammals and chelonians) and species cited as consumed and traded in our study cities were similar to those traded in other Amazonian localities (Bodmer and Lozano 2001; van Vliet et al. 2014). These species are commonly hunted for subsistence and trade by rural populations throughout Amazonia (e.g., Peres 2000; Lopes et al. 2012) and in other Neotropical regions (El Bizri et al. 2015). In particular, tapir and white-lipped peccary were among the top three species cited in our surveys. Both species are listed as vulnerable, following IUCN Red List criteria, and hunting is one of the main threats. Both species are declining in central Amazonia (Parry and Peres 2015). Other highly cited species, such as lowland paca, are also affected by hunting in Amazonia (e.g., Valsecchi et al. 2014; El Bizri et al. 2018), but are listed as least concern by IUCN.

In central Amazonia, governmental statistics for each municipality are useful to predict wild meat consumption at large scales. We found that the proportion of rural inhabitants within a municipality was correlated with the proportion of inhabitants that declared consuming wild meat in cities, the reported frequency of consumption, and the prices per kilogram in the market. This pattern may be a result of the economic connectivity between urban and rural sectors in these municipalities. Thus, in municipalities where the rural population is larger, urban people are able to buy wild meat more frequently from rural people who hunt. Because these small cities are often isolated and only accessible by boat, domestic and processed products become more expensive due to higher transportation costs. As a consequence, wild meat prices are higher in small cities, where rural inhabitants outnumber urban ones, because trading in wild meat is one of the most prevalent and cost-effective activities in localities where the sale of agricultural commodities do not have a large local market and are uncompetitive due to the high costs and long transportation times (Wilkie et al. 2016). Moreover, we argue that the price of the wild meat may also be anchored to the price of domestic meat or other important products for local inhabitants, such as oil.

The relationship between price and species' body mass reflects the fact that smaller species, although more abundant and easier to capture, are sold at a higher price because they yield less meat. Conversely, large-bodied species, although more profitable in terms of meat obtained, are less abundant and therefore more difficult to capture. This explains the U-shaped curve in this relationship and shows that hunters meeting urban demand do not kill prey randomly, but consider prey profitability when choosing which prey to kill and how to price it (Rowcliffe et al. 2004). Our results also indicated that larger species are generally more consumed than smaller species, and this relationship may be caused partially by price differences. However, considering that fewer game taxa were cited as consumed than in rural areas in Amazonia (e.g. 30 species [Vieira et al. 2015], 27 species [Kirkland et al .2018]), the range of species reaching urban markets may be limited by consumer taste and taboos.

Studies reporting the contribution of wild meat to local economies indicate a large informal sector, often as large as formal sectors, such as timber harvesting or agriculture (Lescuyer & Nasi 2016). Because wild meat trade in Brazil is prohibited, the harvest and selling of this product is excluded from official statistics. Nevertheless, the wild meat market was predicted to generate a great deal of money in central Amazonia ($35.1 million). Compared with other products, it is three times lower than mineral ($102.9million) production and similar to fish ($40.1 million) and timber production ($39.9 million) in the

Amazonas state (SEPLANCTI/DEPI 2018; ANM 2019). However, considering that a large proportion of these economic activities, including the wild meat trade, are carried out illegally, these numbers must be considered an underestimate. Most municipalities in the Amazonas state have >40% of their populations living on less than half minimum wage (IBGE 2018); thus, wild meat represents an important product for the income of several rural and urban families in the region. Hunters are not the only ones who generate income from wild meat; rather, several different actors involved in the commodity chain generate income for themselves. In Peru commercial hunters can supply wild meat directly to wholesalers, restaurants, or market traders, who in turn supply meat to the customers; price of the meat increases at each step (Fang et al. 2008). The same has been observed for the trade of tortoise meat in four cities in Amazonia, where intermediaries between hunters and urban vendors benefit significantly and obtain high profits (Morcatty et al. 2015). This highlights the necessity of finding solutions to regulate this sector in Amazonia and to reduce the impacts of wild meat trade in urban centers on Amazonian wildlife.

Our maps provide the first large-scale estimation of the amount of urban wild meat consumption for the Amazon, from which one may determine hotspots of wildlife extraction and where implementation of conservation strategies is more urgent. The high consumption rates of wild meat predicted for large cities, such as Coari and the capital Manaus, where there is an offer of domestic meat, signal that wild meat consumption is not strictly related to dietary necessity or poverty, but possibly a maintenance of the rural heritage and the thrill of local dwellers for diversifying their diet (Wilkie et al. 2016). Many cities in the western Amazon, which are more accessible due to their location downstream on Amazon River, were predicted to have both per capita and total wild meat consumption at relevant levels, likely because of the combination of high GDP and surrounding rural populations. Therefore, the replacement of the wild meat by domestic meat at a more accessible price, which is a very common suggested strategy to reduce wild meat demand in cities (Rushton et al. 2005), may not be sufficient to solve the problem. In addition, law enforcement and surveillance actions face several barriers in the Amazon, especially due to the large extent of the territory and difficult access. Accordingly, the current prohibition on wildlife commerce in most areas of the Amazon has been driving a hidden market that hampers control. Furthermore, captive breeding of wild species, although suggested as an alternative to keep wild meat consumption at sustainable levels (Nogueira-Filho et al. 2011), may not produce enough individuals to supply the demand at an affordable price (Wilkie 2016).

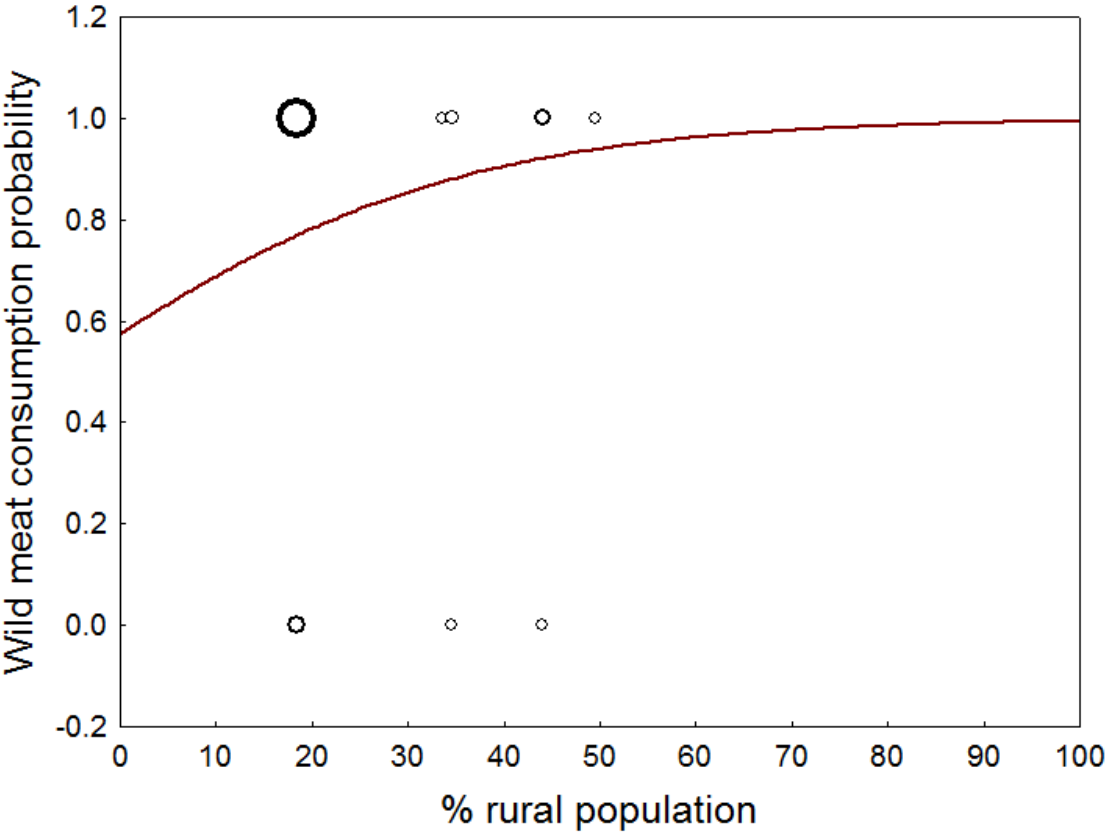
Given the magnitude of the trade of wild meat we found, we suggest the regulation of this unconstrained activity is a fundamental and urgent matter to resolve. Plans that support the sustainable management of wild meat in the surrounding forests should bring regulated wild meat trade into the formal economy and promote the improvement of rural livelihoods. Wildlife trade regulations could include policies designed to allow the trade of more resilient species and to protect or restrict the trade of those more sensitive to hunting. Some of these more resilient species are already among the most consumed taxa in the region, so acceptance of this policy is most likely. This strategy would generate income for those involved in the market chain and adequately control harvests of wildlife species while guaranteeing conservation of threatened species.

3.6 Acknowledgments

This work was supported by the grant agreement for Instituto de Desenvolvimento Sustentável Mamirauá of the Gordon and Betty Moore Foundation (number 5344) and the National Council for Scientific and Technological Development (CNPq) (grant numbers 300005/2013-0, 452908/2016-7, 201475/2017-0). We thank K. Henle, M. Auliya, and C. Ferreira, from the Helmholtz Centre for Environmental Research (UFZ), for their useful comments on the manuscript. H.R.E.B. thanks the German Federal Ministry of Education and Research (BMBF) for his Green Talents Award, which supported this work. T.Q.M. is supported by the WCS Graduate Scholarship Program, a program of the Wildlife Conservation Society and the Christensen Conservation Leaders Scholarship, and by the Wildlife Conservation Network Scholarship Program through the Sidney Byers Scholarship award.

3.7 Supporting Information

Appendix S1. A figure showing the relationship between the percentage of rural population within each municipality and the wild meat consumption probability in the cities (Estimate = 0.04896, $p<0.01$). The size of the markers refers to the frequency of citations for wild meat consumption (1 = consume wild meat; 0 = does not consume wild meat) in each surveyed city. The formula obtained through this model ($y = 2.72^{(0.30311884+0.04896433*x)}/1+2.72^{(0.30311884+0.04896433*x)}$) was used to predict the percentage of potential consumers of wild meat for each urban population of the 62 municipalities in Central Amazonia.



Appendix S2. A table containing details on the game species cited as consumed in five cities in Central Amazonia, with their gross body weight, net body weight after evisceration, conservation status, number and percentage of citations, and wild meat biomass and number of individuals estimated to be consumed annualy.

Common name (Taxon)	Gross body weight (kg)	Net body weight (kg)	Conservation status (IUCN 2019)	N of citations (%) kg (N individuals) consumed yearly					
				Alvarães (n=130)	Coari (n=51)	Fonte Boa (n=20)	Maraã (n=22)	Tefé (n=552)	Total[a]
White-lipped peccary (*Tayassu pecari*)	35	20	VU	120 (22.56) 9448.2 (472.41)	47 (24.87) 56088.16 (2804.41)	19 (22.35) 12826.75 (641.34)	19 (20.65) 12745.05 (637.25)	377 (32.25) 36754.72 (1837.74)	582 (24.54) 127862.87 (6393.14)
Tapir (*Tapirus terrestris*)	140	90	VU	63 (11.84) 4960.3 (55.11)	31 (16.4) 36994.32 (411.05)	13 (15.29) 8776.2 (97.51)	14 (15.22) 9391.09 (104.35)	189 (16.17) 18426.11 (204.73)	310 (14.98) 78548.01 (872.76)
Lowland paca (*Cuniculus paca*)	8	6	LC	99 (18.61) 7794.76 (1299.13)	28 (14.81) 33414.22 (5569.04)	14 (16.47) 9451.29 (1575.21)	15 (16.3) 10061.88 (1676.98)	109 (9.32) 10626.7 (1771.12)	265 (15.1) 71348.85 (11891.47)
Agouti (*Dasyprocta fuliginosa*)	5	2	LC	47 (8.83) 3700.54 (1850.27)	9 (4.76) 10740.29 (5370.14)	13 (15.29) 8776.2 (4388.1)	11 (11.96) 7378.71 (3689.36)	49 (4.19) 4777.14 (2388.57)	129 (9.01) 35372.88 (17686.44)
Deer (*Mazama* spp.)	18.5	12.5	-	33 (6.2) 2598.25 (207.86)	11 (5.82) 13127.02 (1050.16)	12 (14.12) 8101.11 (648.09)	5 (5.43) 3353.96 (268.32)	18 (1.54) 1754.87 (140.39)	79 (6.62) 28935.2 (2314.82)
Armadillos (Family Dasypodidae)	6	4	-	33 (6.2) 2598.25 (649.56)	3 (1.59) 3580.1 (895.02)	3 (3.53) 2025.28 (506.32)	0	22 (1.88) 2144.84 (536.21)	61 (2.64) 10348.46 (2587.12)
Howler monkey (*Alouatta seniculus*)	6	4	LC	1 (0.19) 78.73 (19.68)	0	0	0	9 (0.77) 877.43 (219.36)	10 (0.19) 956.17 (239.04)
Capybara (*Hydrochoerus hydrochaeris*)	30	12	LC	0	2 (1.06) 2386.73 (198.89)	3 (3.53) 2025.28 (168.77)	1 (1.09) 670.79 (55.9)	5 (0.43) 487.46 (40.62)	11 (1.22) 5570.26 (464.19)
Collared peccary (*Pecari tajacu*)	25	13	LC	6 (1.13) 472.41 (36.34)	0	0	0	2 (0.17) 194.99 (15)	8 (0.26) 667.4 (51.34)
Monkey (Order Primates)	6	4	-	2 (0.38) 157.47 (39.37)	0	0	0	5 (0.43) 487.46 (121.87)	7 (0.16) 644.93 (161.23)
Manatee (*Trichechus inunguis*)	400	256	VU	1 (0.19) 78.73 (0.31)	13 (6.88) 15513.75 (60.6)	0	0	3 (0.26) 292.48 (1.14)	17 (1.46) 15884.96 (62.05)
Tayra (*Eira barbara*)	4	2.4	LC	1 (0.19) 78.73 (32.97)	0	0	0	0	1 (0.04) 78.73 (32.97)

Reptilia									
Yellow-spotted river turtle (*Podocnemis unifilis*)	8	3.5	VU	35 (6.58) 2755.72 (787.35)	26 (13.76) 31027.49 (8865)	3 (3.53) 2025.28 (578.65)	7 (7.61) 4695.54 (1341.58)	174 (14.88) 16963.72 (4846.78)	245 (9.27) 57467.75 (16419.36)
Six–tubercled Amazon river turtle (*Podocnemis sextuberculata*)	3	1.5	VU	46 (8.65) 3621.81 (2414.54)	16 (8.47) 19093.84 (12729.23)	4 (4.71) 2700.37 (1800.25)	6 (6.52) 4024.75 (2683.17)	120 (10.27) 11699.11 (7799.41)	192 (7.72) 41139.88 (27426.59)
Giant South American turtle (*Podocnemis expansa*)	40	18	LR/CD	7 (1.32) 551.14 (30.62)	0	1 (1.18) 675.09 (37.51)	6 (6.52) 4024.75 (223.6)	8 (0.68) 779.94 (43.33)	22 (1.94) 6030.93 (335.05)
Yellow-footed tortoise (*Chelonoidis denticulatus*)	8	3	VU	8 (1.5) 629.88 (209.96)	0	0	2 (2.17) 1341.58 (447.19)	8 (0.68) 779.94 (259.98)	18 (0.87) 2751.4 (917.13)
Caimans (Family Alligatoridae)	182.5	91.3	-	0	0	0	0	2 (0.17) 194.99 (2.14)	2 (0.03) 194.99 (2.14)
Aves									
Curassow (*Crax* spp.; *Mitu* spp.)	3	2.2	-	28 (5.26) 2204.58 (1002.08)	1 (0.53) 1193.37 (542.44)	0	6 (6.52) 4024.75 (1829.43)	42 (3.59) 4094.69 (1861.22)	77 (3.18) 11517.39 (5235.18)
Muscovy duck (*Cairina moschata*)	3	2	LC	1 (0.19) 78.73 (39.37)	2 (1.06) 2386.73 (1193.37)	0	0	26 (2.22) 2534.81 (1267.4)	29 (0.69) 5000.27 (2500.14)
Anhinga (*Anhinga anhinga*)	3	2	LC	0	0	0	0	1 (0.09) 97.49 (48.75)	1 (0.02) 97.49 (48.75)
Tinamous (Family Tinamidae)	1	0.6	-	1 (0.19) 78.73 (131.22)	0	0	0	0	1 (0.04) 78.73 (131.22)
Total				532 (100) 41887.01 (9278.16)	189 (100) 225546 (39689.34)	85 (100) 57382.83 (10441.75)	92 (100) 61712.85 (12957.12)	1169 (100) 113968.87 (23405.75)	2067 (100) 500497.56 (95772.12)

[a]Average percentage of citations per species is applicable.

Appendix S3. A table containing details on the estimated amounts of biomass sold, prices and annual monetary movement of 17 taxa cited as traded in five cities in central Amazonia

	City															Total monetary movement	
	Alvarães			Coari			Fonte Boa			Maraã			Tefé				
Taxon	Estimated bought biomass (kg)	Selling price ± SD (USD)	Mean annual monetary value (max CI – min CI) (USD)	Estimated bought biomass (kg)	Selling price ± SD (USD)	Mean annual monetary value (max CI – min CI) (USD)	Estimated bought biomass (kg)	Selling price ± SD (USD)	Mean annual monetary value (max CI – min CI) (USD)	Estimated bought biomass (kg)	Selling price ± SD (USD)	Mean annual monetary value (max CI – min CI) (USD)	Estimated bought biomass (kg)	Selling price ± SD (USD)	Mean annual monetary value (max CI – min CI) (USD)	Estimated bought biomass (kg)	Mean annual monetary value (max CI – min CI) (USD)
Mammals																	
White-lipped peccary (*Tayassu pecari*)	7157.73	2.65 ± 0.47	18966.08 (18357.8-19574.36)	46216.64	2.4 ± 0.51	110780.09 (103988.71-117571.47)	10261.4	2.69 ± 0.12	27631.51 (27080.16-28182.86)	11011.72	1.77 ± 0.33	19528.15 (17898.91-21157.38)	27896.83	2.41 ± 0.7	67207.92 (65244.55-69171.29)	102,544.32	244113.73 (232570.11-255657.36)
Tapir (*Tapirus terrestris*)	3757.81	2.67 ± 0.51	10021.59 (9543.84-10499.33)	30483.32	2.26 ± 0.43	68845.88 (64266.94-73424.83)	7020.96	2.83 ± 0.2	19835.14 (19079.77-20590.52)	8113.9	1.96 ± 0.45	15863.17 (13945.85-17780.49)	13985.41	1.35 ± 2.47	18830.49 (13909.93-23751.05)	63,361.40	133396.28 (120746.33-146046.22)
Lowland paca (*Cuniculus paca*)	5905.12	2.67 ± 0.73	15785.39 (14940.88-16629.9)	27533.32	1.99 ± 0.49	54855.81 (49869.13-59842.5)	7561.03	2.71 ± 0.3	20467.78 (19277.73-21657.84)	8693.46	1.4 ± 0.45	12212.59 (10237.21-14187.98)	8065.66	2.24 ± 0.72	18029.25 (16938.28-19120.23)	57,758.59	121350.83 (111263.21-131438.45)
Agouti (*Dasyprocta fuliginosa*)	2803.44	2.62 ± 0.54	7334.05 (6901.48-7766.62)	8850	4.33 ± 1.76	38288.62 (28114.09-48463.15)	7020.96	2.57 ± 0.23	18011.65 (17145.03-18878.27)	6375.21	1.9 ± 0	12133.02 (12133.02-12133.02)	3625.85	2.98 ± 1.57	10791.17 (9199.08-12383.26)	28,675.46	86558.51 (73492.7-99624.32)
Manatee (*Trichechus inunguis*)	1968.37	0 ± 0	0 (0-0)	10816.66	5.72 ± 2.65	61836.69 (44895.4-78777.98)	6480.88	0 ± 0	0 (0-0)	2897.82	1.14 ± 0	3309.01 (3309.01-3309.01)	1331.94	3.9 ± 1.51	5200.43 (4271.45-6129.42)	23,495.67	70346.13 (52475.85-88216.4)
Deer (*Mazama* spp.)	1968.37	2.7 ± 0.56	5319.35 (4940.35-5698.36)	2950	2.33 ± 0.58	6885.07 (4948.38-8821.75)	1620.22	2.69 ± 0.12	4359.64 (4139.91-4579.37)	0	1.33 ± 0.27	0 (0-0)	1627.93	1.77 ± 0.51	2878.23 (2531.03-3225.43)	8,166.52	19442.28 (16559.67-22324.9)
Armadillos (Family Dasypodidae)	59.65	2.49 ± 0.45	148.39 (96.18-200.59)	0	2.18 ± 0.54	0 (0-0)	0	1.01 ± 0.38	0 (0-0)	0	0 ± 0	0 (0-0)	665.97	2.58 ± 0.52	1717.12 (1490.48-1943.77)	725.62	1865.51 (1586.66-2144.36)
Capybara (*Hydrochoerus hydrochaeris*)	0	2.52 ± 0	0 (0-0)	1966.67	2.62 ± 0	5154.24 (5154.24-5154.24)	1620.22	3.03 ± 0.38	4912.27 (4217.42-5607.11)	579.56	1.52 ± 0	882.4 (882.4-882.4)	369.98	1.07 ± 1.96	396.55 (-240.54-1033.64)	4,536.43	11345.46 (10013.53-12677.4)
Collared peccary (*Pecari tajacu*)	357.89	2.86 ± 0.29	1021.8 (938.49-1105.1)	0	0 ± 0	0 (0-0)	0	0 ± 0	0 (0-0)	0	0 ± 0	0 (0-0)	147.99	2.16 ± 0.61	319.8 (193.99-445.62)	505.88	1341.6 (1132.48-1550.72)
Howler monkey (*Alouatta seniculus*)	119.3	0 ± 0	0 (0-0)	0	0 ± 0	0 (0-0)	0	0 ± 0	0 (0-0)	0	0 ± 0	0 (0-0)	369.98	1.47 ± 0	545.12 (545.12-545.12)	489.28	545.12 (545.12-545.12)
Tayra (*Eira barbara*)	59.65	0 ± 0	0 (0-0)	12783.33	0 ± 0	0 (0-0)	0	0 ± 0	0 (0-0)	0	0 ± 0	0 (0-0)	221.99	0 ± 0	0 (0-0)	13,064.97	0 (0-0)
Monkey (Order Primates)	59.65	0 ± 0	0 (0-0)	0	0 ± 0	0 (0-0)	0	0 ± 0	0 (0-0)	0	0 ± 0	0 (0-0)	0	0 ± 0	0 (0-0)	59.65	0 (0-0)
Reptilia																	

Yellow-spotted river turtle (*Podocnemis unifilis*)	2087.67	9.8 ± 2.27	20449.78 (18877.91-22021.66)	25566.65	12.84 ± 4.4	328188.17 (284920.08-371456.27)	1620.22	2.71 ± 2.07	4387.27 (585.59-8188.94)	4056.95	5.87 ± 6.64	23827.04 (3864.2-43789.89)	12875.46	7.13 ± 2.73	91737.92 (86509.33-96966.52)	46,206.95	468590.19 (394757.11-542423.27)
Six–tubercled Amazon river turtle (*Podocnemis sextuberculata*)	2743.79	5.98 ± 2.81	16416.37 (14189.49-18643.24)	15733.33	10.06 ± 5.59	158308.72 (115214.03-201403.4)	2160.29	6.82 ± 5.33	14736.8 (3455.79-26017.82)	3477.38	5.08 ± 3.59	17650.23 (7667.42-27633.05)	8879.63	4.51 ± 2.56	40065.91 (35994.41-44137.42)	32,994.42	247178.04 (176521.14-317834.93)
Giant South American turtle (*Podocnemis expansa*)	417.53	8.68 ± 4.91	3622.99 (2103.35-5142.63)	0	0 ± 0	0 (0-0)	540.07	0 ± 0	0 (0-0)	3477.38	4.23 ± 2.44	14711.84 (7918.37-21505.3)	591.98	5.13 ± 3.92	3037.55 (1428.79-4646.3)	5,026.96	21372.38 (11450.51-31294.24)
Yellow-footed tortoise (*Chelonoidis denticulatus*)	477.18	3.36 ± 3.43	1603.02 (469.19-2736.85)	0	0 ± 0	0 (0-0)	0	0 ± 0	0 (0-0)	1159.13	0 ± 0	0 (0-0)	591.98	0 ± 0	0 (0-0)	2,228.29	1603.02 (469.19-2736.85)
Caiman (Family Alligatoridae)	0	0.76 ± 0	0 (0-0)	0	0 ± 0	0 (0-0)	0	0 ± 0	0 (0-0)	0	0 ± 0	0 (0-0)	147.99	0 ± 0	0 (0-0)	147.99	0 (0-0)
Aves																	
Curassow (*Crax* spp.; *Mitu* spp.)	1670.14	7.79 ± 2.38	13004.69 (11533.7-14475.67)	983.33	11.23 ± 0	11044.79 (11044.79-11044.79)	0	0 ± 0	0 (0-0)	3477.38	8.56 ± 1.35	29781.05 (26036.56-33525.54)	3107.87	5.96 ± 2.43	18519.5 (16238.41-20800.59)	9,238.72	72350.03 (64853.46-79846.59)
Muscovy duck (*Cairina moschata*)	59.65	4.41 ± 0.89	262.96 (158.83-367.09)	1966.67	7.49 ± 2.65	14726.39 (7510.46-21942.32)	0	0 ± 0	0 (0-0)	0	0 ± 0	0 (0-0)	1923.92	3.13 ± 0.86	6023.56 (5386.23-6660.9)	3,950.24	21012.92 (13055.52-28970.31)
Anhinga (*Anhinga anhinga*)	0	0 ± 0	0 (0-0)	0	0 ± 0	0 (0-0)	0	0 ± 0	0 (0-0)	0	0 ± 0	0 (0-0)	74	0 ± 0	0 (0-0)	74.00	0 (0-0)
Tinamous (Family Tinamidae)	59.65	0 ± 0	0 (0-0)	0	0 ± 0	0 (0-0)	0	0 ± 0	0 (0-0)	0	0 ± 0	0 (0-0)	0	0 ± 0	0 (0-0)	59.65	0 (0-0)
Total	31732.58	4.13 ± 1.35	113956.45 (103051.5-124861.39)	185849.9	5.45 ± 1.63	858914.47 (719926.24-997902.7)	45906.26	3.01 ± 1.01	114342.07 (94981.4-133702.74)	53319.9	3.16 ± 1.41	149898.5 (103892.94-195904.06)	86502.37	3.19 ± 1.54	285300.53 (259640.5-310960.55)	403311.01	1522412.02 (1281492.59-1763331.45)

Appendix S4. Details of the best-fit models using GAMLSS for each response variable, with the family of distribution, link function, delta AIC in relation to the second best model (ΔAIC) and p-value for each variable. Non-linear effects were fit using P-spline smoother (*pb*) function provided by *gamlss* R-package. Families of distributions are represented by Generalised Inverse Gaussian (GIG), Reverse Gumbel (RG) and Box-Cox t (BCTo).

Best fitted model[a]		Link function	Estimate	p-value	Family of distribution	ΔAIC
Response variables	Predictor variables					
Consumption of wild meat						
Frequency of consumption	Intercept +	Log	2.155	<0.0001	GIG	3.141
	% rural population +		0.02504	<0.0001		
	Gross Domestic Product		0.000139	<0.0001		
Taxa consumed						
% of citations per taxon	Intercept +	Identity	4.337549	<0.0001	RG	2.081
	Gross body mass +		0.076604	<0.0001		
	random (Taxa)					
Wild meat price						
Meat price	Intercept +	Log	0.984462	<0.0001	BCTo	6.02
	pb(Gross body mass) +		-0.00136	<0.0001		
	% rural population +		0.00470	<0.0001		
	Random (Taxa)					

3.8 References

Antunes, A. P., Rebêlo, G. H., Pezzuti, J. C. B., de Mattos Vieira, M. A. R., Constantino, P. D. A. L., Campos-Silva, J. V., Fonseca, R., Durigan, C. C., Ramos, R. M., Valsecchi, J., Pimenta, N. C., Ranzi, T. J. D., Lima, N. A. S., Shepard Jr., G. H. 2019. A conspiracy of silence: subsistence hunting rights in the Brazilian Amazon. *Land Use Policy* 84:1–11.

Baía-Júnior, P. C., Guimarães, D. A., Le Pendu, Y. 2010. Non-legalized commerce in game meat in the Brazilian Amazon: a case study. *Revista de Biología Tropical* 58:1079-1088.

Bodmer, R. E., Lozano, E. P. 2001. Rural development and sustainable wildlife use in Peru. *Conservation Biology* 15:1163-1170.

Chaves, W. A., Wilkie, D. S., Monroe, M. C., Sieving, K. E. 2017. Market access and wild meat consumption in the central Amazon, Brazil. *Biological Conservation* 212:240-248.

Cowlishaw, G., Mendelson, S., Rowcliffe, J. M. 2005. Structure and operation of a bushmeat commodity chain in southwestern Ghana. *Conservation Biology* 19:139-149.

Merode, E., Homewood, K., Cowlishaw, G. 2004. The value of bushmeat and other wild foods to rural households living in extreme poverty in Democratic Republic of Congo. *Biological Conservation* 118:573–581.

Dounias, E. 2016. From subsistence to commercial hunting: technical shift in cynegetic practices among southern Cameroon forest dwellers during the 20th Century. *Ecology and Society* 21(1):23.

El Bizri, H. R., Morcatty, T. Q., Lima, J. J., Valsecchi, J. 2015. The thrill of the chase: uncovering illegal sport hunting in Brazil through YouTube™ posts. *Ecology and Society* 20: 30.

El Bizri, H. R., Fa, J. E., Bowler, M., Valsecchi, J., Bodmer, R., Mayor, P. 2018. Breeding seasonality in the lowland paca (*Cuniculus paca*) in Amazonia: interactions with rainfall, fruiting, and sustainable hunting. *Journal of Mammalogy* 99(5):1101-1111.

Fa, J. E., Albrechtsen, L., Johnson, P. J., Macdonald, D. W. 2009. Linkages between household wealth, bushmeat and other animal protein consumption are not invariant: evidence from Rio Muni, Equatorial Guinea. *Animal Conservation* 12: 599-610.

Fa, J. E., Olivero, J., Real, R., Farfán, M. A., Márquez, A. L., Vargas, J. M., Ziegler, S., Wegmann, M., Brown, D., Margetts, B., Nasi, R. 2015. Disentangling the relative effects of bushmeat availability on human nutrition in central Africa. *Scientific Reports* 5: 8168.

Fang, T., Bodmer, R., Puertas, P., Mayor, P., Perez, P., Acero, R., Hayman, D. 2008. *Certificación de pieles de pecaries (Tayassu tajacu y T. pecari) en la Amazonía peruana: una estrategia para la conservación y manejo de fauna Silvestre en la Amazonia peruana*. Wust Editions-Darwin Institute, Lima, Peru.

García, J. B., Acosta, N. B., Olivares, L. V. 2004. Técnicas de preservación y factor de conversión de fauna silvestre en la región Loreto, Perú. In *Memorias del VI congreso internacional sobre el manejo de fauna silvestre en la Amazonía y Latinoamérica*, edited by R. Bodmer, pp. 427–433. Universidad Nacional de la Amazonía Peruana; Durrell Institute of Conservation and Ecology; and Wildlife Conservation Society, Iquitos, Peru.

Instituto Brasileiro de Geografia e Estatística – IBGE. 2001. *Sinopse preliminar do Censo Demográfico: 2000*. IBGE, Rio de Janeiro, Brazil.

Instituto Brasileiro de Geografia e Estatística – IBGE. 2018. Cidades. Available online at https://cidades.ibge.gov.br/ (accessed on 15 June 2018).

Kirkland, M., Eisenberg, C., Bicerra, A., Bodmer, R. E., Mayor, P., Axmacher, J. C. 2018. Sustainable wildlife extraction and the impacts of socio-economic change among the Kukama-Kukamilla people of the Pacaya-Samiria National Reserve, Peru. *Oryx* doi: 10.1017/S0030605317001922.

Kümpel, N., Milner-Gulland, E., Cowlishaw, G., Rowcliffe, J. 2010. Incentives for hunting: The role of bushmeat in the household economy in rural Equatorial Guinea. *Human Ecology* 38:251-264.

Lescuyer, G., Nasi, R. 2016. Financial and economic values of bushmeat in rural and urban livelihoods in Cameroon: Inputs to the development of public policy*. International Forestry Review* 18:93-107.

Lopes, G. P., Valsecchi, J., Vieira, T. M., Costa, E. W. M. 2012. Hunting and hunters in lowland communities in the region of the middle Solimões, Amazonas, Brazil. *Uakari* 8:7-18.

Morcatty, T. Q., Valsecchi, J. 2015. Social, biological, and environmental drivers of the hunting and trade of the endangered yellow-footed tortoise in the Amazon. *Ecology and Society* 20(3): 3.

Morsello, C., Yagüe, B., Beltreschi, L., van Vliet, N., Adams, C., Schor, T., Quiceno-Mesa, M. P., Cruz, D. 2015. Cultural attitudes are stronger predictors of bushmeat consumption and preference than economic factors among urban Amazonians from Brazil and Colombia. *Ecology and Society* 20(4):21.

Nasi, R., Taber, A., van Vliet, N. 2011. Empty forests, empty stomachs? Bushmeat and livelihoods in the Congo and Amazon Basins. *International Forestry Review* 13:355-368.

Nogueira, S. S. C., Nogueira-Filho, S. L. G. 2011. Wildlife farming: an alternative to unsustainable hunting and deforestation in Neotropical forests? *Biodiversity and Conservation* 20:1385-1397.

Ojasti, J. 1996. *Wildlife utilization in Latin America: current situation and prospects for sustainable management*. FAO Conservation Guide 25. Food and Agriculture Organization, Rome, Italy.

Parry, L., Peres, C. A. 2015. Evaluating the use of local ecological knowledge to monitor hunted tropical-forest wildlife over large spatial scales. *Ecology and Society* 20(3):15.

Parry, L., Barlow, J., Pereira, H. 2014. Wildlife harvest and consumption in Amazonia's urbanized wilderness. *Conservation Letters* 7:565-574.

Peres, C. A. 2000. Effects of subsistence hunting on vertebrate community structure in Amazonian forests. *Conservation Biology* 14(1):240-253.

Robinson, J. G., Redford, K. H.1986. Body size, diet, and population density of Neotropical forest mammals. *The American Naturalist* 128:665-680.

Rowcliffe, J. M., de Merode, E., Cowlishaw, G. 2004. Do wildlife laws work? Species protection and the application of a prey choice model to poaching decisions. *Proceedings of the Royal Society of London B: Biological Sciences* 271:2631-2636.

Rushton, J., Viscarra, R., Viscarra, C., Basset, F., Baptista, R., Brown, D. 2005. *How important is bushmeat consumption in South America: now and in the future*. ODI Wildlife Policy Briefing, Number 11, ODI, United Kingdom.

SEPLANCTI/DEPI 2018. *Anuário Estatístico do Amazonas 2018*. Departamento Estadual de Estatística, Manaus, Brasil.

Valsecchi, J., El Bizri, H. R., Figueira, J. E. C. 2014. Subsistence hunting of *Cuniculus paca* in the middle of the Solimões River, Amazonas, Brazil. Brazilian *Journal of Biology* 74:560-568.

van Vliet, N., Cruz, D., Quiceno-Mesa, M., Neves de Aquino L. J., Moreno, J., Rairon, R., Fa, J. E. 2015. Ride, shoot, and call: wildlife use among contemporary urban hunters in Três Fronteiras, Brazilian Amazon. *Ecology and Society* 20(3):8.

van Vliet, N., Mesa, M. P. Q., Cruz-Antia, D., Neves de Aquino, L. J. N., Moreno, J., Nasi, R. 2014. The uncovered volumes of bushmeat commercialized in the Amazonian trifrontier between Colombia, Peru & Brazil. *Ethnobiology and Conservation* 3:7.

Vieira, M., von Muhlen, E. M., Shepard Jr, G. H. 2015. Participatory monitoring and management of subsistence hunting in the Piagaçu-Purus reserve, Brazil. *Conservation and Society* 13:254-264.

Wilkie, D. S., Wieland, M., Boulet, H., Le Bel, S., van Vliet, N., Cornelis, D., BriacWarnon, V., Nasi, R., Fa, J. E. 2016. Eating and conserving bushmeat in Africa. *African Journal of Ecology* 54:402-414.

Chapter 4. Breeding seasonality in the lowland paca (*Cuniculus paca*) in Amazonia: interactions with rainfall, fruiting, and sustainable hunting

Published in *Journal of Mammalogy*

El Bizri, H. R., Fa, J. E., Bowler, M., Valsecchi, J., Bodmer, R., & Mayor, P. (2018). Breeding seasonality in the lowland paca (*Cuniculus paca*) in Amazonia: interactions with rainfall, fruiting, and sustainable hunting. *Journal of Mammalogy*, *99*(5), 1101-1111. DOI: 10.1093/jmammal/gyy102.

4.1 Abstract

The resilience of a given species to hunting is conditioned by the effect of potential threats upon the more sensitive periods in its life history, such as when animals are breeding. We investigated the environmental drivers of breeding seasonality in the lowland paca (*Cuniculus paca*), and the potential impact of hunting on the species. As part of a participative study with hunters in 2 Amazonian sites, we obtained reproductive organs of pacas as well as information on the hunters' daily wild meat extraction. Using data on rainfall, river water level, and fruiting phenology from the 2 study sites, we applied generalized additive models (GAMLSS) to examine the effect of climatic and environmental factors on paca reproduction. Forest fruiting was directly linked to higher pregnancy rates in pacas, and when lactation and weaning of offspring mostly occurred. Hunting was highly seasonal in all studied years and positively correlated with higher levels of river water. The coincidence between hunting patterns and paca reproductive cycles during the wet season resulted in more

pregnant females being harvested. In addition to the known slow reproductive rate of pacas, the disproportionate offtake of pregnant females may affect the long-term sustainability of hunting of this species. Reducing hunting during the flooded season may not be feasible because the lowland paca provides most of wild meat consumed by thousands of rural Amazonians during this period. However, options to offset the negative effects of killing of pregnant females could include the zoning of hunting areas or encouraging hunters to target primarily males. Our results indicate that strategies for the sustainable harvest of paca and other heavily hunted Amazonian mammals should consider the interaction between the species' reproductive cycles and hunting by local people in order to enhance conservation and management efforts.

4.2 Introduction

In high latitudes, where climatic variability between seasons is greatest, most species produce a large number of offspring in a short period of time, most of which do not survive (Bronson 1985). By contrast, in more stable environments with less seasonal variation, such as tropical forest regions, species generally produce a constant, low number of offspring over the year (McNaughton 1975). However, in the Amazon basin, the extreme variation in river levels, caused by seasonal meltwater in the Andes or rainfall, affects food availability (particularly tree fruits) to such an extent that frugivorous mammals may exhibit a greater than expected reproductive seasonality for this environment (Dubost et al. 2005). Furthermore, seasonal patterns in water levels also determine patterns of hunting and fishing by humans (Endo et al. 2016).

Animal populations are regulated by factors that impact mortality and recruitment (Caughley 1977). Understanding the population dynamics of exploited species is essential to determine sustainable harvest rates for wildlife populations. Harvesting individuals can have direct effects on the growth rate of a population by increasing mortality rates. There is increasing evidence that harvesting can also have indirect effects on population growth. For instance, harvest can disrupt the sex and age structure of a population, which can in turn affect fecundity rates (Milner et al. 2007; Bunnefeld et al. 2009). Furthermore, sex-skewed harvesting can have potentially deleterious effects on long-term fecundity (defined as the number of young born) and lead to population collapse, as shown for ungulates (Ginsberg and Milner-Gulland 1994; Freeman et al. 2014). In addition, overhunting of females in seasonally breeding animals, during periods when more females are pregnant, may negatively influence the population dynamics of the species.

In this paper, we evaluate how hunting may affect the population dynamics of the lowland paca (*Cuniculus paca*). The paca is a large, frugivorous caviomorph rodent that occurs throughout the Neotropics, inhabiting primarily broadleaf forests from east-central Mexico to northern Argentina. (Collet 1981; Pérez 1992; Aquino et al. 2009). Studies to date, in primary broadleaf forest, suggest that pacas occupy relatively small home ranges (Marcus 1984; Beck-King et al. 1999), and are patchily distributed in mosaic landscapes with scattered resources (Marcus 1984; Beck-King et al. 1999; Ulloa et al. 1999). Pacas feed mostly on fruits and seeds, and occasionally consume leaves and flowers (Beck-King et al. 1999; Dubost 2017).

Pacas are of conservation and management interest throughout their geographic range, as a popular game species for people (e.g., Read et al.

2010; El Bizri et al. 2015, 2016; Gutiérrez-Granados 2015; Mayor et al. 2015), an important prey of large carnivores, and as seed dispersers (Dubost and Henry 2006; Aquino et al. 2009). However, there is concern that current levels of hunting may be unsustainable, as observed in several Amazonian sites (e.g., Zapata-Ríos et al. 2009; Valsecchi et al. 2014). Given the importance of the paca as a source of protein to human residents of tropical forests, identifying the factors that may affect paca numbers remains fundamental.

Here, in 2 sites in Amazonian Peru and Brazil, we first assess how environmental factors such as rainfall patterns affect fruit availability, and in turn show how this correlates with the reproductive seasonality of pacas. We then assess the impact of harvest rates during the different phases of the reproductive cycle of pacas using data gathered from a 15-year participatory hunting study for the 2 study sites.

4.3 Materials and Methods

4.3.1 Study sites

The Yavarí-Mirín River (YMR; 04º19’53” S, 71º57’33” W) is located in the western Peruvian Amazon, encompassing 107,000 ha of continuous upland forests containing a single indigenous community of 307 inhabitants (Figure 1). The Amanã Sustainable Development Reserve (ASDR; 01º54’00” S, 64º22’00” W) is a 2,313,000-ha reserve of predominantly upland forests in the central Brazilian Amazon, between the Negro and Japurá rivers. Approximately 4,000 riverine people inhabit 23 communities and some isolated settlements within this reserve (Figure 1). In both study sites, local communities rely on agriculture for income and on hunting and fishing for subsistence. River water levels at both sites change seasonally, varying up to 12 m between the dry and flood peaks (Ramalho et al. 2009). Climate in both study sites is typically equatorial with annual temperatures ranging between 22°C and 36°C, relative humidity of 80%, and an annual rainfall of 1,500 – 3,000 mm.

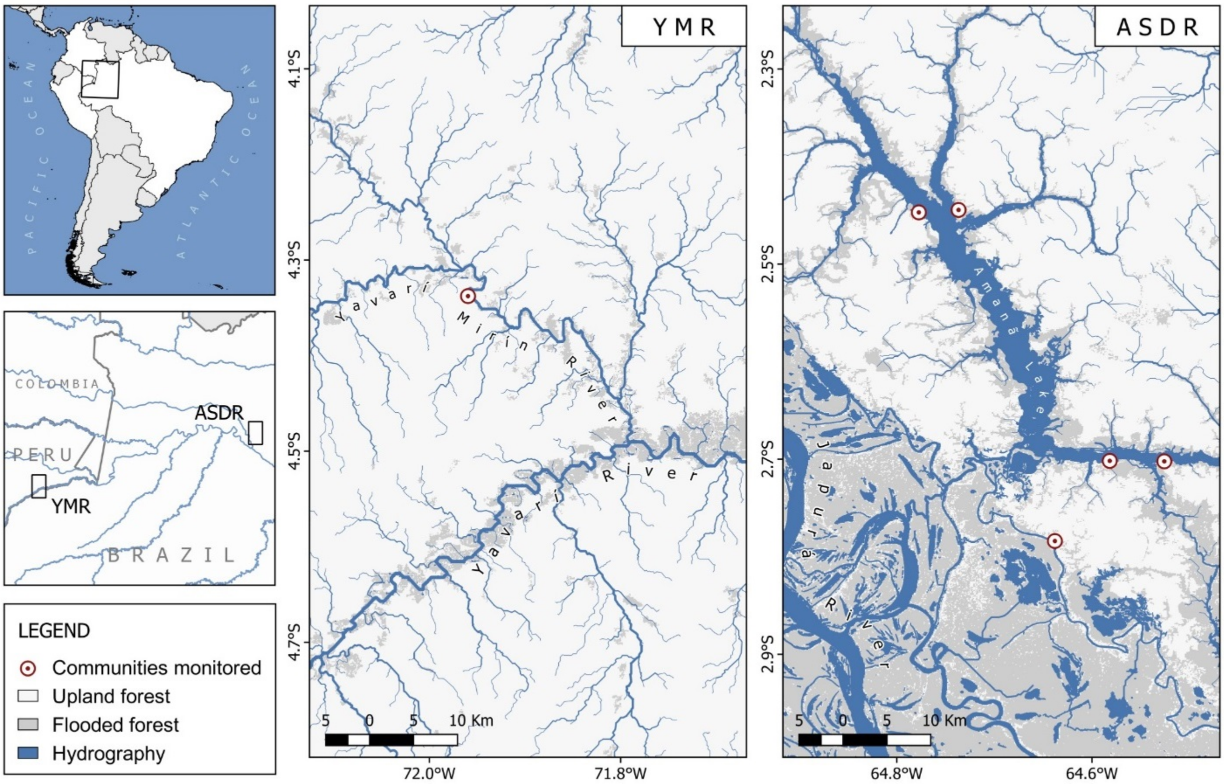


Figure 1. Location of the 2 study sites (YMR: Yavarí-Mirín River, ASDR: Amanã Sustainable Development Reserve) in Amazonia and the communities participating in the monitoring of hunting and collection of biological material on lowland pacas (*Cuniculus paca*).

4.3.2 Water level and rainfall

For the YMR, we calculated monthly average river water level (as meters above sea level – m.a.s.l.) and rainfall (in mm) on the Yavarí River, from data provided by a Brazilian National Water Agency hydrological station, c. 50 km from the study site (HidroWeb, Estirão do Repouso station, rainfall: 1962 – 1999, water level: 1980 – 2017, http://www.snirh.gov.br/hidroweb/). In the ASDR, we used data on average rainfall (mm) for the Tefé municipality, c. 90 km from the study area, from information also provided by the Brazilian National Water Agency (HidroWeb, Tefé station, 2005 – 2017, http://www.snirh.gov.br/hidroweb/). We used data on river water levels from the Mamirauá Sustainable Development Institute for the Amanã Lake station inside the ASDR (1990 – 2018, https://mamiraua.org.br/pt-br/pesquisa-e-monitoramento/monitoramento/fluviometrico/).

4.3.3 Ripe fruit availability

We determined annual changes in ripe fruit availability, the main item in the diets of pacas (Dubost et al. 2005), by monitoring tree fruit abundance in 3 transects between March 2004 and February 2005. Two transects, started at random points, were in upland forests in the YMR, and a third transect was located in *aguajal*, upland swamp forest dominated by palms. Two transects were 5 m wide and one in the upland forest was 20 m wide (Pitman et al. 2003). We tagged and identified every tree of a diameter at breast height (DBH) >10 cm, as well as every vine or liana of DBH >7 cm (Ayres 1986). We marked plants until the rate of discovery of new species plateaued (Sutherland 2000), which determined the length and area of each transect. Starting mid-month, we observed the canopy of each tagged tree or vine once per month with binoculars and a small telescope, recording the presence or absence of ripe fruits in each sampled individual plant. Because fruits of the moriche palm (*Mauritia flexuosa*) constitute an important part of the diet of pacas (Mendieta-Aguilar et al. 2015), we also obtained more detailed fruiting data from the 38 individuals found within the transects and analyzed it independently.

4.3.4 Paca reproduction and hunting

We trained local hunters in the YMR community and in 5 ASDR communities to remove all abdominal and pelvic organs from harvested specimens and to store these materials in buffered 4% formaldehyde solution (Mayor et al. 2017). From 2000 to 2015, local hunters collected and voluntarily donated genitalia from 300 female pacas (212 in the YMR and 88 in the ASDR), each labeled with the hunting date. Since hunters do not consume these organs, we avoided encouraging additional mortality to supply our study. In parallel, between 2000 and 2015 in the YMR, and between 2002 and 2015 in the ASDR, hunters recorded all harvested pacas, including sex and hunting date. In each monitored community in YMR and ASDR, local hunters were provided with datasheets in which they voluntarily recorded information on their daily hunting events. To ensure data were accurately collected, we conducted regular workshops and meetings (at least once per year) with all data providers and members of the participating communities. In this study, we only used the data for harvested females.

4.3.5 Data analysis

We removed the conceptuses from all pregnant females. Using a metal caliper (maximum 300 mm) and a tape measure (1.0 mm accuracy), we measured the crown-rump length and longitudinal length of each embryo or fetus, from rostral edge of nose to distal portion of the tail. Conception dates were determined by backdating the date of collection of each embryo or fetus from their estimated age, using the age formula for paca fetuses in El Bizri et al. (2017). Predicted parturition dates were estimated by summing a standard gestation length of 149 days (Guimarães et al. 2008) to the derived conception dates. We then calculated the monthly number and percentage of conceptions and parturitions during the study period. Hunting data on females collected by local people were also used to calculate the monthly percentage of female pacas harvested in each site within each monitored year (hereafter known as hunting rates). Additionally, we estimated the pregnancy period (from conception to parturition dates) for each paca, and summed the cumulative number of pregnant pacas per month to obtain a monthly percentage of pregnant females among all collected samples in a year (hereafter known as pregnancy rate). We also estimated the monthly percentage of weaned offspring by summing a standard lactation length of 21 days to the parturition dates, which correspond to the period after which the offspring, although still suckling, starts eating solid food (Collett 1981). In addition, we calculated the average longitudinal length of the embryos or fetuses per month in each locality.

We applied generalized additive models for location, scale, and shape (GAMLSS) (Stasinopoulos and Rigby 2007) to assess the relationship between climate, fruiting, paca reproductive events, and hunting. By using GAMLSS, it is possible to test across a wide set of distribution families, ensuring the best fit to the data is selected. Analyses were conducted in 3 sets using a theoretical framework of likely direct relationships between the variables. In set (1), we evaluated the relationship between monthly rainfall (predictor variable) and monthly fruiting percentage in the 3 YMR environments. In set (2), we evaluated the relationship between monthly fruiting percentage in the 3 environments (predictor variables) and paca reproductive events (percentage of conceptions, parturitions, and weaning, and pregnancy rates) for the YMR; in this second set, we also tested rainfall as a predictor variable for conceptions in both areas (YMR and ASDR), since this factor has been reported as a possible cue for conceptions in several mammal species. In set (3), we evaluated the relationship between river water level and paca reproductive events (predictor variables) with hunting rates. For the latter, we calculated the monthly percentage of harvested females in each year in both areas and related these values with the monthly average water level and percentage reproductive events, which were considered constants among months, independently of the year.

We tested all combinations of predictor variables in each set in linear or non-linear forms using different distribution families. Final models were selected based on ∆AIC values, i.e., the difference between the value of Akaike's information criterion (AIC) for the model being evaluated and the model with the lowest AIC value (Burnham and Anderson 2004); ∆AIC values smaller than 2 indicated models with good support. Among these models, we chose the simplest one as final, i.e., the model with fewest degrees of freedom and with fewest predictor variables in the model. We used R 3.3.3 software (R Core Team 2017) for all statistical analyses. GAMLSS were run using the *gamlss* R-package. Values are expressed as the mean ± standard deviation ($\overline{X}$ ± *SD)*.

4.3.6 Compliance

All research followed guidelines of the American Society of Mammalogists for the ethical use of wild animals in research (Sikes et al. 2016) and was conducted in compliance with the research protocol approved by the Research Ethics Committee for Experimentation in Wildlife at the Dirección General de Flora y Fauna Silvestre from Peru (License 0229-2011-DGFFS-DGEFFS), by the Instituto Chico Mendes for Biodiversity Conservation from Brazil (License SISBIO No 29092-1), and by the Committee on Ethics in Research with Animals of the Federal Rural University of the Amazon (UFRA CEUA protocol 007/2016.

4.4 Results

4.4.1 Ripe fruit availability

We sampled 589 trees and vines in 8,970 m² of upland forests, and 386 trees and vines in 5,150 m² of swamp forests. Fruiting patterns in the YMR varied according to habitat type. In upland forests, fruiting trees were present throughout the year, with peaks in March (6.62% plants fruiting) and December (4.68% plants fruiting; Figure 2). In swamp forests, fruiting peaked between February and May (6.12 ± 0.83% plants fruiting), with no trees fruiting in September and October. *Mauritia flexuosa* showed marked fruiting during the low rainfall period (May - August), with the highest number of fruiting trees recorded in June (34.21%); no fruits were observed during the remaining months of the year (Figure 2). Upland forest fruiting was positively correlated with rainfall (Figure 3, Table 1), but there was no correlation between rainfall and *M. flexuosa* or swamp forest fruiting (Table 1).

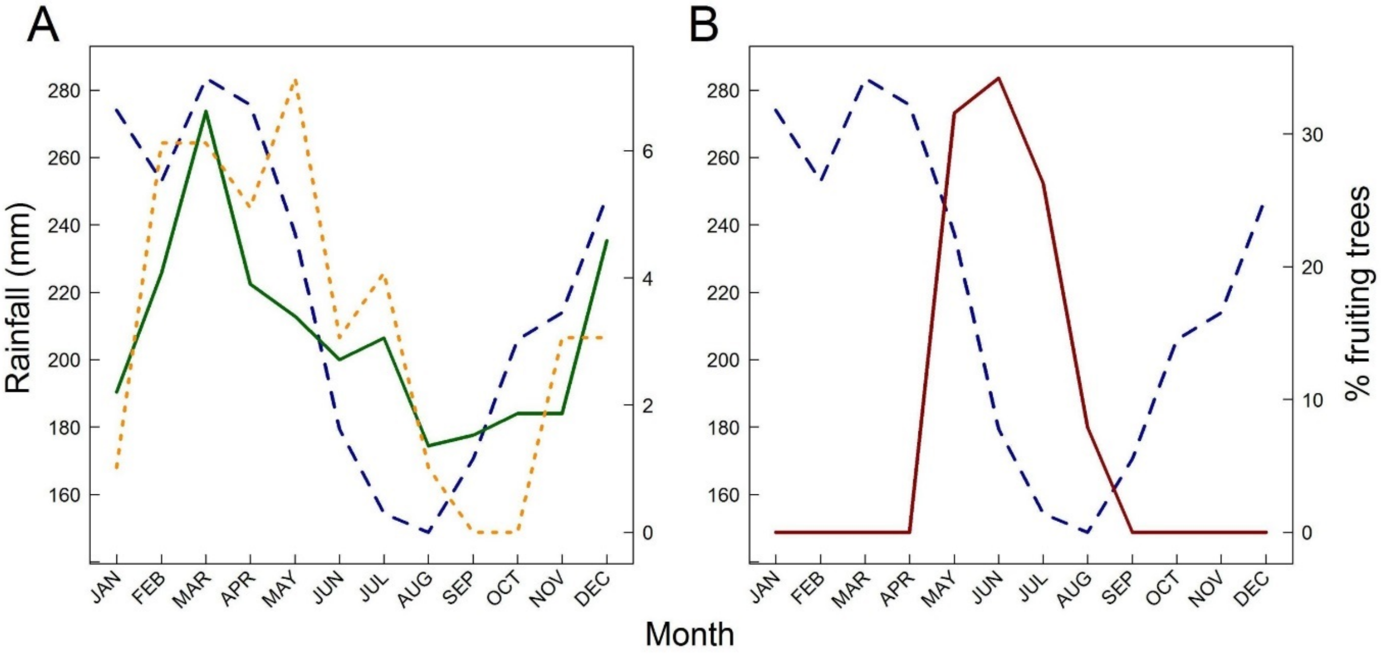


Figure 2. Trends in (A) rainfall (dashed line) and percentage of trees bearing fruits in upland forests (solid line) and swamp forest (dotted line); and (B) rainfall (dashed line) and percentage of *M. flexuosa* trees bearing fruits (solid line) along the year in the Yavarí-Mirín River, western Amazonia.

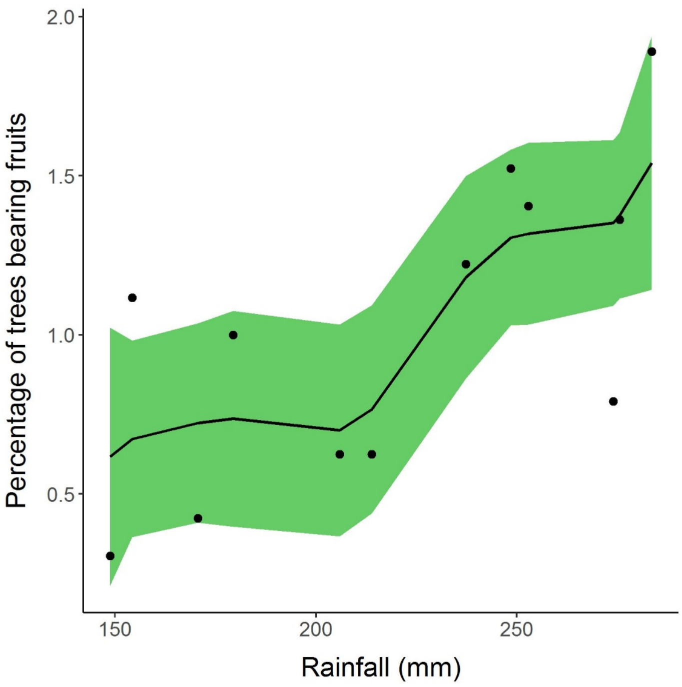


Figure 3. Relationship between rainfall (mm) and percentage of trees bearing fruits in upland forests in the Yavarí-Mirín River, western Amazonia. The gray area represents 95% confidence intervals. The response variable is plotted on the y-axis in a scale of variation around the mean (μ = 0) calculated from the original data used to build the model.

4.4.2 Paca reproductive seasonality

There were 157 (52.3%) pregnant pacas among all sampled females, 100 (47.2%) in the YMR and 57 (64.8%) in ASDR (Figure 4). Average fetal length was 11.30 ± 10.58 cm in the YMR and 17.43 ± 9.74 cm in the ASDR, with a significant difference between sites ($t_{155} = 3.59$, $P < 0.01$). Paca reproductive events occurred during different periods of the year in the 2 study sites. In YMR, conceptions occurred mainly between October and January (50.0%), while parturitions primarily took place between March and June (49.0%). In ASDR, most conceptions occurred between March and June (45.6%), while most parturitions happened between August and November (42.1 %; Figure 5). Nevertheless, conceptions and parturitions occurred throughout the year in both sites. There was a positive relationship between conceptions and rainfall in both study sites (Figs. 6A and B), but there was a negative relationship between conceptions and fruiting in upland forests in the YMR (Figure 6C; Table 1). Pregnancy rates were positively associated with fruiting in upland forest (Figure 6D), while the higher weaning rates were related to higher fruiting periods in swamp forest (Figure 6E) and of *M. flexuosa* (Figure 6F, Table 1). On the other hand, there was no relationship between parturition and fruiting in any environment (Table 1).

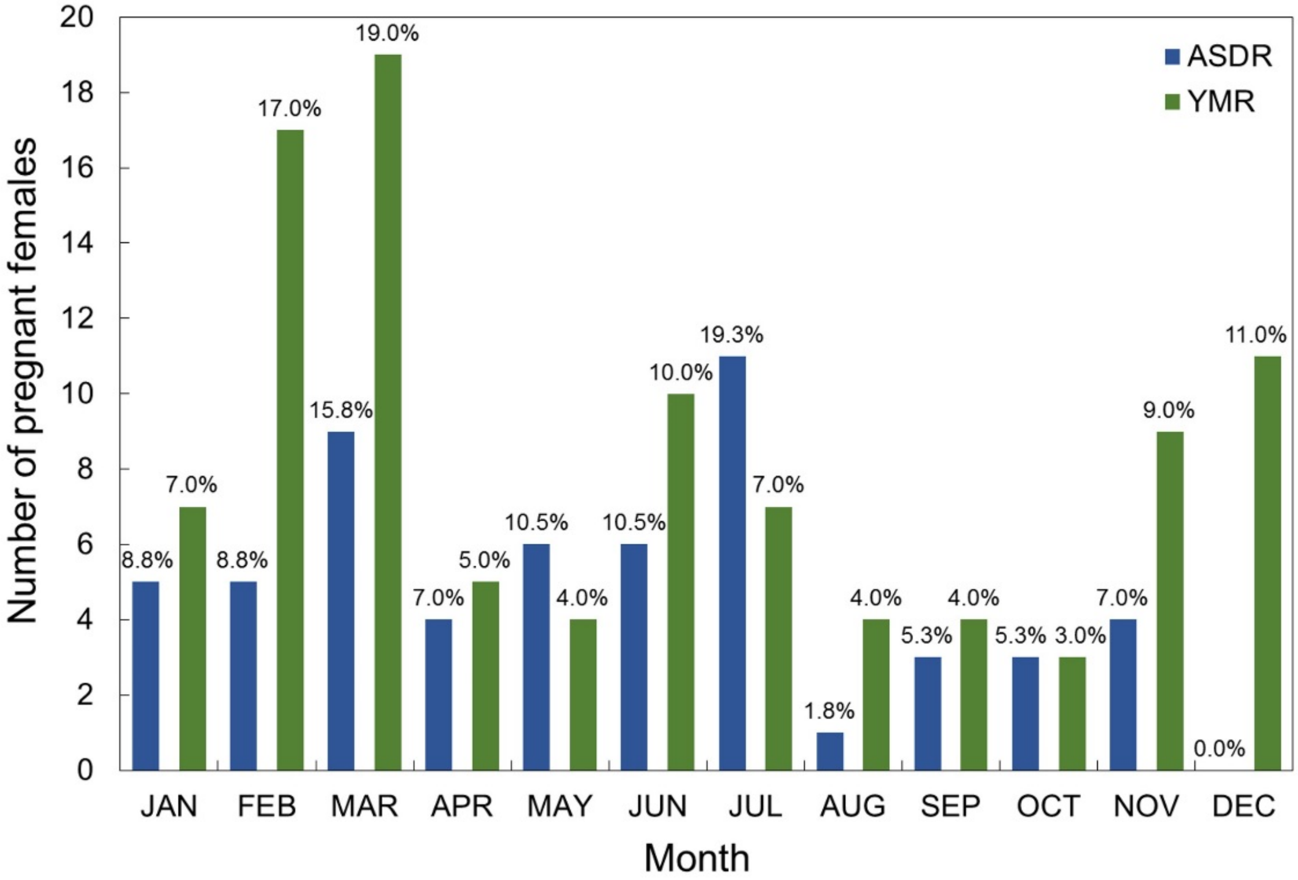


Figure 4. Number and percentage of lowland paca (*Cuniculus paca*) samples that included a uterus showing signs of pregnancy, collected in each month over the monitoring years in the Amanã Sustainable Development Reserve (ASDR) and Yavarí-Mirín River (YMR), Amazonia.

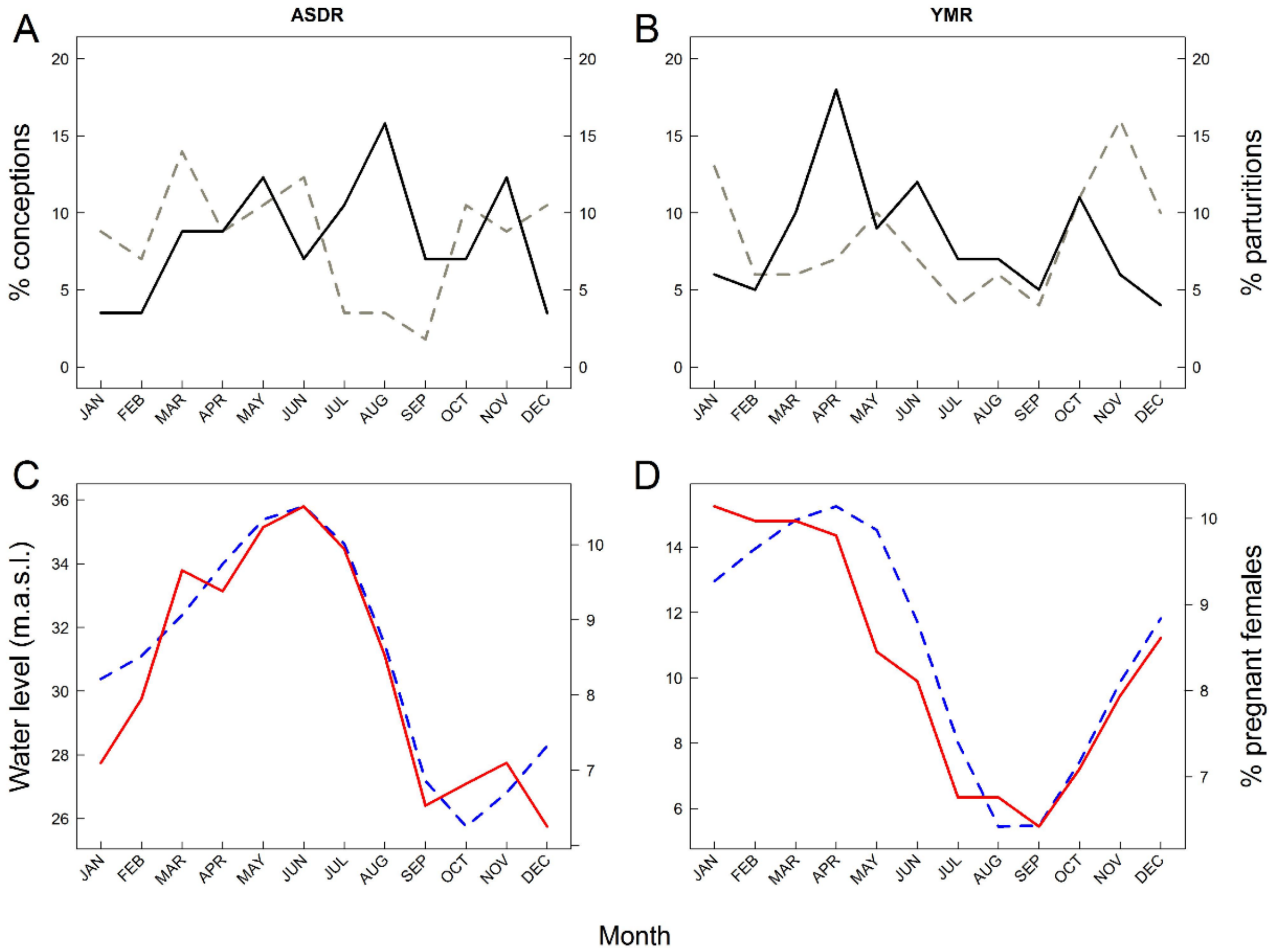


Figure 5. Trends in (A, B) the percentage of paca conceptions (dashed gray lines) and parturitions (solid black lines); and (C, D) average river water level (dashed lines) and percentage of pregnant female pacas (solid lines) along the year in the Amanã Sustainable Development Reserve (ASDR) and Yavarí-Mirín River (YMR), Amazonia.

4.4.3 Hunting vulnerability of pregnant pacas

A total of 803 harvested paca females were recorded in the communities, 288 in the YMR and 515 in the ASDR. Hunting rates varied between months, which were cyclical along the years (Figs. 7A and B) and showed a positive relationship with the river water level in both study sites (Figs. 7C and D, Table 1). A strong positive relationship between hunting rates and pregnancy rates was observed (Figs. 7E and F, Table 1). There were no relationships between conceptions, parturitions, and weaned offspring and hunting rates (Table 1).

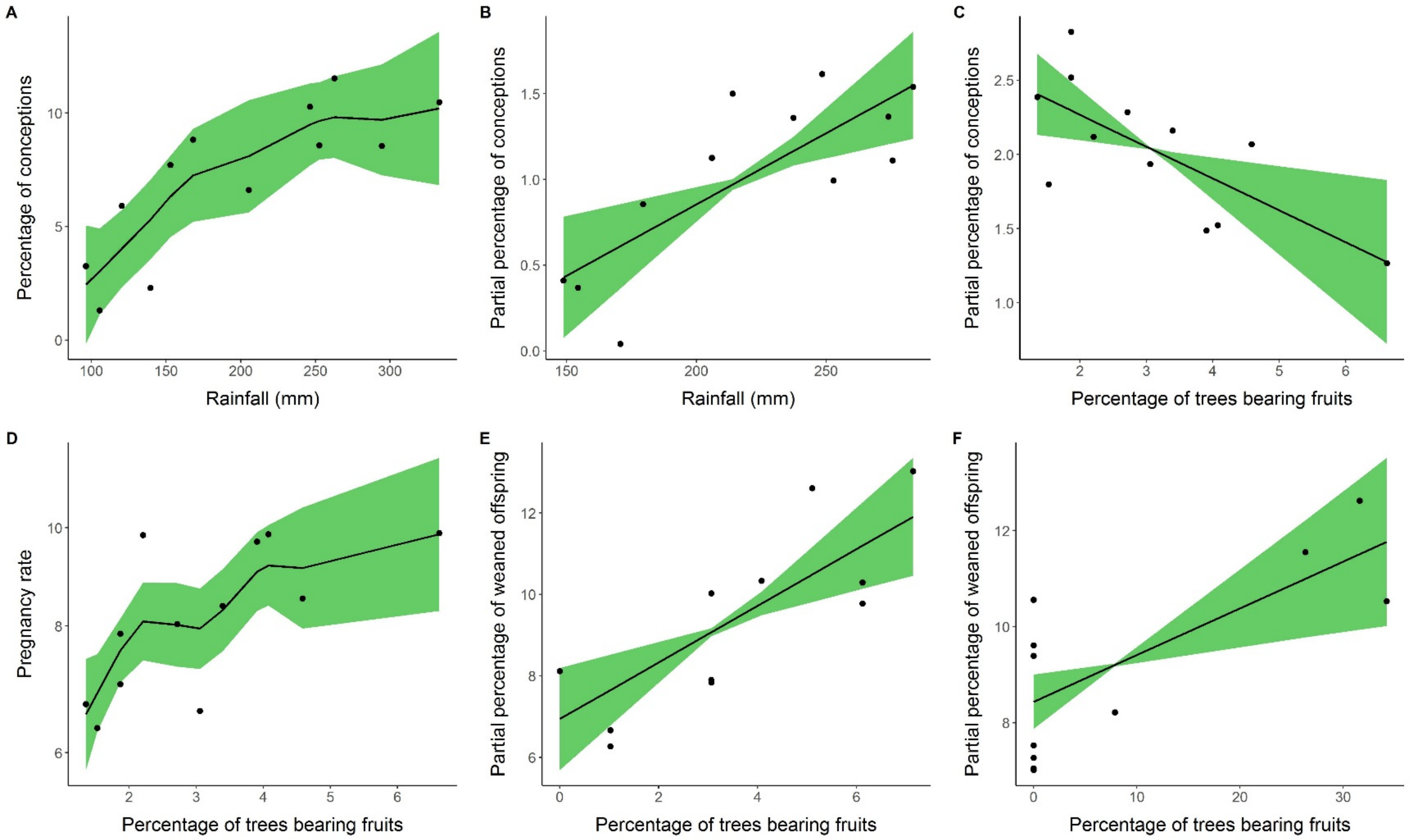


Figure 6. Relationship between (A) rainfall and the percentage of paca conceptions in the Amanã Sustainable Development Reserve, central Amazonia; (B) rainfall and percentage of paca conceptions in the Yavarí-Mirín River, western Amazonia; (C) percentage of trees bearing fruits in upland forest and percentage of paca conceptions in the Yavarí-Mirín River, western Amazonia; (D) percentage of trees bearing fruits in upland forest and pregnancy rate in the Yavarí-Mirín River, western Amazonia; (E) percentage of trees bearing fruits in swamp forest and percentage of weaned offspring, and (F) percentage of *M. flexuosa* trees bearing fruits and percentage of weaned offspring in the Yavarí-Mirín River, western Amazonia. The green area represents 95% confidence intervals. The points are normalized residuals.

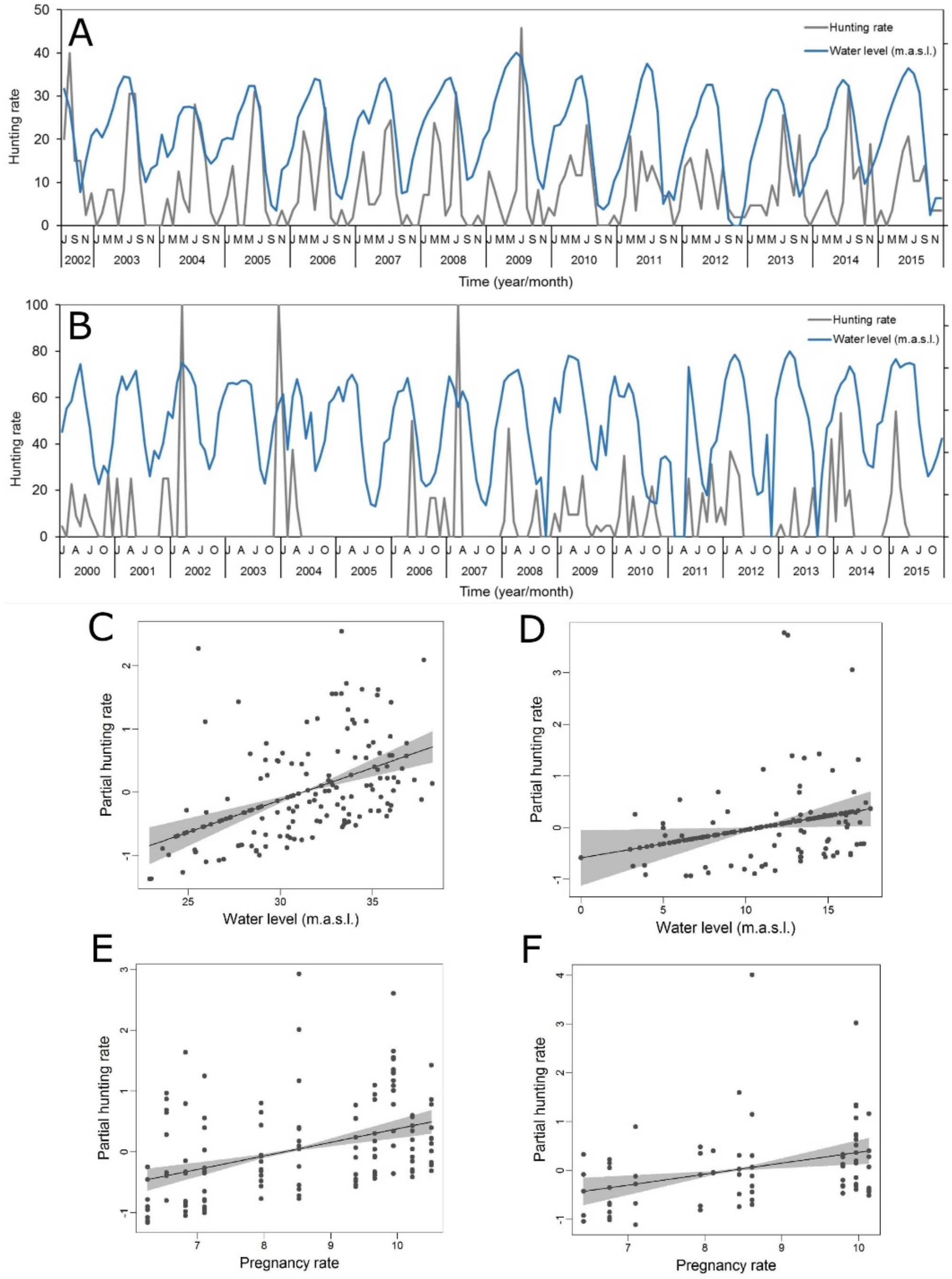


Figure 7. Temporal trends of the river water level and hunting rates (monthly percentage of harvested females within each year) in the (A) Amanã Sustainable Development Reserve, and (B) Yavarí-Mirín River, in Amazonia. Relationship between river water level and hunting rates in the (C) Amanã Sustainable Development Reserve and (D) Yavarí-Mirín River, in Amazonia. Relationship between pregnancy rate and hunting rates in the (E) Amanã Sustainable Development Reserve and (F) Yavarí-Mirín River, in Amazonia. The gray area represents 95% confidence intervals. Response variables are plotted on the y-axis in a scale of variation around the mean (μ = 0) calculated from partial normalized residuals of the models.

4.5 Discussion

4.5.1 Paca reproductive seasonality and fruit availability

Although pregnant females were present year-round in our study sites, most pregnancies occurred during periods of greater fruit availability in upland forests, when rainfall was highest. The greater food supply during this period can sustain larger numbers of pregnant females. When most females are in their last third of gestation, a period of greatest absolute fetal growth and when pregnant individuals demand more energy, fruit availability is, in fact, at its peak. A similar pattern has been observed for the ring-tailed coati (*Nasua nasua*) where the gestation period, concentrated between November and March, coincided with greater fruit availability in upland and swamp forests in the YMR (Mayor et al. 2013*a*). However, mammals with less selective diets are aseasonal breeders, as in the case of the white-lipped peccary (*Tayassu pecari*), collared peccary (*Pecari tajacu*), and the red brocket deer (*Mazama americana*) (Mayor et al. 2009, 2010, 2011), because these species consume green leaves, insects, and small vertebrates when fruit is less available (Dubost and Henry 2017). This pattern has also been confirmed by Dubost and Henry (2017) in French Guiana, who showed that mammals that consume more fruits were highly seasonal breeders.

4.5.2 Changing energy demands and seasonality in food supply

There is evidence from Amazonia that a seasonal increase in rainfall triggers fruit maturation in several habitat types, including non-flooded forests (Haugaasen and Peres 2005). Since rainfall and river water levels vary in different regions of the Amazon, reproductive events of the paca occur at different phases of the year in each of our studied sites, according to local variations in climate and fruit production. Paca reproduction is therefore plastic and opportunistically seasonal (Mayor et al. 2013*b*). Thus, for fruit-dependent species, rainfall, in contrast to photoperiod, may drive conceptions to take place some months prior to fruit ripening, and pregnancies and births will coincide with the period of higher fruit abundance. The observation made by Dubost and Henry (2006) that non-pregnant pacas consumed less seeds than pregnant animals also suggests that conceptions occur during periods of low food availability so that pregnancies mostly occur during periods of higher fruit and seed availability. Our results also show that the greatest number of conceptions occurred when fruit availability in upland forests was low; pregnant pacas could take advantage of the subsequent periods of greater food supply. Similarly, in free-ranging, provisioned rhesus macaques (*Macaca mulatta)* on islands in Puerto Rico, more conceptions occurred during the spring rainfall period, just before the main tree-fruiting season (Rawlins and Kessler 1985).

In Amazonia, swamp forest species and *M. flexuosa* in particular (the most important source of food during the drought period) play a major role in sustaining lactating females and their young, which start weaning during the low-water period. Since during lactation females consume up to 5 times more food than before pregnancy (Randolph et al. 1977), the availability of ripe fruits during this period is of extreme importance. For several species of flying foxes (*Pteropus* spp.), O'Brien (1993) showed that lactation and offspring weaning occur during periods when fruit supply is at its peak. In addition, Lee et al. (2017) showed that giraffe (*Giraffa camelopardalis*) calves born during the dry season in Tanzania had a higher survival probability due to the greater energy reserves accumulated by mothers during the rainy season as well as the higher protein concentration of available browse during the late dry-season rains.

4.5.3 Hunting and reproduction in quarry species

Different prey can cope with human harvest according to their population dynamics and biological capacity (Cardillo et al. 2005), but their patterns of reproduction reflect their response to environmental and human disturbance. Predator–prey systems often co-evolve slowly through generations by the action of natural selection, with the appearance of phenotypical and behavioral traits in prey species that avoid their extinction (Kooijman and Lika 2014). However, the current reproductive strategies in wild species are not adapted to the typically more intensive levels of human predation, especially when hunting is directly impacting pregnant females and affecting the species' recruitment potential.

Water levels and hunting rates were shown to have a similar cyclical pattern over the period of 15 years for which data were available. Other studies in the Amazon basin have also demonstrated that hunters maximize their captures by taking into account seasonal water level changes (Kvist et al. 2001; Endo et al. 2016). This temporal convergence between heavier hunting and pregnancies in pacas is thus likely to adversely impact the species' population dynamics. A probable indication that hunting of pregnant paca females during high-water periods may affect populations of the species is available for the ASDR, where Valsecchi et al. (2014) demonstrated that paca hunting is unsustainable and the species' abundance at this site significantly dropped over an 8-year period.

Table 1. Details of the best-fit models using GAMLSS for each response variable, with the family of distribution, ΔAIC in relation to the null model (ΔAIC null), and generalized R^2. Non-linear effects were fit using cubic spline (*cs*) functions provided by *gamlss* R-package. Families of distributions are represented by log-Normal (LOGNO), Normal (NO), Zero-Adjusted Gamma (ZAGA), Gamma (GA), Box-Cox t (BCTo), inverse Gaussian (IG), Gumbel (GU), Inverse Gamma (IGAMMA) and reverse Gumbel (RG). Generalized R^2 were calculated using the function Rsq of the *gamlss* package. Null models are indicated by 1.

Best fitted model[a]						
Response variables	Predictor variables	Estimate	*P*-value	Family of distribution (link function)	ΔAIC null	Generalized *R*²
Yavarí-Mirín River						
Fruiting						
intercept +		-0.4638	0.29			
% plants fruiting U.F.	*cs*(rainfall)	0.0068	0.011	LOGNO (identity)	5.45	62.0
intercept +		3.3163	<0.001			
% plants fruiting S.F.	1	-	-	NO (identity)	0	
intercept +		3.2189	<0.001			
% plants fruiting *M.f.*	1	-	-	ZAGA (log)	0	
Paca reproductive events						
intercept +		0.8665	0.085			
% conceptions	rainfall	0.0083	0.011	LOGNO (identity)	3.97	48.5
	% plants fruiting U.F.	-0.2147	0.027			
intercept +		2.120	<0.001			
% parturitions	1	-	-	IG (log)	0	
intercept +		6.1337	<0.001			
% weaned offspring	% plants fruiting S.F.	0.6945	0.009	GU (identity)	11.95	73.5
	% plants fruiting *M.f.*	0.0972	0.041			
intercept +		1.8672	<0.001			
pregnancy rate	*cs*(plants fruiting U.F.)	0.0734	0.007	IGAMMA (log)	5.60	67.0
Paca hunting						
intercept +		2.3929	<0.001			
hunting rates	water level	0.0541	0.033	ZAGA (log)	6.02	6.7
	pregnancy rate	0.2239	0.003			
Amanã Reserve						
Paca reproductive events						
intercept +		0.3517	0.83			
% conceptions	*cs*(rainfall)	0.0333	0.001	RG (identity)	3.97	53.6
Paca hunting						
intercept +		-0.9121	0.11			
hunting rates	water level	0.1020	<0.001	ZAGA (log)	7.22	29.1
	pregnancy rate	0.2223	<0.001			

[a] abbreviations for plants fruiting – U.F.: upland forest; S.F.: swamp forest; *M.f.*: *Mauritia flexuosa*.

4.5.4 Management implications

Pacas provide the largest proportion of wild meat consumed by local populations and even urban dwellers in the Amazon (Bodmer and Lozano 2001; Suárez et al. 2009; van Vliet et al. 2015). However, the species has a relatively low reproductive output, in which females only produce 1 young per pregnancy (Mayor et al. 2013*b*; El Bizri et al. 2017, Mayor et al. 2016). The results presented here highlights the necessity for developing sustainable harvest strategies that are compatible with the target species' life history and their reproductive patterns. These strategies could include focusing hunting efforts on males or reducing hunting during the pregnancy season. However, avoiding hunting pacas during high water levels may not be possible for hunters. During the flooded period, fishing becomes difficult and hunting becomes the main source of meat supply during this period (Valsecchi et al. 2014; Endo et al. 2016), thus making it unlikely for a shift away from hunting pacas during the wet season. On the other hand, since male pacas can fertilize several females, hunting males exclusively during the high-water period, when pregnant females are more common, is feasible since rural Amazonian hunters pursue pacas by "spotlighting" (Valsecchi et al. 2014), thus permitting the identification of the sex of the animal and even the pregnancy stage of females (H. R. El Bizri, pers. obs.).

Another strategy to improve the state of hunted paca populations is to encourage the use of rotating hunting areas over the years or to protect areas during the hunting season that could act as refugia for females. This strategy would create a source-sink system where protected grounds would function as sources of individuals to repopulate areas depleted by hunting. This strategy has already been advocated as efficient to conserve species such as the culpeo fox (*Pseudalopex culpaeus*) in the Argentine Patagonia (Novaro et al. 2005) as well as ungulates in the Neotropics (Novaro et al. 2001; Naranjo and Bodmer 2007). A similar approach was effectively applied to recover giant Arapaima (*Arapaima gigas*) populations by encouraging community-based source-sink schemes; this system is now successfully applied throughout the Amazon (Campos-Silva et al. 2017). Here, we argue that source-sink systems could be equally applied for pacas. However, as all systems, these also need to be continuously monitored and adapted especially because the demand for paca meat is likely to increase in line with human population growth. Thus, additional measures such as setting quotas of the paca population that can be harvested per family, hunter, or community may be needed. Finally, since palm species are essential for pacas, and probably other Amazonian species, to achieve their highest reproductive potential, actions focused on conservation of swamp forest palm species, which are largely exploited by humans (Peters et al. 1989; Rull and Montoya 2014), are also critical.

Due to the fact that most hunting in Amazonia is determined by the annual variation in river water level, we argue that the impact we have observed in pacas could be mirrored in other species, and hence might affect the sustainability of wild meat, so vital for numerous inhabitants. Accordingly, strategies that ensure the sustainability of hunted Amazonian species must be based on reproductive information to minimize the impact on their populations when they are most vulnerable.

4.6 Acknowledgments

We sincerely thank the people from the Yavarí-Mirín River and the Amanã Sustainable Development Reserve, without whom this work would not be possible. We also thank J. R. Gonçalves for making the map, and T.Q. Morcatty for aid in the statistical analysis. This work was supported by the Gordon and Betty Moore Foundation, the National Council for Scientific and Technological Development (CNPq) [grant numbers 300005/2013-0; 452908/2016-7; 201475/2017-0], the IVITA (Instituto Veterinario de Investigaciones de Tropico y de Altura), the Museo de la Universidad Nacional de la Amazonía Peruana, the Earthwatch Institute and the Fundacion Autonoma Solidaria.

4.7 References

Aquino, R., Gil, D., Pezo, E. 2009. Aspectos ecológicos y sostenibilidad de la caza del majás (*Cuniculus paca*) en la cuenca del río Itaya, Amazonía peruana. *Revista Peruana de Biología* 16:67-72.

Ayres, J. M. 1986. *The white Uakaris and the Amazonian flooded forests*. PhD dissertation, University of Cambridge, UK.

Beck–King, H., Helversen, O., Beck–King, R. 1999. Home Range, population density, and food resources of *Agouti paca* (Rodentia: Agoutidae) in Costa Rica: A study using alternative methods. *Biotropica* 31(4):675-685.

Bodmer, R. E., Lozano, E. P. 2001. Rural development and sustainable wildlife use in Peru. *Conservation Biology* 15:1163-1170.

Bronson, F .H. 1985. *Mammalian reproduction: an ecological perspective. Biology of Reproduction* 32:1-26.

Burnham, K.P., Anderson, D.R. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research* 33:261-304.

Bunnefeld, N., Baines, D., Newborn, D., Milner-Gulland, E. J. 2009. Factors affecting unintentional harvesting selectivity in a monomorphic species. *Journal of Animal Ecology* 78:485–492.

Campos-Silva, J. V., Peres, C. A., Antunes, A. P., Valsecchi J., Pezzuti, J. 2017. Community-based population recovery of overexploited Amazonian wildlife. *Perspectives in Ecology and Conservation* 15:266-270.

Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R. P., Sechrest, W., Orme, C.D.L., Purvis, A. 2005. Multiple causes of high extinction risk in large mammal species. *Science* 309(5738):1239-1241.

Caughley, G. 1977. *Analysis of Vertebrate Populations*. John Wiley & Sons, London, United Kingdom.

Collet, S.F. 1981. *Population characteristics of Agouti paca (Rodentia) in Colombia*. Michigan: Michigan State University, East Lansing, USA.

Dubost, G., Henry, O., Comizzoli, P. 2005. Seasonality of reproduction in the three largest terrestrial rodents of French Guiana forest. *Mammalian Biology* 70:93-109.

Dubost, G., Henry, O. 2006. Comparison of diets of the acouchy, agouti and paca, the three largest terrestrial rodents of French Guianan forests. *Journal of Tropical Ecology* 22:641-651.

Dubost, G., and Henry, O. 2017. Seasonal reproduction in Neotropical rainforest mammals. *Zoological Studies* 56:2.

El Bizri, H. R., Morcatty, T., Lima, J., Valsecchi, J. 2015. The thrill of the chase: uncovering illegal sport hunting in Brazil through YouTube™ posts. *Ecology and Society* 20:30.

El Bizri, H. R., da Silva Araújo, L. W., da Silva Araújo, W., Maranhão, L., Valsecchi, J. 2016. Turning the game around for conservation: using traditional hunting knowledge to improve the capture efficiency of Amazon lowland pacas. *Wildlife Biology* 22:1-6.

El Bizri, H. R., Monteiro, F. O. B., de Andrade, R. S., Valsecchi, J., Guimarães, D. A. A., and Mayor, P. 2017. Embryonic and fetal morphology in the lowland paca (*Cuniculus paca*): A precocial hystricomorph rodent. *Theriogenology* 104:7-17.

Endo, W., Peres, C. A., Haugaasen, T. 2016. Flood pulse dynamics affects exploitation of both aquatic and terrestrial prey by Amazonian floodplain settlements. *Biological Conservation* 201:129-136.

Freeman, E. D., Larsen, R. T., Peterson, M. E., Anderson Jr., C. R., Hersey K. R., McMillan, B. R. 2014. Effects of male-biased harvest on mule deer: implications for rates of pregnancy, synchrony, and timing of parturition. *Wildlife Society Bulletin* 38:806-811.

Ginsberg, J. R., Milner-Gulland, E. J. 1994. Sex-biased harvesting and population dynamics in ungulates: implications for conservation and sustainable use. *Conservation Biology* 8:157-166.

Guimarães, D. A. A., Bastos, L. V., Ferreira, A. C. S., Luz-Ramos, R. S., Ohashi, O. M., Ribeiro, H. L. 2008. Características reprodutivas da paca fêmea (*Agouti paca*) criada em cativeiro. *Acta Amazonica* 38:531-538.

Gutiérrez-Granados, G. 2015. Assessment on the size-bias in hunting preferences for bush meat consumption in a Mexican tropical rainforest. *Global Journal of Advanced Biological Sciences* 1:50-54.

Haugaasen, T., Peres, C. A. 2005. Primate assemblage structure in Amazonian flooded and unflooded forests. *American Journal of Primatology* 67:243-258.

Kooijman, S. A., Lika, K. 2014. Resource allocation to reproduction in animals. *Biological Reviews* 89:849-859.

Kvist, L. P., Gram, S., Ore, I. 2001. Socio-economy of flood plain households in the Peruvian Amazon. *Forest Ecology and Management* 150:175-186.

Lee, D. E., Bond, M. L., Bolger, D. T. 2017. Season of birth affects juvenile survival of giraffe. *Population Ecology* 59:45-54.

Marcus, M. J. 1984. *Behavioral ecology of paca (Agouti paca) on Barro Colorado Island, Panama*. Doctoral Dissertation, University of Maine, Orono, USA.

Mayor, P., Bodmer, R. E., Lopez-Bejar, M. 2009. Reproductive performance of the wild white-lipped peccary (*Tayassu pecari*) female in the Peruvian Amazon. *European Journal of Wildlife Research* 55:631-634.

Mayor, P. G., Bodmer, R. E., Bejar, M. L. 2010. Reproductive performance of the wild collared peccary (*Tayassu tajacu*) female in the Peruvian Amazon. *European Journal of Wildlife Research* 56:681-684.

Mayor, P., Bodmer, R. E., Lopez-Bejar, M., López-Plana, C. 2011. Reproductive biology of the wild red brocket deer (*Mazama americana*) female in the Peruvian Amazon. *Animal Reproduction Science* 128:123-128.

Mayor, P., Montes, D., López-Plana, C. 2013a. Functional morphology of the female genital organs in the wild ring-tailed coati (*Nasua nasua*) in the northeastern Peruvian Amazon. *Canadian Journal of Zoology* 91:496-504.

Mayor, P., Guimarães, D. A., López, C. 2013b. Functional morphology of the genital organs in the wild paca (*Cuniculus paca*) female. *Animal Reproduction Science* 140:206-215.

Mayor, P., Pérez-Peña, P., Bowler, M., Puertas, P., Kirkland, M., Bodmer, R. 2015. Effects of selective logging on large mammal populations in a remote indigenous territory in the northern Peruvian Amazon. *Ecology and Society* 20: 36.

Mayor, P., El Bizri, H., Bodmer, R. E. and Bowler, M. 2017. Assessment of mammal reproduction for hunting sustainability through community-based sampling of species in the wild. *Conservation Biology* 31:912–923.

McNaughton, S. 1975. r-and K-selection in Typha. *The American Naturalist* 109:251-261.

Mendieta-Aguilar, G., Pacheco, L. F., and Roldán, A. I. 2015. Dispersión de semillas de *Mauritia flexuosa* (Arecaceae) por frugívoros terrestres en Laguna Azul, Beni, Bolivia. *Acta Amazonica* 45: =45-56.

Milner, J. M., Nilsen, E. B., Andreassen, H. P. 2007. Demographic side effects of selective hunting in ungulates and carnivores: review. *Conservation Biology* 21:36–47.

Naranjo, E. J, Bodmer, R. E. 2007. Source–sink systems and conservation of hunted ungulates in the Lacandon Forest, Mexico. *Biological Conservation* 138:412-420.

Novaro, A. J., Redford, K. H., Bodmer, R. E. 2001. Effect of hunting in source-sink systems in the Neotropics. *Conservation Biology* 14:713-721.

Novaro, A. J., Funes, M. C., Walker, R. S. 2005. An empirical test of source–sink dynamics induced by hunting. *Journal of Applied Ecology* 42:910-920.

Pitman, N., Vriesendorp, C., Moskovits, D. 2003. *Peru: Yavari. Rapid Biological Inventories Report 11*. The Field Museum, Chicago, USA.

Pérez, E. M. 1992. *Agouti paca*. *Mammalian Species* 404:1-7.

Peters, C. M., Balick, M. J., Kahn, F., Anderson, A. B. 1989. Oligarchic forests of economic plants in Amazonia: utilization and conservation of an important tropical resource. *Conservation Biology* 3:341-349.

O'Brien, G. M. 1993. Seasonal reproduction in flying foxes, reviewed in the context of other tropical mammals. *Reproduction, Fertility and Development* 5:499-521.

R Core Team. 2017. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL: https://www.R-project.org/.

Ramalho, E. E., Macedo, J., Vieira, T. M., Valsecchi, J., Marmontel, M., Queiroz, H. L. 2009. Ciclo hidrológico nos ambientes de várzea da Reserva de Desenvolvimento Sustentável Mamirauá – médio rio Solimões, período de 1990 a 2008. *Uakari* 5:61-87.

Randolph, P. A., Randolph, J. C., Mattingly, K., Foster, M. M. 1977. Energy costs of reproduction in the cotton rat *Sigmodon hispidus*. *Ecology* 58:31-45.

Rawlins, R. G., Kessler, M. J. 1985. Climate and seasonal reproduction in the Cayo Santiago macaques. *American Journal of Primatology* 9:87-99.

Read, J., Fragoso, J. M. V., Silvius, K. M., Luzar, J., Overman, H., Cummings, A., Giery, S. T., Oliveira, L. F. 2010. Space, place, and hunting patterns among indigenous peoples of the Guyanese Rupununi region. *Journal of Latin American Geography* 9:213-243.

Rull, V., Montoya, E. 2014. *Mauritia flexuosa* palm swamp communities: natural or human-made? A palynological study of the Gran Sabana region (northern South America) within a Neotropical context. *Quaternary Science Reviews* 99:17-33.

Suárez, E., Morales, M., Cueva, R., Utreras Bucheli, V., Zapata-Ríos, G., Toral, E., Torres, J., Prado, W., Vargas Olalla, J. 2009. Oil industry, wild meat trade and roads: indirect effects of oil extraction activities in a protected area in north-eastern Ecuador. *Animal Conservation* 12: 364-373.

Sikes, R. S., and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy* 97:663–688.

Stasinopoulos, D. M., Rigby, R. A. 2007. Generalized additive models for location, scale and shape (GAMLSS) in R. *Journal of Statistical Software* 23(7):1-46.

Sutherland, W. J. 2000. *The conservation handbook: Techniques in research, management and policy*. Blackwell Science, Oxford, United Kingdom.

Ulloa L., Rodriguez, D., Sanchez, P. 1999. Movimientos y uso del tiempo y el espacio por una guartinaja (*Agouti paca*) en la Sierra Nevada De Santa Marta, Colombia. *Revista de Academia Colombiana de Ciencias* 23:687–694.

Valsecchi, J., El Bizri, H. R., Figueira, J. E. C. 2014. Subsistence hunting of *Cuniculus paca* in the middle of the Solimões River, Amazonas, Brazil. *Brazilian Journal of Biology* 74:560-568.

van Vliet, N., Quiceno-Mesa, M. P., Cruz-Antia, D., Tellez, L., Martins, C., Haiden, E., Oliveira, M. R., Adams, C., Morsello, C., Valencia, L., Bonilla, T., Yagüe, B., Nasi, R. 2015. From fish and bushmeat to chicken nuggets: the nutrition transition in a continuum from rural to urban settings in the Tri frontier Amazon region. *Ethnobiology and Conservation* 4:1-12.

Zapata-Ríos, G., Urgilés, C., Suárez, E. 2009. Mammal hunting by the Shuar of the Ecuadorian Amazon: is it sustainable? *Oryx* 43:375-385.

Chapter 5. Age at sexual maturity, first parturition and reproductive senescence in wild lowland pacas (*Cuniculus paca*): implications for harvest sustainability

Published in *Animal Reproduction Science*

El Bizri, H. R., Fa, J. E., Valsecchi, J., Bodmer, R., & Mayor, P. (2019). Age at sexual maturity, first parturition and reproductive senescence in wild lowland pacas (*Cuniculus paca*): implications for harvest sustainability. *Animal Reproduction Science*, *205*: 105-114. DOI: 10.1016/j.anireprosci.2019.04.009.

5.1 Abstract

Generation length (GL) of a mammal, calculated through the age at sexual maturity, first reproduction and reproductive senescence can be used to assess the capacity of a population of a species to withstand differing amounts of hunting pressure by humans without depletion of animal numbers. Due to the lack of reproductive data for wild mammals, the GL is often difficult to determine for most species. In the present study, the GL parameters were assessed for the wild lowland paca (*Cuniculus paca*) from a sample of 119 female genitalia obtained during a 15-year hunter participatory program in the Amazon. The probability of female pacas being sexually active, with observable ovarian functionality or pregnancy, increased as both body and genitalia masses increased. The average body mass at puberty was 5.46 kg. Puberty was estimated to occur at 4 months of age, from which there was estimation when age at first parturition would occur 9 months after birth. Additionally, there was no indication that there was a decrease in parturition rate at more advanced

ages. The estimated age of first reproduction for pacas was much less than previous estimates, most from assessments of captive animals. In addition, because there was no evidence of reproductive senescence, it is suggested that the average age of mature hunted pacas should be used to determine optimal harvesting rates of pacas by humans. The present study highlights the importance of *in situ* studies on reproduction of animals in their natural habitat because these will yield more accurate reproductive variable estimates than those obtained from captive animals. It is suggested that similar methods be used to accurately assess reproductive parameters of other tropical species that are hunted by humans.

5.2 Introduction

Generation length (GL) for mammals has been defined as the “average age of parents of the current cohort” (IUCN 2001, 2012*a*), and the “age at which half of total reproductive output is achieved by an individual” (IUCN 2004); the latter calculated as the average age at which reproduction occurs first and last in an animal’s life. The GL has been used as a reference time-frame in a multitude of ecological analyses to assess a species extinction risk (Gaillard et al. 2005; Perry et al. 2005; Jiguet et al. 2007; Mace et al. 2008; IUCN 2012*b*). An accurate estimation of the GL of any species is also important in determining its capacity to withstand additional death losses imposed by humans.

Although GL is often difficult to determine due to the paucity of detailed reproductive data from species in their natural habitat, overall patterns are based on published metrics as well as taxonomic and allometric species relationships (e.g., Di Marco et al. 2012; Pacifici et al. 2013). Long-lived species are usually characterized by having a large body size, relatively lower reproductive rates, slower sexual maturation, greater parental care and a long GL (Clutton-Brock 1998; Andrade et al. 2017). Long-lived species are especially vulnerable to hunting pressures; short-lived species of smaller body size, greater reproductive rates, earlier puberty and a shorter GL are generally more resilient to human hunting pressure (Peres 2000; Jerozolimski and Peres 2003; Smucny et al. 2004; Nasi et al. 2008; Ripple et al. 2016, 2017).

Reproductive variables, including the GL of game species, are important elements in most mathematical models used for assessing the capacity of a species' population to withstand hunting by humans at a sustainable level over time (Weinbaum et al. 2013). For example, the intrinsic rate of population increase of a species, r_{max}, is calculated based on the annual birth rate of female offspring, age at first parturition, and age at last parturition during its lifetime (Cole 1954), and is useful in predicting how a target species may respond to various harvesting levels (Greene et al. 1998). Gathering empirical data on the reproductive variables of hunted wild species is laborious. This has meant that r_{max} calculations for most game mammals are based on measures derived from captive animals (Robinson and Redford 1986).

While data from captive animals are important and can be useful, reproductive variables may differ from populations in their natural habitat due to differences in stress levels, lack of natural predation and diseases, and the constancy of resources, mates and territories. Accordingly, if values for reproductive variables from captive animals are used in hunting assessments, they can under or overestimate the numbers of animals that can be sustainably harvested from populations (Miller-Gulland and Akçakaya 2001). In a study of ten Amazonian mammals, wild populations of five species had birth rates that were less than those derived from captive animals (Mayor et al. 2017).

Furthermore, values for reproductive variables currently used to calculate GL such as age at the time of an animal's first and last parturition can differ from estimates for captive animals and, therefore, the data are not reliable for population sustainability assessments.

The lowland paca (*Cuniculus paca*) is a large-sized rodent, currently the most hunted Neotropical species (El Bizri et al. 2015, 2016). Paca reproduction has been extensively studied in captivity for about five decades (see Kleiman et al. 1979; Pérez and Hernandes 1979; Matamoros and Pashov 1984; Smythe 1991). The paca is a polyestrous species with spontaneous ovulation and an estrous cycle of 32.5 (± 3.69) days that breeds throughout the year in captivity (Guimarães et al. 2008). Additionally, the paca is a uniparous species with rare cases of twin gestations (Pérez and Hernandes 1979; Meritt 1989; Oliveira et al. 2003; Oliveira et al. 2007). In the Amazon, the lowland paca in its natural habitat has 1.37 to 1.48 annual parturitions that are seasonally distributed depending on the amounts of fruitification and river water, with a long estimated farrowing interval of 247 to 266 days (Mayor et al. 2013; El Bizri et al. 2018).

In contrast to captive studies, little reproductive data are available for wild pacas. For example, the age at first parturition used for r_{max} calculations, 365 days (Robinson and Redford 1986; Collet 1981) is known to vary between 225 and 703 days (Merrit 1989; Smythe 1991; Nogueira et al. 2006; Belaunde 2008; Guimarães et al. 2008). Because most estimates were obtained from captive populations, this variation may be explained by using differing diagnostic methods and environmental conditions in studies that can affect the behaviour and physiology of the animals. In contrast, an analysis of paca female reproduction for animals in their natural habitat was conducted using dental cementum and these animals reached a maximum age of around 12.5 years, and were still reproductively active (Colett 1981). There is no further detailed information on the decrease of reproduction capacity with aging (i.e., age of reproductive senescence) in pacas and other Neotropical game mammals, and few studies have been conducted to investigate reproductive variables by direct examination of reproductive organs.

In the present study, there was examination of a large sample of genitalia of wild lowland paca females, from which there were calculations of age at sexual maturity and first parturition. From these data, there was also an investigation of whether there was reproductive senescence in the species. These refinements allowed for the discussion of potential effects of using new GL values on the results of models assessing sustainable harvest rates of wild lowland paca populations for human purposes.

5.3 Materials and Methods

5.3.1. Study sites

Materials used in this study were obtained from two study sites, the Yavarí-Mirín River (YMR, 04º19’53” S; 71º57’33” W) and the Amanã Sustainable Development Reserve (ASDR, 01º54’00” S; 64º22’00” W). The YMR is located in the Western Amazon, and encompasses 107,000 ha of continuous upland forests with one single indigenous community of 307 inhabitants. The ASDR is a 2,313,000 ha reserve of predominantly upland forests in the Central Amazon, between the Negro and Japurá Rivers. Approximately 4,000 riverine people inhabit 23 communities and some isolated settlements within ASDR. In both areas, local residents rely mainly on agriculture for income and on hunting and fishing for subsistence. The climate in both study areas is typically equatorial with annual temperatures ranging from

22 to 36ºC, relative humidity of 80%, and annual rainfall between 1500 and 3000 mm.

5.3.2 Biological material and data collection

Local hunters from the one community in the YMR and from five communities in the ASDR were trained to remove abdominal and pelvic organs from hunted animals and to store these in buffered 4% formaldehyde solution (v/v). From 2000 to 2016, local hunters collected and voluntarily donated genitalia from a total of 119 female pacas; 44 in the YMR and 75 in the ASDR. All genitalia were individually labelled with the hunting date and the specimen's body mass.

In addition, between 2002 and 2015, hunters in the ASDR recorded data from all pacas onto datasheets (n = 1027), including sex, body mass and date harvested. Only data related to females (n = 522) were utilized in the present study. All research was conducted in compliance with the research protocol approved by the Research Ethics Committee for Experimentation in Wildlife at the Dirección General de Flora y Fauna Silvestre from Peru (License 0350-2012-DGFFS-DGEFFS), by the Instituto Chico Mendes for Biodiversity Conservation from Brazil (License SISBIO No 29092-1), and by the Committee on Ethics in Research with Animals of the Federal Rural University of the Amazon (UFRA CEUA protocol 007/2016).

5.3.3 Laboratory procedures

Genital organs of females were examined for evidence of conceptuses. In addition, the two ovaries of non-pregnant females were sliced and analyzed using a magnifying glass to evaluate the presence of ovarian structures:

corpora lutea (CL) and antral follicles larger than 2 mm. Two classes of sexually active females were defined: i) pregnant females with conceptuses (i.e., pregnant females); and ii) non-pregnant females with at least one CL and/or large antral follicles (i.e., non-pregnant estrous cycling females) (Mayor et al. 2013). In contrast, non-pregnant females without a CL or large antral follicles were considered to be anestrous.

The tubular genital organs (uterine horns, cervix and vagina) of non-pregnant females as well as the conceptuses of pregnant females were weighed using a digital weigh scale (0.1 g accuracy; characterized as genitalia mass). Uterine characteristics of pregnant females were not assessed.

5.3.4. Data analysis

A one-way ANOVA with a *post-hoc* Tukey test was used to assess whether the average body mass differed among anestrus, estrous cycling-non-pregnant and pregnant females, including the body mass of pregnant females with and without the conceptus mass. A T-test was used to compare the uterine mass between anestrus and estrous cycling females. Generalized Additive Models for Location, Scale and Shape (GAMLSS) (Stasinopoulos and Rigby 2007) with the binomial distribution were used to assess the likelihood of females being sexually active (estrous cycles or pregnancy occurring) based on the body mass for all females in the study and to the genitalia mass for non-pregnant females.

Using the probability curve that was developed, there were calculations of the body mass of individuals with a 75% probability of initiation of estrous cycles as a result of pubertal onset and considered this as the average at which most pacas would become pubertal (i.e., pubertal females). There was also calculation of the body mass at which there was a 50% and 100% probability of puberty occurring, using these as the minimum and maximum range of body mass for puberty to occur in females, respectively. There was a subsequent classification as pubertal females of all female pacas that were harvested in the ASDR that were within this body mass range. There was a cross-correlation of the monthly percentages of births in pacas as reported by El Bizri et al. (2018) with the percentages of harvested females that were pubertal to estimate the best fitted time-lag (in months) corresponding to the onset of puberty. The GAMLSS were then used to assess the relationship between the percentage of harvested pubertal females corrected by the selected time-lag and the percentage of births. The same analysis was used to assess the relationship between conceptus mass and pregnant female mass.

To assess whether there is reproductive senescence or a decrease in reproductive rate with advancing age, the GAMLSS analysis was used to evaluate the relationship between the individual body mass of non-pregnant females and the genitalia mass, both in absolute values and relative percentage in relation to the body mass. The existence of an asymptote or decrease in genitalia mass in females with greater body mass may indicate the cessation of capacity to become pregnant at a certain body mass value.

In all GAMLSS models, linear or non-linear relationships and different families of distribution were tested. Families of distribution and final models were selected based on ∆AIC values (Burnham and Anderson 2004), in which ∆AIC < 2 indicated best fit models. Among the best fit models, those with higher coefficient of determination (R^2) obtained using the *Rsq* function were selected. In addition to the AIC ranking, normal distribution of the residuals (Q-Q Plot) was also checked for selecting the best-fitted family of distribution. The R 3.3.3

software (http://www.Rproject.org/) was used for all statistical analyses, and GAMLSS models were tested using the *gamlss* R-package.

5.4 Results

5.4.1 Ovarian structure determinations, genitalia mass and pregnancy diagnosis

Among the females (*n* = 111) for which there were ovarian structures detected that indicated there had been onset of estrous cycles and in which there was pregnancy diagnoses, there were nine that were anestrous (8.1%) and 102 (91.9%) that had initiated estrous cycles. Among females that were post-pubertal, 18 (17.6%) were non-pregnant and 84 (82.4%) were pregnant (Figure 1). Post-pubertal females had a larger body mass (7.4 ± 1.8) compared to anestrous females (4.2 ± 1.6 kg; *F* = 18.36, df = 3, *P*<0.0001), however, there was no difference between post-pubertal non-pregnant and pregnant females when assessments were made with or without conceptus mass (*t* = 0.86, df =166, *P* = 0.39).

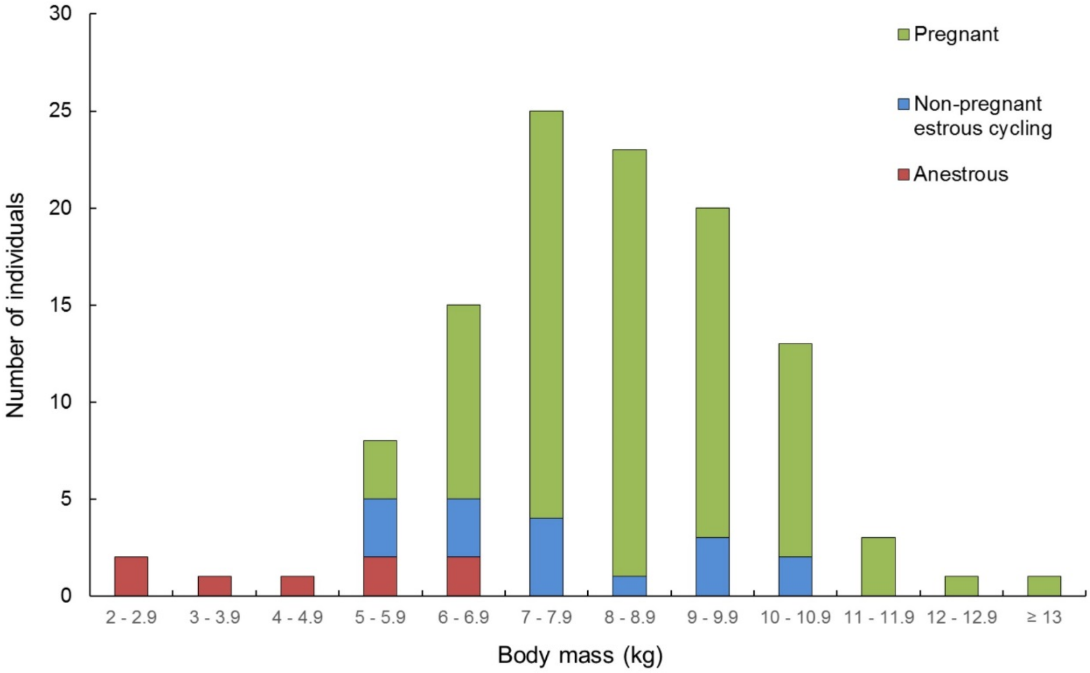


Figure 1. Distribution of number and percentage of lowland paca female genitalia samples according to their reproduction activity diagnosed through ovarian activity and pregnancy (N = 111) along the increase in female body mass in Amazonia.

Estrous cycling females had a larger genitalia mass compared to anestrous females (t = 3.22, df = 25, P = 0.0035; Table 1). Ovarian structures, indicating there had been onset of estrous cycles, were observed in pacas with greater than 5 kg of body mass, and all females with more than 65 g of genitalia mass had ovaries that contained a corpus luteum or large follicles. In addition, the probability of female pacas being estrous cycling increased with an increase in both body and genitalia masses (Figure 2, Table 2).

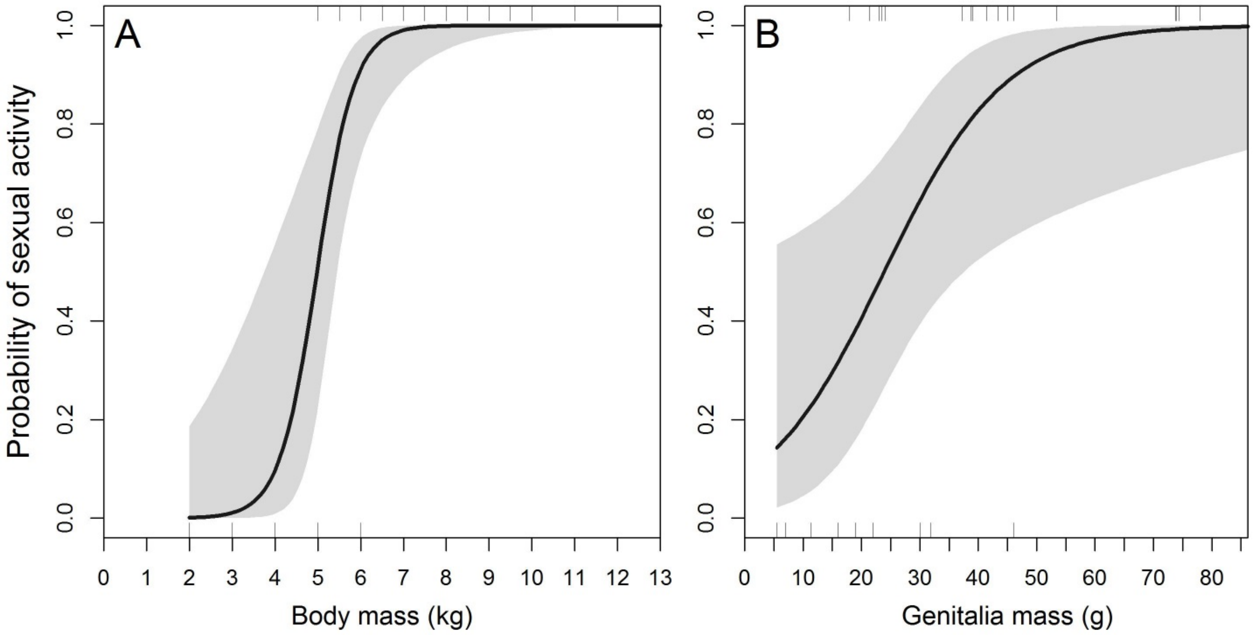


Figure 2. Probability of reproductive tracts being sexually active (estrous cycling or pregnant) in the lowland paca (*Cuniculus paca*), diagnosed A - by the presence of ovarian structures or pregnancy according to body mass; and B - by the presence of ovarian structures according to genitalia mass.

5.4.2 Age at sexual maturity, first parturition and onset of reproductive senescence

Based on the curve between body mass and the probability of females being sexually active (estrous cycling or pregnant) (Sexual activity = $e^{(-11.36+2.28*\text{Body mass})}/1+ e^{(-11.36+2.28*\text{Body mass})}$), there were calculations of the average body mass at the time of puberty to be 5.46 kg (75% of probability), ranging from 4.98 kg (50% of probability) to 6.73 kg (~100% of probability).

Table 1. Categorization of females based on the presence of pregnancy and ovarian structures that are indicative of the onset of estrous cycles along with number of samples and comparison of mean body mass and mass of tubular genital organs; Distinct letters between values within the same column indicate differences $P<0.05$

Category	Ovarian functionality	*n* (Number of samples)	Mean body mass (kg) ± SD	Mean genitalia mass (g) ± SD
Non-pregnant	Inactive	9	4.2 ± 1.6^{a}	20.96 ± 13.16^{a}
	Active	18	7.4 ± 1.8^{b}	46.69 ± 21.92^{b}
Pregnant without conceptus mass	Active	84	8.0 ± 1.5^{b}	-
Pregnant with conceptus mass	Active	-	8.2 ± 1.5^{b}	-
Non-pregnant	Unidentified	8	-	-
Overall	-	119	7.6 ± 1.9	40.61 ± 25.68

Using the probability curve, there was a determination of the number and percentage of pubertal females among all pacas harvested in the ASDR. Monthly percentage of pubertal females peaked in March (24.0%), August (20.9%) and September (25.8%) (Figure 3). There was a positive relationship between percentage births and percentage pubertal females with a -4 months time lag ($r^2 = 0.31$; Figure 4; Table 2). There was also a positive relationship ($r^2 = 0.28$) between conceptus mass and pregnant female body mass (Figure 5, Table 2). Similarly, in non-pregnant estrous cycling females there was an obvious non-linear positive relationship between body mass and the absolute and relative genitalia mass (Figure 6, Table 2).

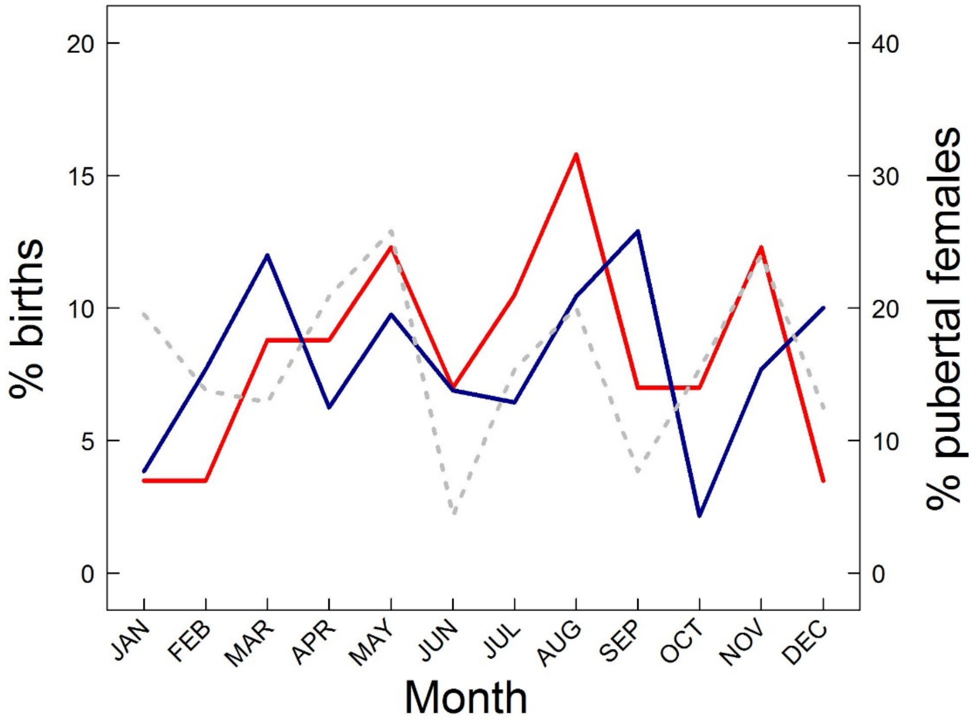


Figure 3. Temporal trend in the monthly percentage of paca births (solid red line) based on El Bizri et al. (2018) and monthly percentage of hunted pubertal females without time lag (solid blue line) and with a -4 month time lag (dashed gray line) in the Amanã Sustainable Development Reserve, Amazonia

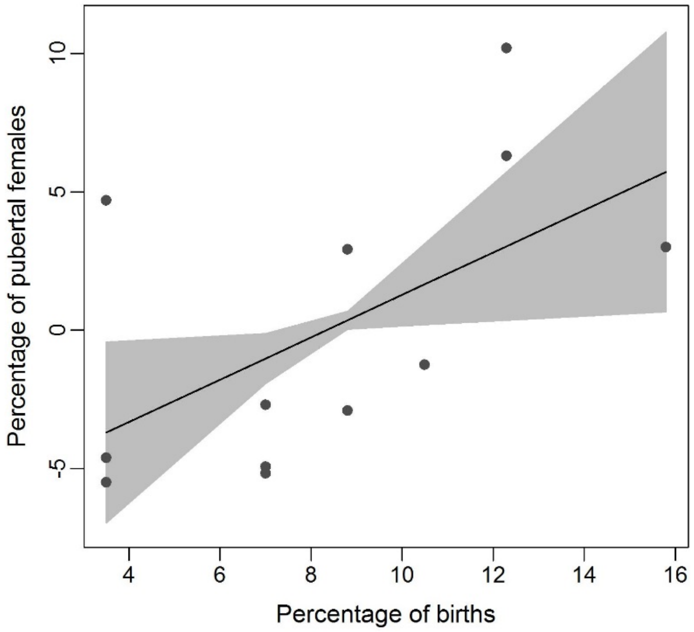


Figure 4. Association between the percentage of pubertal females and the percentage of births with a -4 month time lag in the Amanã Sustainable Development Reserve; response variable is plotted on the y-axis in a scale of variation around the mean (μ = 0) calculated from the normalized residuals used to develop the model.

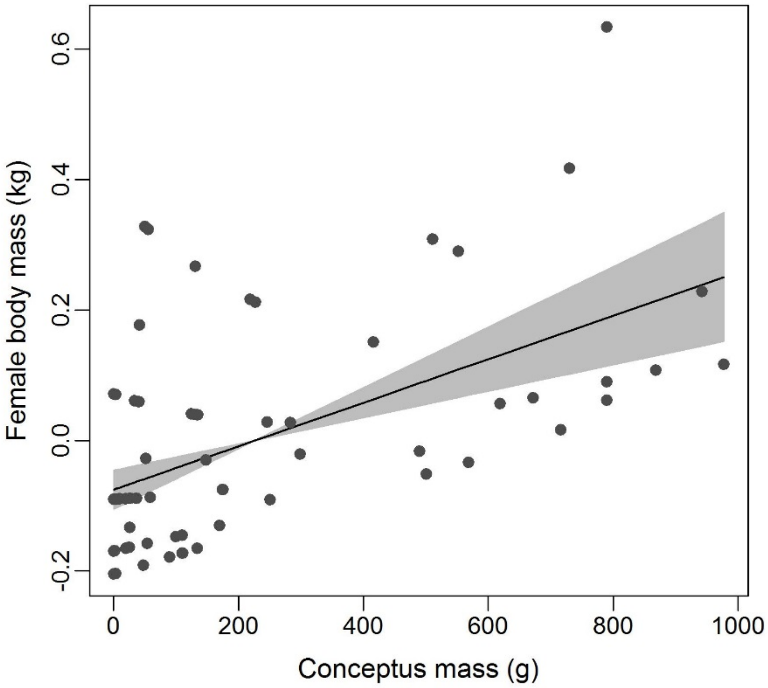


Figure 5. Relationship between conceptus and body mass of pregnant females; response variable is plotted on the y-axis in a scale of variation around the mean (μ = 0) calculated from the normalized residuals used to develop the model.

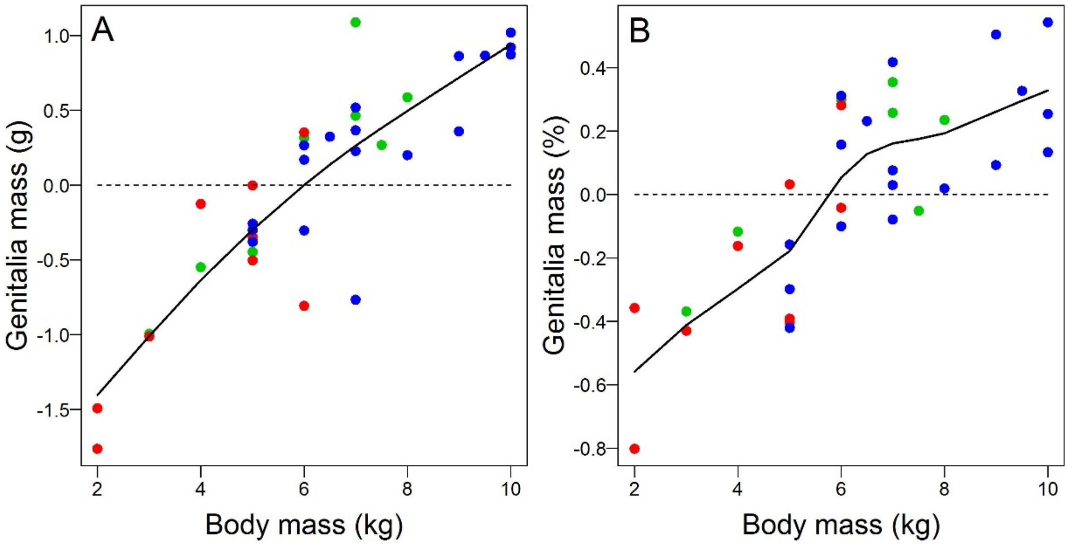


Figure 6. Relationship between body mass and A - absolute mass of tubular genital organs and B – relative genitalia mass of non-pregnant pacas in Amazonia (*n* = 35); Red dots: anestrous females (*n* = 9); blue dots: estrous cycling females (*n* = 18); green dots: ovarian characteristics unidentified due to lack of ovaries (*n* = 8); dashed line represents the average absolute genitalia mass (40.61 g) and average relative genitalia mass (0.006%), while the y-axis is in a scale of variation around the mean (μ = 0) calculated from the normalized residuals used to develop the model.

Table 2. Details of the best-fit models using GAMLSS for each response variable, with the family of distribution, delta AIC in relation to the null model (ΔAIC null) and generalized R^2 Non-linear effects were fit using penalized beta splines (*pb*) and cubic smoothing splines (*cs*) functions provided by gamlss R-package; Families of distributions are represented by Binomial (BI), Gumbel (GU), Weibull (WEI3), Generalized Gamma (GG) and Box-Cox t original (BCTo); Generalized R^2 were calculated using the function *Rsq* of the gamlss package

Best fitted model		Estimate	*P* (*P*-value)	Family of distribution	ΔAIC null	Generalized R^2
Response variables	Predictor variables					
Sexual activity						
Presence of ovaries' structures/pregnancy	Body mass (kg)	2.281	0.0035	BI	37.71	30.07
Presence of ovaries' structures	Genitalia mass (g)	0.097	0.0286	BI	8.82	33.01
% Hunted pubertal females – 4 months	% Births	0.766	0.0376	GU	2.53	31.42
Pregnancy						
Female body mass (kg)	Conceptus mass (g)	0.00033	<0.0001	WEI3	19.30	27.58
Reproductive senescence						
Non-pregnant genitalia mass (absolute values)	*pb*(Body mass)	0.283	<0.0001	GG	46.94	57.07
Non-pregnant genitalia mass (relative values)	*cs*(Body mass)	0.114	<0.0001	BCTo	18.51	53.11

5.5 Discussion

Reproductive variables such as age at sexual maturity, age at first parturition and decreased reproductive rate as a result of aging in a game species are important for determining the sustainability of populations of hunted species. In the present study, it was possible to obtain more realistic measures of these variables by using genitalia of animals that were harvested in their natural habitat. Ovarian functionality was initiated in pacas that had about 5.5 kg of body mass. There was determined that these pubertal pacas would have about 4 months of age. In addition, all females larger than 6.5 kg were pregnant or had ovaries that did contained a corpus luteum and/or large follicles indicating there had been onset of estrous cycles, thus all pacas with these ovarian structures or pregnancy were considered to be sexually mature. If a pregnancy length of 149 days is considered (Guimarães et al. 2008), first parturition in the pacas in their natural habitat would occur from 9 months of age onwards. This is much earlier in life than most of these previous estimates for this species where parturition on the average was estimated to occur at about 1 year of age (Collett 1981; Merrit 1989; Smythe 1991; Nogueira et al. 2006; Belaunde 2008; Guimarães et al. 2008).

Although this estimate indicates that sexual maturity happens earlier in life than was previously thought to occur, this value is validated by body mass growth curves for pacas. Available body mass growth curves indicate that the female paca would weigh 4.54 (Collett 1981), 4.65 (Rodríguez and Arroyo 2008), 5.15 (Belaunde 2008), or 8.35 (Santos et al. 2006) kg at 4 months of age. Realizing that there is a broad range in body weights in these various studies, the average of these values (5.67 kg) is consistent with the estimated average body mass for pubertal females in the present study (5.46 kg, 75% of maturity probability). Furthermore, pacas are considered precocial, having a longer gestation period and a relatively greater intrauterine fetal development than several other rodent species. This results in pacas giving birth to well-developed neonates that are relatively independent in their extra-uterine life and with a lesser need for parental care (El Bizri et al. 2017). In precocial species, there is a relatively greater metabolic energy utilization during pregnancy with compensation occurring as a result of less time devoted to lactation and offspring care, leading to earlier maturity of the offspring (Derrickson 1992; Martin et al. 2005). It is, therefore, unlikely that female offspring would require a long maturation period before the time of pubertal onset and ultimately pregnancy occurring.

Previous studies of reproduction of lowland pacas have been conducted using captive animals, so differences between age at sexual maturity and first parturition in the present and past studies may be related to this difference. For example, although pacas are solitary in the wild, animals have been maintained in large colony groups of males and females in some studies. In these situations, first parturitions have been recorded between 14.9 and 23.4 months of age (Merrit 1989; Perez-Torres 1996; Belaunde 2008). The grouping of animals has been imposed in confinement to enhance the reproductive performance in several hystricomorphs. In colonial hystricomorph rodents, such as the wild cavies, *Cavia aperea*, and domestic guinea-pig, *Cavia aperea* f. *porcellus*, puberty occurs in captive females in the presence of males more than 15 days before those housed without males (Trillmich et al. 2006). Furthermore, maintaining individuals in large groups may also result in suppression of reproductive functions (Wasser and Barash 1983; Kaplan et al. 1986; Abbott et al. 1988).

In many rodents, reproductive suppression is a consequence of the relatively lesser concentrations of luteinizing hormone (Faulkes et al. 1990), urinary chemo-signals or pheromones (Brown and MacDonald 1984), or by hierarchical competition where a dominant individual induces stress in subordinates through agonistic behavior. Wild Cape ground squirrel (*Xerus inauris*) females in large groups have a delayed sexual maturation compared to those in smaller groups (Waterman 2002). This reproductive suppression occurs in both captive and wild colonies and it appears as though naked mole-rat (*Heterocephalus glaber*) females in large group environments are reproductively suppressed for their entire lifespan as a result of relatively lesser concentrations of luteinizing hormone than breeding females (Faulkes et al. 1990). In addition, other factors such as photoperiod, temperature and feeding habits in captivity can affect reproduction and may differ substantially from what occurs in the animal's natural habitat (Trillmich 2000). Thus, it is likely that these factors contribute to a delayed sexual maturation in the captive lowland paca.

The present study is the first in which there has been an attempt to assess the onset of reproductive senescence of pacas in their natural habitat using characteristics of reproductive organs as the biological markers to do so. There was no indication, based on findings in the present study, of reproductive senescence because there was no asymptote of genitalia mass or absence of structures indicative of onset of estrous cycles in ovaries in large females. There was a consistent positive relationship between body weight and uterine mass of lowland pacas in the present study, thus, there were no indications of uterine involution occurring in the older pacas, at least in hunted populations. The largest females in the present study were pregnant at the time tissues were collected. These findings indicate pacas can reproduce as their age advances, and possibly at a high rate. This interpretation is plausible considering there is not generally a post-reproductive female lifespan in mammals with this being limited to humans and a few species of toothed whales (Ellis et al. 2018). Consistent with findings in the present study there have been estimates of lowland paca age in a previous study through dental enamel analyses. Findings indicated that when there was not hunting of wild pacas by humans in their natural habitat sites in Colombia, these pacas could be 12.5 years of age and still be reproductively active, while the maximum recorded age was 8 years in sites where harvesting of pacas for human purposes occurred (Collett 1981). This means that senescent paca females are unlikely to exist in hunted populations because larger, and therefore older, individuals are generally harvested for human purposes. These factors can have a substantial effect when considering the effect of paca hunting on population sustainability assessments.

In biological terms, to determine whether there is reproductive senescence in pacas, in-depth studies of pacas in their natural habitat should be conducted because the captive environment may result in an improved fitness and longer lifespan. For example, grey mouse lemur (*Microcebus murinus*) females lived 50% longer in captivity than females in their natural habitat (Hämäläinen et al. 2014). In addition, there needs to be further studies conducted where there is assessment of more precise age data (from skulls) and maturity information from ovaries similar to what occurred in the present study to further ascertain whether there is reproductive senescence in the paca. For paca population sustainability assessments when hunting occurs, the results of the present and a previous study (Collett 1981) indicate there is no cessation of reproduction, thus, it is suggested that the average age at harvest, as a result of hunting of mature female pacas, be considered the age of the last reproduction event.

The implementation of conservation programs for hunted species is often guided by assessments of their vulnerability to extinction or sustainability of hunting (Bowler et al. 2014). Because previous calculations of reproductive processes of pacas are likely biased, refinements in conservation programs should occur as a result of the enhanced knowledge from the present study regarding the age at sexual maturity. These findings imply that there should be substantial changes to calculations of the GL and, in turn, the calculation of intrinsic rate of population growth (r_{max}) for this species. Using the most current calculation of birthrate of female offspring (0.71; Mayor et al. 2017), the age of first reproduction calculated in conducting the present study (9 months, or 0.75 years) and the classic measure of age at last reproduction (12.5 years; Collett 1981), the revised r_{max} for paca would be 0.60. This is greater than the refined value that was recently published (0.54; Mayor et al. 2017), but still 10.4% less than the established estimate (0.67; Robinson & Redford 1986). Hence, even when there is consideration of the findings in the present study that pacas sexually mature earlier than what was previously reported, pacas still reproduce less efficiently than expected when calculations were based on data from previous studies. In addition, pacas produce one offspring per gestation and in Amazonia there is an unexpected seasonal pattern of reproduction that converges with periods when there is greater hunting intensity and consequently the harvesting of a large number of pregnant females for human consumption (Oliveira et al. 2007; Mayor et al. 2013, 2017; Valsecchi et al. 2014; El Bizri et al. 2018). When results of the present and previous studies are considered, there needs to be a critical review of previous population sustainability assessments for the species, and calculations of sustainable yields for future *in situ* management actions (i.e., establishment of hunting quotas) should be more conservative.

The results of the present study indicate that estrous cycling and pregnant females of lowland paca in their natural habitat have a larger body mass than anestrous females. Ovarian functionality was observed in animals with greater than a 5 kg body mass, and all females with more than 65 g genitalia mass had ovaries containing structures indicative that there had been an onset of estrous cycles before the time of harvest. It is estimated that puberty occurs at about 4 months of age, implying that first parturition occurs at 9 months of age. In addition, there is no evidence that reproductive senescence occurs in the lowland paca. The enhanced information, as a result of the present study, about reproduction of the paca should be considered when conducting population sustainability assessments for the species in areas where hunting occurs.

In addition, results of the present study highlight the importance of *in situ* studies in understanding the reproduction of species in their natural habitat. These investigations yield more precise information about factors affecting population size of a hunted species in their natural habitat. As ascertained from results of the present study, age at sexual maturity as well as parturition patterns of species in their natural habitat can be obtained and made available to help refine hunting sustainability models. The manner in which the present study was conducted also emphasizes the opportunities to involve local hunter communities in a participatory manner to allow for the collection of large amounts of biological material (see also Mayor et al. 2017). We recommend this method because users of the resource are themselves able to gain directly from the knowledge generated from such studies.

5.6 Acknowledgements

We sincerely thank all the people from the communities in the Yavarí-Mirín River and the Amanã Sustainable Development Reserve, without whom this work would not be possible. We also thank T. Q. Morcatty for useful suggestions and comments on the manuscript. This research was supported by the Gordon and Betty Moore Foundation [Grant Agreement for Instituto de Desenvolvimento Sustentável Mamirauá, #5344], the National Council of Technological and Scientific Development (CNPq) [grant numbers 300005/2013-0; 452908/2016-7; 201475/2017-0], the IVITA (Instituto Veterinario de Investigaciones de Trópico y de Altura), the Museo de la Universidad Nacional de la Amazonía Peruana, the Earthwatch Institute and the Fundación Autónoma Solidaria.

5.7 References

Abbott, D. H., Hodges, J. K., George, L. M. 1988. Social status controls LH secretion and ovulation in female marmoset monkeys (*Callithrix jacchus*). *Journal of Endocrinology* 117:329-339.

Belaunde, S. A. 2008. *Determinación de parámetros productivos y reproductivos en la zoocria del "jochi pintado" Cuniculus paca*. Tesis de licenciatura en biología, Universidad Autónoma Gabriel René Moreno, Santa Cruz. 95 p.

Bowler, M., Anderson, M., Montes, D., Perez, P., Mayor, P. 2014. Refining reproductive parameters for modelling sustainability and extinction in hunted primate populations in the Amazon. *PloS One* 9(4):e93625.

Brown, R. E., MacDonald, D. W. 1984. *Mammalian Social Odours*. Oxford University Press, Oxford, United Kingdom.

Burnham, K. P., Anderson, D. R. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research* 33:261–304.

Clutton-Brock, T. H. 1988. *Reproductive success*. University of Chicago Press, Chicago and London.

Cole, L. 1954. The population consequences of life-history phenomena. *The Quarterly Review of Biology* 29:103–137.

Collett, S. F. 1981. *Population characteristics of Agouti paca (Rodentia) in Colombia*. Publications of the Museum, Michigan State University, East Lansing, Michigan. *Biological Series Volume* 5:485–602.

de Andrade, R. D. S., Monteiro, F. O. B., El Bizri, H. R., Vicente, W. R. R., de Araujo Guimarães, D. A., Mayor, P. 2018. Fetal development of the Poeppig's woolly monkey (*Lagothrix poeppigii*). *Theriogenology* 110:34-43.

Derrickson, E. M., 1992. Comparative reproductive strategies of altricial and precocial eutherian mammals. Functional Ecology 6(1):57-65.

Di Marco, M., Possingham, H. P., Wilson, K. A., Blomberg, S. P., Boitani, L. Rondinini, C. 2012. A novel approach for global mammal extinction risk reduction. Conservation Letters 5(2):134-141.

El Bizri, H. R., Morcatty, T. Q., Lima, J. J. S., Valsecchi, J. 2015. The thrill of the chase: uncovering illegal sport hunting in Brazil through YouTube™ posts. *Ecology and Society* 20:30.

El Bizri, H. R., da Silva Araújo, L. W., da Silva Araújo, W., Maranhão, L., Valsecchi, J. 2016. Turning the game around for conservation: using traditional hunting knowledge to improve the capture efficiency of Amazon lowland pacas. Wildlife Biology 22:1-6.

El Bizri, H. R., Monteiro, F. O. B., de Andrade, R. D. S., Valsecchi, J., de Araújo Guimarães, D. A., Mayor, P. (2017). Embryonic and fetal morphology in the lowland paca (*Cuniculus paca*): A precocial hystricomorph rodent. *Theriogenology* 104:7-17.

El Bizri, H. R., Fa, J. E., Bowler, M., Valsecchi, J., Bodmer, R., Mayor P. 2018. Breeding seasonality in the lowland paca (*Cuniculus paca*) in Amazonia: interactions with rainfall, fruiting, and sustainable hunting. *Journal of Mammalogy* 99:1101–1111.

Ellis, S., Franks, D. W., Nattrass, S., Cant, M. A., Bradley, D. L., Giles, D., Balcomb, K.C., Croft, D. P. 2018. Postreproductive lifespans are rare in mammals. *Ecology and Evolution* 8:2482-2494.

Faulkes, C. G., Abbott, D. H., Jarvis, J. U. M. 1990. Social suppression of ovarian cyclicity in captive and wild colonies of naked mole-rats, *Heterocephalus glaber*. *Journal of Reproduction & Fertility* 88:559-568.

Gaillard, J. M., Yoccoz, N. G., Lebreton, J. D., Bonenfant, C., Devillard, S., Loison, A., Pontier, D., Allaine, D. 2005. Generation Time: A Reliable Metric to Measure Life-History Variation among Mammalian Populations. *The American Naturalist* 166:119–123.

Greene C., Umbanhowar, J., Mangel, M., Caro, T. 1998. Animal breeding systems, hunter selectivity, and consumptive use in wildlife conservation. In *Behavioral ecology and conservation biology*, edited by T. Caro, pp. 271–305, Oxford University Press, Oxford, United Kingdom.

Guimarães, D. A., Bastos, L. V., Ferreira, A. C. S., Luz-Ramos, R. S., Ohashi, O. M., Ribeiro, H. L. 2008. Características reprodutivas da paca fêmea (*Agouti paca*) criada em cativeiro. *Acta Amazonica* 38:531–538.

Hämäläinen, A., Dammhahn, M., Aujard, F., Eberle, M., Hardy, I., Kappeler, P. M., Perret, M., Schliehe-Diecks, S., Kraus, C. 2014. Senescence or selective disappearance? Age trajectories of body mass in wild and captive populations of a small-bodied primate. *Proceedings of the Royal Society B* 281:20140830.

IUCN. 2001. *IUCN Red List Categories and Criteria*: *Version 3.1*. IUCNSpecies Survival Commission. IUCN, Gland, Switzerland and Cambridge, United Kingdom.

IUCN. 2004. *Guidelines for Using the IUCNRed List Categories and Criteria. Standards and Petitions Subcommittee*. URL: http://www.globaltrees.org/downloads/RedListGuidelines.pdf [accessed 2018-9-11]

IUCN. 2012a. *The IUCN Red List of Threatened Species. Version 2012.2.* http://www.iucnredlist.org [accessed 2018-9-11]

IUCN. 2012b*. IUCN Red List Categories and Criteria: Version 3.1.* Second edition. IUCN, Gland, Switzerland and Cambridge, United Kingdom. http://www.iucnredlist.org/technical-documents/categories-and-criteria [accessed 2018-9-11]

Jerozolimski, A., Peres, C.A. 2003. Bringing home the biggest bacon: A cross-site analysis of the structure of hunter–kill profiles in Neotropical forests. *Biological Conservation* 111:415–425.

Jiguet, F., Gadot, A. S, Julliard, R., Newson, S.E., Couvet, D. 2007. Climate envelope, life history traits and the resilience of birds facing global change. *Global Change Biology* 13:1672-1684.

Kaplan, J. R., Adams, M. R., Koritnik, D. R., Rose, J. C., Manuk, S.B. 1986. Adrenal responsiveness and social status in intact and ovariectomized *Macaca fascicutaris*. *American Journal of Primatology* 11:181-193.

Mace, G. M., Collar, N. J., Gaston, K. J., Hilton-Taylor, C., Akçakaya, H. R., Leader-Williams, N., Millner-Gulland, E. J., Stuart, S. N. 2008

Quantification of extinction risk: IUCN's system for classifying threatened species. Conservation Biology 22:1424-1442.

Martin, R. D., Genoud, M., Hemelrijk, C. K. 2005. Problems of allometric scaling analysis: examples from mammalian reproductive biology. *Journal of Experimental Biology* 208:1731-1747.

Matamoros, Y., Pashov, B. 1984. Ciclo estral del tepezcuinte (*Cuniculus paca*, Brisson), en cautiverio. *Brenesia* 22:249-260.

Mayor, P., Guimarães, D. A., Lopez, C. 2013. Functional morphology of the genital organs in the wild paca (*Cuniculus paca*) female. *Animal Reproduction Science* 140:206-215.

Mayor, P., El Bizri, H., Bodmer, R., Bowler, M. 2017. Assessment of mammal reproduction for hunting sustainability through community-based sampling of species in the wild. *Conservation Biology* 31:912–923.

Merrit, D. 1989. The husbandry and management of the Paca (*Cuniculus paca*) at Lincoln Park Zoo, Chicago. *International Zoo Yearbook* 28:264-267.

Milner-Gulland, E. J., Akçakaya, H. R. 2001. Sustainability indices for exploited populations. *Trends in Ecology and Evolution* 16:686–692.

Nasi, R., Brown, D., Wilkie, D., Bennett, E., Tutin, C., van Tol, G., Christophersen, T. 2008. *Conservation and use of wildlife-based resources: the bushmeat crisis.* Technical Series no. 33, Secretariat of the Convention on Biological Diversity, Montreal, and Center for International Forestry Research (CIFOR), Bogor, Indonesia.

Nogueira, T., Giannoni, M., Toniollo, G. 2006. Observações preliminares sobre a reprodução de uma colônia de pacas *Agouti paca* Linnaeus, 1766 em cativeiro. *Cadernos do CEAM-Núcleo de Estudios Agrários* 6:83-95.

Oliveira, F. S., Machado, M. R. F., Canola, J. C. 2003. Real time B-mode ultrasound in pacas pregnancy (*Agouti paca*, L.1766). *Brazilian Journal of Veterinary Research and Animal Science* 40:73-78.

Oliveira, F. S., Machado, M. R. F., Canola, J. C., Camargo, M. H. B. 2007. Uniparidade em pacas criadas em cativeiro (*Agouti paca*, Linnaeus, 1766). *Arquivo Brasileiro de Medicina Veterinária e Zootecnia* 59:387-389.

Pacifici, M., Santini, L., Di Marco, M., Baisero, D., Francucci, L., Grottolo Marasini, G., Visconti, P., Rondinini, C. 2013. Database on generation length of mammals. 5427 data records. Online at http://doi.org/10.5061/dryad.gd0m3, version 1.0 (last updated on 2013-08-27), Resource ID: 10.5061/dryad.gd0m3, Data Paper ID: doi: 10.3897/natureconservation.5.5734

Peres, C. A. 2000. Effects of subsistence hunting on vertebrate community structure in Amazonian forests. Conservation Biology 14:240-253.

Perez-Torres, J. 1996. *Guía para el manejo y cría de la "Paca" Agouti paca*. Convenio Andrés Bello. Bogotá, Colombia.

Pérez, H. C., Hernández, F. Z. 1979. Comportamiento reproductivo y datos de la alimentación de *Agouti paca*. *Acta Zoologica Lilloana* 35:283-385.

Perry, A. L., Low, P. J., Ellis, J. R., Reynolds, J. D. 2005. Climate change and distribution shifts in marine fishes. *Science* 308:1912–1915.

Ripple, W. J., Abernethy, K., Betts, M. G., Chapron, G., Dirzo, R., Galetti, M., Levi, T., Lindsey, P. A., MacDonald, D. W., Machovina, B., Newsome, T. M., Peres, C. A., Wallach, A. D., Wolf, C., Young, H. Bushmeat hunting and extinction risk to the world's mammals. *Royal Society Open Science* 3:160498.

Ripple, W. J., Wolf, C., Newsome, T. M., Hoffmann, M., Wirsing, A. J., McCauley, D. J. 2017. Extinction risk is most acute for the world’s largest and smallest vertebrates. *PNAS* 114:10678-10683.

Robinson, J. G., Redford, K. H. 1986. Body size, diet, and population density of Neotropical forest mammals. *The American Naturalist* 128:665–680.

Rodríguez, M. A. B., Arroyo, M. D. B. 2008. Efecto de la dieta sobre la ganancia de peso en individuos de *Agouti paca* (Rodentia: Agoutidae) en cautiverio. *Revista Mexicana de Mastozoología* 12:6-16.

Santos, R., Lima, A. L., Barbosa W. A., Vargas Junior, J. G. 2006. Determinação da curva de crescimento em pacas (*Agouti paca* L.) criadas em cativeiro do nascimento ao desmame. IX Encontro Latino Americano de Iniciação Científica e V Encontro Latino Americano de Pós-graduação, Universidade do Vale do Paraíba. Univap, Vale do Paraíba, São Paulo.

Smucny, D. A., Abbott, D. H., Mansfield, K. G., Schultz-Darken, N. J., Yamamoto, M. E., Alencar, A. I., Tardif, S. D. 2004. Reproductive output, maternal age, and survivorship in captive common marmoset females (*Callithrix jacchus*). *American Journal of Primatology* 64:107-121.

Smythe, N. 1991. Steps toward domesticating the paca (*Agouti* = *Cuniculus paca*) and prospects for the future. In *Neotropical wildlife use and conservation*, edited by J. G. Robinson, K. H. Redford, pp. 202–216. University of Chicago Press, Chicago, Illinois, USA.

Stasinopoulos, D. M., Rigby, R. A. 2007. Generalized additive models for location, scale and shape (GAMLSS) in R. *Journal of Statistical Software* 23:1-46.

Trillmich, F. 2000. Effects of low temperature and photoperiod on reproduction in the female wild guinea pig (*Cavia aperea). Journal of Mammalogy* 81:586-594.

Trillmich, F., Laurien-Kehnen, C., Adrian, A., Linke, S. 2006. Age at maturity in cavies and guinea-pigs (*Cavia aperea* and *Cavia aperea f. porcellus*): influence of social factors. *Journal of Zoology* 268:285-294.

Valsecchi, J., El Bizri, H. R., Figueira, J. E. C. 2014. Subsistence hunting of *Cuniculus paca* in the middle of the Solimões River, Amazonas, Brazil. *Brazilian Journal of Biology* 74:560-568.

Wasser, S. K., Barash, D. P. 1983. Reproductive suppression among female mammals: implications for biomedicine and sexual selection theory. *The Quarterly Review of Biology* 58:513-538.

Waterman, J. M. 2002. Delayed maturity, group fission and the limits of group size in female Cape ground squirrels (Sciuridae: *Xerus inauris*). Journal of Zoology 256:113-120.

Weinbaum, K. Z., Brashares, J. S., Golden, C. D., Getz, W. M. 2013. Searching for sustainability: are assessments of wildlife harvests behind the times? *Ecology Letters* 16:99-111.

Chapter 6. Involving local communities for effective citizen science: determining game species' reproductive status to assess hunting effects in tropical forests

Published in *Journal of Applied Ecology*

El Bizri, H. R., Fa, J. E., Lemos, L. P., Campos-Silva, J. V., Vasconcelos Neto, C. F., Valsecchi, J., & Mayor, P. (2020). Involving local communities for effective citizen science: Determining game species' reproductive status to assess hunting effects in tropical forests. *Journal of Applied Ecology*. DOI: 10.1111/1365-2664.13633.

6.1 Abstract

Involving communities in sustainable wildlife management in tropical forests can ensure food security and livelihoods of millions of forest dwellers that depend on wild meat, and also safeguard hunted species. Mathematical models have been developed to assess hunting sustainability; but these require empirical information on reproductive parameters of the prey species, often challenging to obtain. Here, we suggest that if local people can accurately identify the reproductive status of hunted animals in the field, these data could fill the existing knowledge gap regarding species' life-history traits and enable better assessments of hunting impacts. We first tested whether local people in 15 rural communities in three Amazonian sites could accurately diagnose, before and after training, the pregnancy status of hunted pacas (*Cuniculus paca*), which we use as our model. We then applied the results from these tests to correct reproductive status data of hunted specimens, voluntarily collected over 17 years (2002-2018) as part of a citizen science project in one of our study sites. We ran generalized additive models to contrast these corrected reproductive rates with those obtained from the direct analysis of genitalia by researchers, and with indices describing game extraction levels (catch-per-unit-effort, CPUE, and age structure of hunted individuals). Before training, interviewees correctly diagnosed pregnancy in 72.5% of tests, but after training, interviewees accurately diagnosed pregnancy in 88.2% of tests, with high improvements especially for earlier pregnancy stages. Monthly pregnancy rates determined by hunters and by researchers were similar. Reported annual pregnancy rates were negatively correlated with CPUE, and positively correlated with the percentage of immatures in the hunted population, in accordance with an expected density-dependent response to variations in hunting levels. We show that the voluntary diagnosis of game species' reproductive status by local people is a feasible method to obtain accurate life-history parameters for hunted tropical species, and to assess hunting effects on game populations. Given that almost half of the protected areas in the world are co-managed by local people, our results confirm the potential of integrating local communities in citizen science initiatives to ensure faster, low-cost, and more accurate data collection for wildlife management.

6.2 Introduction

Ensuring the sustainability of wildlife hunting in tropical forests is crucial to guarantee the conservation of game species and safeguard the food security and livelihoods of millions of forest dwellers (Coad et al. 2019). Since the early 1990s, a wide range of mathematical models have been developed to assess hunting sustainability (Weinbaum et al. 2013). These models require accurate information on population abundance, reproductive and mortality patterns of the hunted species (Weinbaum et al. 2013).

Reproductive performance of wild vertebrates is usually studied by directly examining animals after capture and restrain, or from direct field observations of births (e.g., Zhang et al. 2007). Because both methods are challenging, especially for tropical forest animals (Fragoso et al. 2016), researchers are limited by the lack of basic information on age of first reproduction, breeding cycles and pregnancy rates of hunted species (Milner-Gulland and Akçakaya 2001). Moreover, such information is also essential for the development of complex demographic models, such as how reproductive rates change in response to the removal of individuals by hunting. These models are rarely applied due to the lack of data; thus, researchers employ simpler ones that perform with much higher uncertainty levels (Weinbaum et al. 2013).

A cost-effective option for gathering large amounts of biological and ecological evidence in the field is via citizen scientists (Dickinson et al. 2010). By involving non-professionals it is possible to obtain vital information on a variety of subjects (Bonney et al. 2014; Steger et al. 2017). In the tropics, indigenous and rural people have been involved in citizen science projects, providing information on animal populations and trends, just as accurately as trained scientists (e.g., Danielsen et al. 2014). Since local communities in tropical forests have extensive knowledge of the environment and are the main direct users of natural resources, their participation in scientific monitoring is central (Pocock et al. 2015).

Mayor et al. (2017) have demonstrated the effectiveness of citizen science through a community-based collection of organs of Amazonian forest mammals to determine reproductive parameters. In this study, local hunters collected and voluntarily donated complete visceras of hunted specimens over an uninterrupted 15-year period. Using this material, Mayor et al. (2017) were able to estimate annual birth rates of female offspring. These estimates differed significantly from those obtained in sustainability assessments that often use data from captive populations.

As shown by Mayor et al. (2017) it is possible to collect accurate reproductive parameters of some hunted species over the long-term through the examination of biological materials brought back to researchers. This is possible for small-bodied animals but not for large species since their viscera are often not brought back from the forest due to their heavy weight (see Mayor et al. 2017). In the current system local people are only responsible for sample collection, since the determination of the reproductive status of animals is done by technicians in laboratories, thus increasing survey costs, and does not involve locals in data processing and analysis, and arguably in using the collected data in decision-making. Conversely, if local people could accurately categorise the reproductive status of hunted specimens where they are hunted, data collection becomes cheaper, easier to implement, and more frequent, therefore substantially increasing sample sizes. Beyond providing more precise estimates of reproductive rates, larger sample sizes would also permit the better understanding of hunting impacts, i.e. by determining how variation in reproductive rates over time relates to density-dependent responses of populations to hunting.

In this study, we used the lowland paca (*Cuniculus paca*) as our model species, because it is amongst the top three most hunted species in the Neotropics (e.g. Peres 2000; El Bizri et al. 2015; El Bizri et al. 2020), allowing us to acquire a large number of samples. Using photographs of genitalia of paca females donated by hunter families, we tested whether an effective method could be implemented for citizen scientists to accurately diagnose the reproductive status of hunted specimens. We first established the local peoples' capacity to determine the reproductive status of female pacas in three Amazonian sites, before and after a period of training. We then used these results to correct the pregnancy rates estimated for the species from data collected by local people on hunted specimens' reproductive status over a 17-year period (2002-2018) in one study site. For this study site, we compared the corrected pregnancy rates with those determined from genitalia samples by trained researchers, and with hunting indices to describe the effects of hunting on the studied game populations.

6.3 Materials and Methods

6.3.1 Study sites

We conducted our study in three Amazonian sites (Figure 1). The Yavarí-Mirín River (YMR, 04º19'53" S; 71º57'33" W) is located in the Western Peruvian Amazon, and encompasses 107,000 ha of continuous upland forests where a single indigenous community of 307 inhabitants live (Figure 1). The Amanã Sustainable Development Reserve (ASDR, 01º54'00" S; 64º22'00" W) is a 2,350,000 ha reserve of predominantly upland forests in the central Brazilian Amazon, between the Negro and Japurá Rivers. Approximately 4,000 riverine people inhabit 80 communities and some isolated settlements within this reserve. The middle Juruá River (MJR) region in southern Brazilian Amazonia (MJR, 5°40'26"S, 67°30'25"W) comprises two protected areas of sustainable natural resources use (Middle Juruá Extractive Reserve and Uacari Sustainable

Development Reserve) with 886,175 ha of lowland and upland forests. These two reserves are occupied by ca. 3,200 people in 57 settlements. In all three areas, local communities rely mainly on agriculture for income and on hunting and fishing for subsistence.

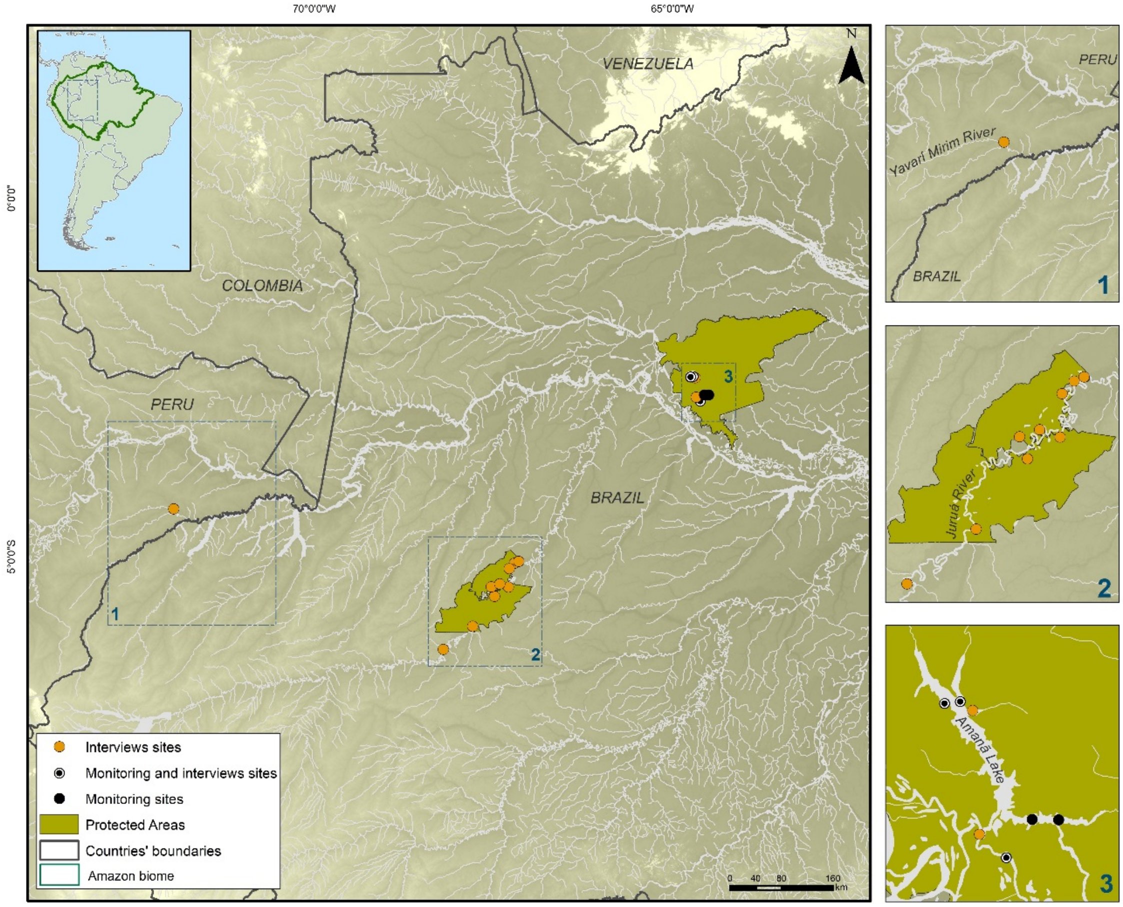


Figure 1. A map showing the three sampled sites with locations of the 15 communities within Amazonia where interviews on the reproductive status of game species were performed (interview sites), between 2017 and 2019, and of the 5 communities where hunting and reproductive data was provided by local people in a citizen-science project between 2002 and 2018 (monitoring sites). Note that three communities in the Amanã Sustainable Development Reserve participated in both interviews and monitoring collections, and thus are classified as “monitoring and interviews sites”.

6.3.2 Local people interviews

Photographs were taken of all paca female genitalia collected (n=300) from animals donated for research by local people in the YMR and ASDR (see El Bizri et al., 2018; Mayor et al., 2017; Mayor, Guimarães, & López, 2013; see

Appendix S1). For pregnant genitalia, we removed the conceptuses and measured their crown-rump length using a metal Vernier calliper (maximum 300 mm).

From the pool of photographs, we selected a total of 42 showing complete genitalia, being 7 (16.7%) photographs of non-pregnant females and 35 (83.3%) from pregnant females with conceptuses ranging from 0.5 cm to 26 cm in length (mean = 7.51 cm; SD = 7.28 cm), depicting the increasing range in conceptus size along gestation. Using these photographs, we asked interviewees to answer whether they thought the specimen was pregnant or not. If they considered the specimen to be pregnant, the interviewee was requested to point out where he/she believed the conceptus was implanted within the uterus.

Considering the time available for the study, we used simple random sampling (Albuquerque et al., 2014) to select the maximum number of young and adults to interview within each sampled community. We interviewed a total of 104 people, 81 men (77.9%) and 23 (22.1%) women. The average age of the men was 38.7 ± 13.9 SD (17-72) years old, and of women 41.3 ± 14.1 SD (24-75). Interviews were conducted in August 2017 in the single YMR community, in May and October 2018, and in January and June 2019 in five ASDR communities, and in November 2018 in nine communities in the MJR.

We held two rounds of interviews for each person during a single interview day. In the first round, we showed the pictures randomly and asked people to determine the reproductive status of each specimen without giving them any clues or guidance on the reproductive biology of the species. In the second round, we used three of the pictures to train interviewees on how pregnancy occurs, explaining where the conceptuses would normally be found in the uterus, and how to determine their presence. We then shuffled the photographs and randomly presented these again for their second diagnosis.

6.3.3 Hunting registers

In the ASDR, a citizen-science hunting monitoring system has been active since 2002 and is ongoing. In this site we trained five local hunters within five separate communities to assemble a wide range of data on the daily hunting activity of community members, including time spent hunting and number of hunters involved, as well as collect data on each specimen hunted: sex and the body mass of hunted individuals, and reproductive status of females (pregnant or non-pregnant). Hunters voluntarily provided information to collectors after returning from their hunts. By the end of 2018, collectors had recorded data for a total of 1236 hunted pacas.

All research was conducted in compliance with the research protocol approved by the Research Ethics Committee for Experimentation in Wildlife at the Dirección General de Flora y Fauna Silvestre from Peru (License 0350-2012-DGFFS-DGEFFS) and by the Instituto Chico Mendes for Biodiversity Conservation from Brazil (License SISBIO No 29092-1).

6.3.4 Data analysis

6.3.4.1 Interview responses

For each interview, responses were scored as 1 if correct and 0 if incorrect. We considered an incorrect answer when the interviewee identified a non-pregnant paca as pregnant (false positive) and a pregnant paca as non-pregnant (false negative), also when the interviewee incorrectly indicated the location where the conceptus was implanted in the uterus.

We analysed all responses using generalized linear mixed models (GLMM) with a binomial distribution to obtain logistic regressions of the probability of interviewees giving correct answers according to a set of predictor variables. We generated separate models for non-pregnant and pregnant females. For non-pregnant specimens, we considered the number of correct and incorrect responses (scores: 0 – incorrect, 1 – correct) as the dependent variable, and the interviewees' sex (man/woman) and age (continuous) as predictor variables. For pregnant specimens, we considered the number of correct and incorrect responses (scores: 0 – incorrect, 1 – correct) as dependent variable, and the interviewees' sex and age and the length of the conceptuses (continuous) as predictor variables. We built a null model (no effect of predictor variables) and models with different combinations of predictor variables, from simple ones (only one predictor variable) to a more complex one (all variables in the model). We independently tested each interview round. Interviews from the same community may not be independent since there were a different number of interviewees for each community, and because we consider that the learning process and sharing of information (of the biological traits of game species) among local people may be nested at the community level. As a result of these two issues, the communities sampled were included as a random categorical factor.

Final models from GLMMs were compared based on Akaike Information Criterion (AIC) values, and all models with the $\Delta AIC < 2$ in relation to the model with lowest AIC were considered as with strong support (see Burnham & Anderson, 2004). To avoid selecting a model that was overfitting due to a large sample size, we also used a likelihood ratio test to compare the significance of these models; if two models were similar ($p>0.05$), we considered the best-fitted model the one with lowest number of parameters, i.e. fewest degrees of freedom. However, we present all models with ΔAIC < 2 in Appendix S2. GLMMs were conducted using the R package *lme4*.

Finally, we assessed the effect of training on the probability of giving more correct answers in the second interview. For both non-pregnant and pregnant specimens, we calculated the difference between the percentages of correct and incorrect responses in the two interview rounds using a chi-square test. In addition, for pregnant specimens, we calculated the difference between the average logistic regression formulas produced in the GLMMs for each round of interview.

6.3.4.2 Corrections of reproductive status and density-dependence effects

Interview results were then used to correct the data on the reproductive status of hunted females collected over the 17-year (2002–2018) monitoring period in the ASDR. Since no systematic training on pregnancy diagnosis was conducted with local people during the monitoring period, we considered they could be categorizing pregnant females as non-pregnant at a similar rate as obtained in the first interview round. On this basis, we therefore applied a correction factor based on two steps. First, we used the formula of the relationship between conceptus length and gestational age in El Bizri et al. (2017) (Crown-rump length = 0.179*Age – 5.28) to obtain the proximate number of pregnancy days up to which hunters would be mistakenly diagnosing pregnant pacas as non-pregnant. For this, we considered the threshold for an accurate diagnosis to be at a conceptus length in which the probability of giving a correct answer was 90%. Second, we used the monthly percentage of paca conceptions presented by El Bizri et al. (2018) as a proxy for the percentage of pacas that would be in the early days of pregnancy, not detectable as pregnant by the hunters. Based on the number of pregnancy days calculated from our first step, we calculated a retroactive monthly percentage of false negatives for each month, thus correcting the number of pregnant and non-pregnant females (see Appendix S3). The gestation length of 149 days for the paca was based on Guimarães et al. (2008).

We used these corrected reproductive data to validate the effectiveness of a long-term citizen science collection of reproductive performance data to: (1) provide reliable information on the reproductive rates for the species, and (2) understand hunting effects. For the first aim (1), we selected females with a body mass ≥5.5 kg, which we considered as mature, following El Bizri et al. (2019a). We then calculated the monthly percentage of pregnant specimens among the mature females sampled each month (hereafter monthly pregnancy rate), independently for each year, and assessed the relationship between monthly pregnancy rate and the expected monthly pregnancy rate of pacas. For this purpose, we considered the published metrics of pregnancy rates in El Bizri et al. (2018), calculated from pregnancy diagnoses from genitalia collected in the ASDR by researchers and examined in the laboratory, as the expected monthly pregnancy rates (see Appendix S3). In this analysis, the month was treated as a fixed factor, while the year of collection was treated as a random factor.

For our second aim (2), we hypothesized that any hunting impact on any animal population would lead to an increase in pregnancy rates over time as a density-dependent response to lower population abundance (e.g. Lima & Jaksic 1998). This increase in pregnancy rate would then be related to an increase in immature individuals in the population due to higher birth rates. We tested for all these relationships by calculating the yearly pregnancy rates of hunted specimens, correlating these with the mean annual catch-per-unit-effort (CPUE, in ind hunter^{-1}hour^{-1}) of hunting events as a proxy of paca abundance (see Rist et al. 2010; Valsecchi et al. 2014; Marrocoli et al. 2019). Afterwards, we correlated the yearly pregnancy rates with the annual percentage of immature individuals (number of individuals < 5.5 kg/total number of individuals hunted) (see Mendes-Oliveira et al. 2012; El Bizri et al. 2018, 2019). Although 848 paca hunting events were recorded, we calculated CPUE for only nocturnal hunts using the 'spotlighting' method (n=519), since paca is strictly nocturnal and spotlighting is a technique that is specifically used to hunt this and no other species, therefore guaranteeing that this index indeed reflected the species' abundance in the study area (see Valsecchi et al. 2014).

To assess the relationship between the monthly pregnancy rate and the expected monthly pregnancy rate of pacas, as well as density-dependent effects, we used a generalized additive model (GAM), which consists of univariate regression analysis that allows each regression variable to have a linear or non-linear relationship with the dependent variable. The type of non-linearity is tested through the use of several smoothers/additive terms in the modelling process. These terms normally add penalizations in the model to prevent overfitting. For the conduction of GAMs, we first tested the best family of distribution fitted to the response variable, comparing these based on QQ-plots of the residuals, and on the difference between AIC values among them. After selecting the best-fitted distribution, we built a null model (no relationship with the predictor variable), and models with the predictor variables in linear and non-linear forms, testing penalized splines and cubic splines as additive terms.

The final model, both in terms of retention of predictor variables and the type of relationship (whether linear or non-linear), was selected based on AIC values (Burnham and Anderson 2004), in which the model with the lowest AIC was selected. For these analyses, the R package *gamlss* was used (Stasinopoulos and Rigby 2007). An advantage of using the *gamlss* package is its flexibility in terms of families of distribution (over 100 continuous, discrete and mixed distributions for modelling the response variable are available), and the various additive terms available compared to other packages. We used R 3.3.3 software for all statistical procedures, and a p-value<0.05 was considered significant.

6.4 Results

6.4.1 The diagnosis of the reproductive status by local people

For non-pregnant females, there was a proportion of 92.6% and 90.4% of correct responses in the first and second round of interviews, respectively, with no significant difference between rounds ($\chi^2=0.17$; p=0.68); no significant effect was observed for any of the predictor variables on the probability of giving correct responses (Table 1).

For pregnant females, the proportion of correct responses was 72.5% for the first interview round. The probability of correctly diagnosing pregnancy varied according to the conceptus size, the smaller the conceptus, the lower the probability (Table 1; Figure 2a). This probability also varied according to the age of the interviewee, with youngers answering correctly more often than older individuals; this difference being greater for small-sized conceptuses (Table 1; Figure 2b). The average probability formula calculated according to conceptus size was: Probability of Correct Responses = $1/1+e^{--(0.19\text{*Foetal size-}0.08)}$.

In the second round of interviews, after training, we recorded a total of 88.2% correct answers. The size of the conceptus still influenced the probability of giving correct answers (Table1; Figure 2c-d). The average probability formula calculated according to conceptus size in the second round was: Probability of Correct Responses = $1/1+e^{-(0.57*\text{Foetal size}+0.45)}$, changing substantially from the first round of interviews due to significant improvements in the diagnosis of pregnancy after training ($\chi^2=236.65$; $p<0.0001$). This improvement occurred for all conceptus sizes, but was higher for pregnant females with smaller conceptuses, between 0.5 and 10 cm (32-85 gestation days, 21.5-57.0% of total gestation length, respectively), with peak at around 5 cm (57 gestation days, 38.3% of total gestation length), for which diagnoses improved by around 25% (Figure 3).

Table 1. Details of the best-fit generalized linear mixed models (GLMMs) for the diagnoses of mature paca (*Cuniculus paca*) females by local people through genitalia pictures, and generalized additive models (GAMs) for the relationship between the corrected monthly pregnancy rate from hunting registers with the expected pregnancy rate from genitalia, the trend in annual pregnancy rates along the monitoring period (2002-2018), and between annual pregnancy rates with the catch-per-unit-effort and proportion of immature individuals in the Amanã Sustainable Development Reserve. The communities were included as a random categorical factor in the GLMMs.

Best-fit model		Estimate (SE)	z-value/t-value	*P*-value	Family of Distribution[a]	Link function	*w*AIC (*k*; df; ∆AIC null)[b]
Response variables	Predictor variables						
Interview - Pregnant pictures							
First round							
Correct answers	(Intercept)	0.433 (0.20)	2.21	0.0272*			
	Conceptus size	0.190 (0.01)	18.01	<0.001*	BI	Logit	0.71 (4; 4; 576.19)
	Interviewee age	-0.001 (0.003)	-2.98	0.0029*			
Second round							
Correct answers	(Intercept)	0.452 (0.16)	2.85	0.0044*	BI	Logit	0.25 (3; 3; 457.06)
	Conceptus size	0.569 (0.05)	11.64	<0.001*			
Interview - Non-pregnant pictures							
First round							
Correct answers	(Intercept)	2.640 (0.30)	8.90	<0.001*	BI	Logit	0.35 (3; 3; 2.53)
	Interviewee sex	1.788 (1.04)	1.72	0.086			
Second round							
Correct answers	(Intercept)	2.687 (0.37)	7.28	<0.001*	BI	Logit	0.50 (3; 3; 2.17)
	Interviewee sex	15.774 (17.42)	0.01	0.993			
Monthly pregnancy rate							
From hunting registers	(Intercept)	-9.910 (4.83)	-2.05	0.042			
	From genitalia	1.042 (0.15)	6.79	<0.001*	BCCGo	Identity	0.65 (14; 15.5; 31.80)
Temporal trends							
Annual pregnancy rate	(Intercept)	-0.002 (0.16)	-146.00	<0.001*	IG	Identity	0.99 (3; 4.9; 15.86)
	pb(Year)	1.169 (0.008)	148.10	<0.001*			
Density-dependent responses							
Annual pregnancy rate	(Intercept)	67.83 (11.56)	5.87	<0.001*	GA	Identity	0.86 (2; 3; 3.58)
	CPUE	-118.95 (44.37)	-2.68	0.018*			
Proportion of immatures	(Intercept)	8.00 (4.11)	1.95	0.072	GU	Identity	0.87 (2; 3; 3.79)
	Annual pregnancy rate	0.26 (0.10)	2.65	0.019*			

Note: *p<0.05. Smoothers were fitted using p-splines (*pb*). IG=Inverse Gaussian; BI = Binomial, BCCGo = Box Cox Cole Green Original, GA = Gamma, GU = Gumbel. SE = Standard Error. *w*AIC = Akaike weights; *k* = number of parameters; df = degrees of freedom; ΔAIC null = difference between the AIC of the selected model and the AIC of the null model.

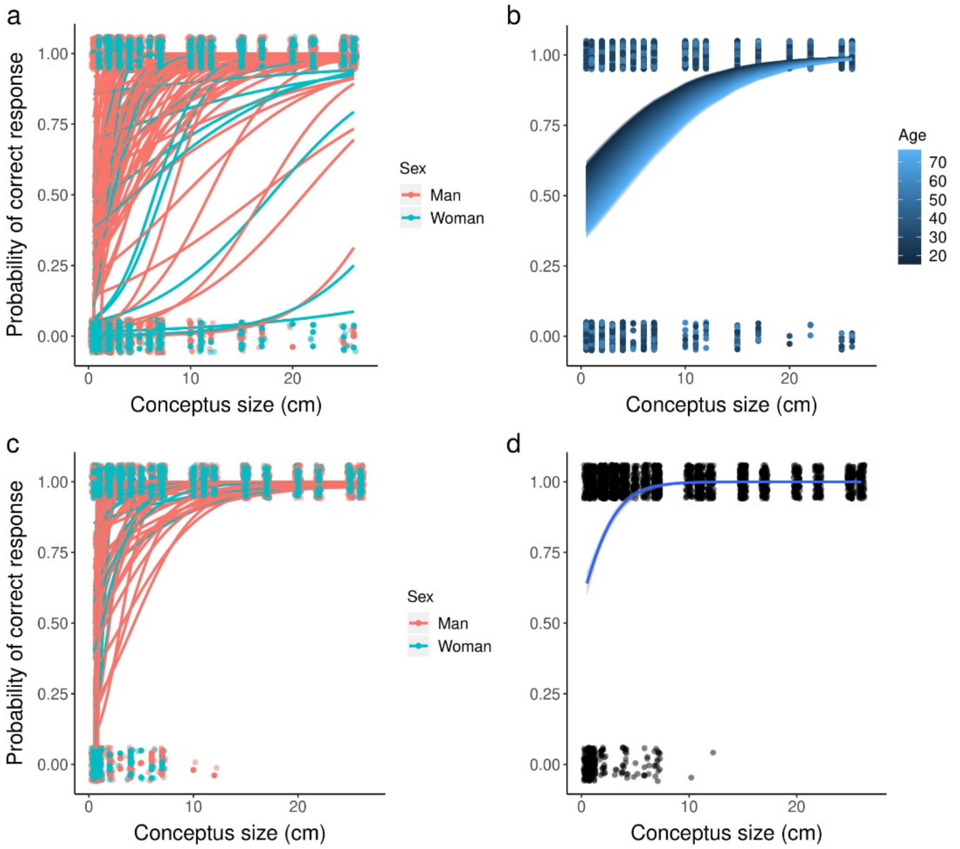


Figure 2. Probability of local people at correctly diagnosing pregnancy in pictures of genitalia of lowland pacas (*Cuniculus paca*) before (*a* and *b*) and after training (*c* and *d*), according to sex and age of the interviewee along the increase in conceptus size in pregnancy. Each line of graphs *a* and *c* represents one of the 104 people interviewed in this study.

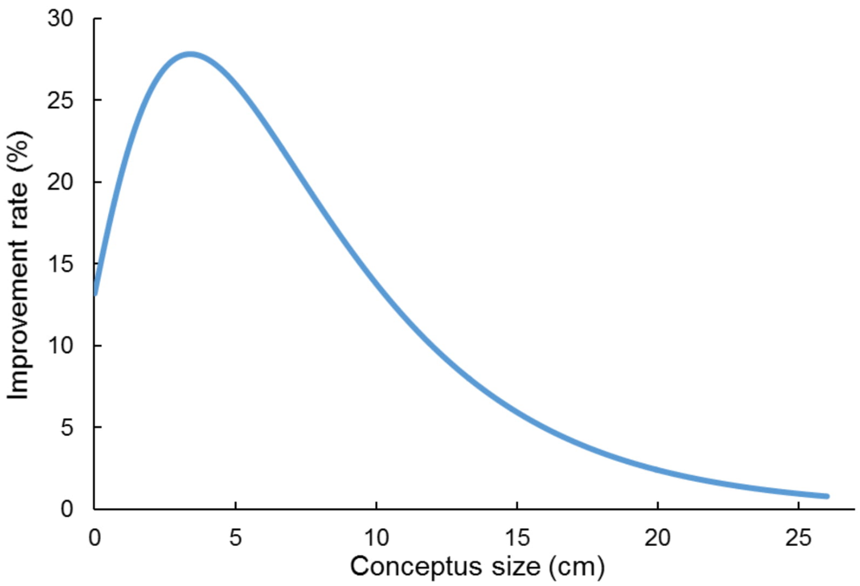


Figure 3. Improvement rate, in percentage, of the probability of local people in Amazonia at correctly diagnosing pregnancy in pictures of genitalia of lowland pacas (*Cuniculus paca*) after a training session.

6.4.2 Estimates of reproductive rates of game species and hunting effects

Out of the total number of hunted individuals recorded in our monitoring programme (n=1236 pacas), 634 were females out of which 554 were mature (87.4%, ≥ 5.5 kg). Among these, local dwellers classified 445 as non-pregnant and 109 as pregnant. Without any correction, the average monthly pregnancy rate from hunting registers was 22.7% (Table 2). Using the formula obtained from the first round of interviews, we estimated that hunters would start diagnosing pregnancies with ≥90% accuracy for conceptuses larger than 12.6 cm in length. This length corresponds to around 100 days of gestational age (El Bizri et al., 2017). Thus, by including a retroactive 3-month time-lag (~ 90 days) to the percentage of conceptions provided by El Bizri et al. (2018), the average monthly pregnancy rate increased by 19.3%, reaching 42.0% with the inclusion of 108 females that were in fact pregnant but incorrectly diagnosed as non-pregnant (Table 2).

Corrected monthly pregnancy rates were positively and significantly correlated with the expected monthly pregnancy rates calculated from genitalia collections (El Bizri et al., 2018) (Table 1; Figure 4). The annual pregnancy rates calculated from hunting registers were on average 39.1%, presenting an inverted U-shaped pattern of changes across years, with a peak in 2012 (Table 3; Figure 5). Pregnancy rates were negatively correlated with the annual CPUE over time (Table 1; Figure 6), and years with higher pregnancy rates had a higher proportion of immature individuals (Table1; Figure 6).

Table 2. Details on the number of mature paca (*Cuniculus paca*) females hunted in the Amanã Sustainable Development Reserve per month with their reproductive status, and the monthly pregnancy rates obtained from hunting registers before and after a correction. For more details on the calculations, see Appendix S3.

Month	Number of mature females			False negatives[a]	Monthly pregnancy rate (%)[b]	Corrected monthly pregnancy rate (%)[c]	Expected monthly pregnancy rate (%)[d]
	Pregnant	Non-pregnant	Total				
January	6	19	25	5.3	24.00	45.33	35.82
February	10	27	37	7.1	27.03	46.23	40.11
March	16	31	47	9.2	34.04	53.71	48.71
April	10	26	36	7.8	27.78	49.32	47.28
May	6	35	41	11.7	14.63	43.09	51.58
June	12	43	55	13.6	21.82	46.51	53.01
July	15	103	118	27.1	12.71	35.68	50.14
August	10	74	84	14.3	11.90	28.91	42.98
September	8	45	53	3.9	15.09	22.54	32.95
October	8	26	34	4.1	23.53	35.60	34.38
November	7	7	14	1.5	50.00	60.53	35.82
December	1	9	10	2.7	10.00	36.84	31.52
Total/Average	109	445	554	108.3	22.7	42.02	42.02

Note: [a]Estimated number of females that were incorrectly diagnosed as non-pregnant when they were in fact pregnant (false negatives). [b]Pregnancy rate calculated from interviews with local people before correction. [c]Pregnancy rate calculated from interviews corrected based on the number of false negatives. [d]Expected monthly pregnancy rates based on calculations using data from genitalia collections obtained in El Bizri et al. (2018).

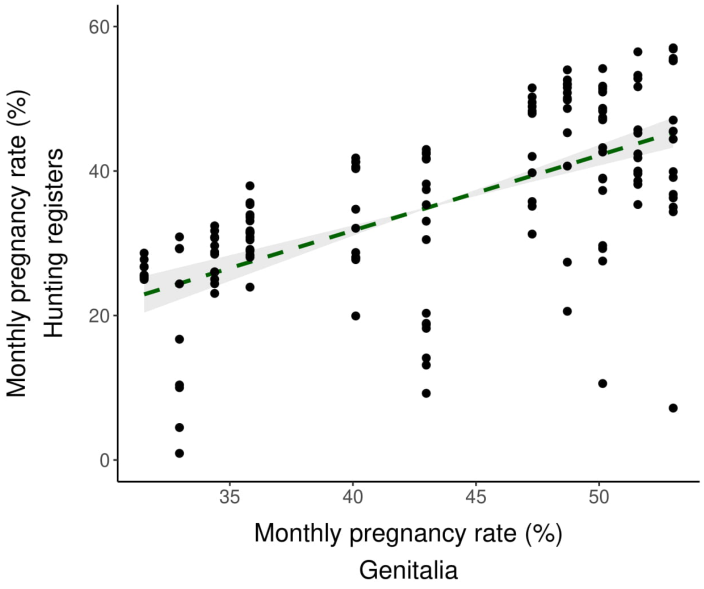


Figure 4. Relationship between the monthly pregnancy rates of lowland pacas (*Cuniculus paca*) determined by researchers through genitalia examinations and by hunting registers conducted by local people along 17 years in the Amanã Sustainable Development Reserve. Data on the pregnancy rates from genitalia were obtained from El Bizri et al. (2018).

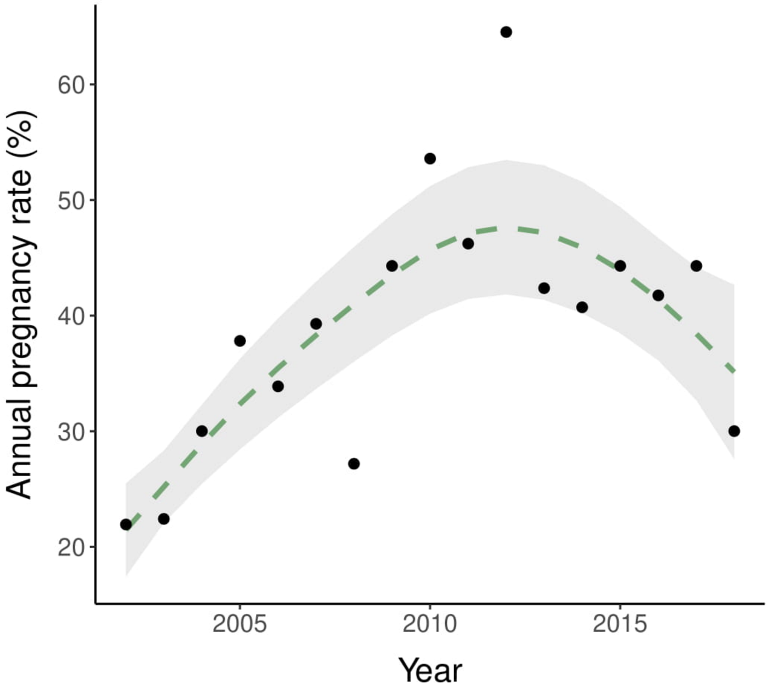


Figure 5. Temporal trends of annual pregnancy rates of lowland pacas (*Cuniculus paca*) determined by hunting registers conducted by local people along 17 years in the Amanã Sustainable Development Reserve.

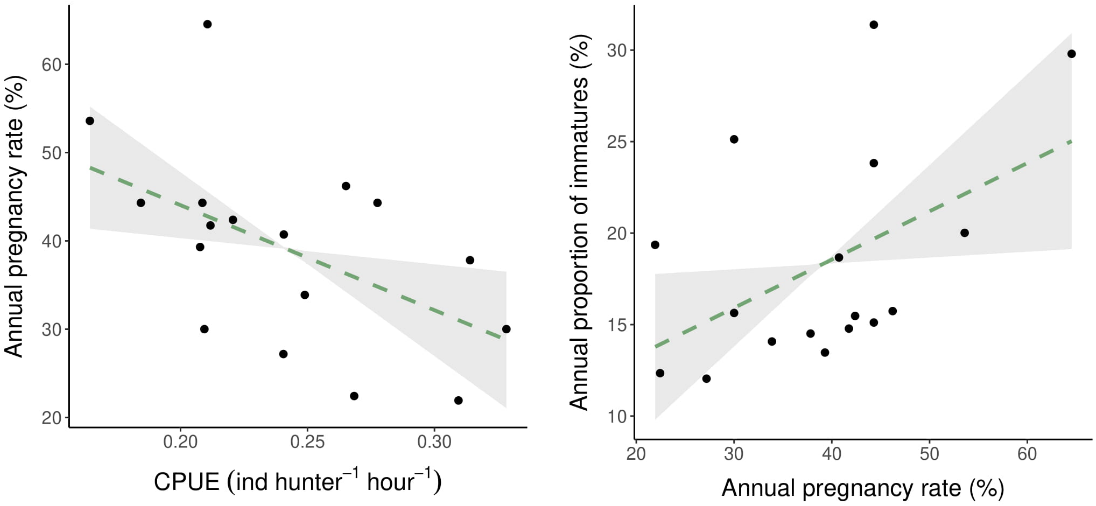


Figure 6. Relationship between the catch-per-unit-effort (CPUE) and annual proportion of immature individuals in hunted populations with the annual pregnancy rates of lowland pacas (*Cuniculus paca*) determined by hunting registers conducted by local people along 17 years (2002-2018) in the Amanã Sustainable Development Reserve.

Table 3. Details on the number of mature paca (*Cuniculus paca*) females hunted in the Amanã Sustainable Development Reserve per year with their reproductive status, the annual pregnancy rates obtained from hunting registers after a correction, the catch-per-unit-effort (ind hunter^{-1} hour^{-1}) (CPUE) of nocturnal paca hunting events and the proportion of immatures (individuals < 5.5 kg) within the total number of individuals hunted. For more details on the calculations, see Appendix S3.

	Number of mature females					
Year	Pregnant	Non-pregnant	Total	Pregnancy rate (%)	CPUE (ind hunter^{-1} hour^{-1})	Proportion of immatures (%)
2002	1	37	38	21.93	0.31	17.57
2003	1	31	32	22.43	0.27	12.05
2004	3	25	28	30.01	0.33	15.63
2005	5	22	27	37.82	0.31	12.24
2006	7	41	48	33.88	0.25	12.77
2007	8	32	40	39.30	0.21	3.37
2008	3	35	38	27.19	0.24	10.38
2009	6	18	24	44.30	0.21	8.57
2010	12	23	35	53.59	0.16	19.40
2011	7	19	26	46.22	0.27	10.00
2012	19	23	42	64.54	0.21	28.41
2013	9	30	39	42.38	0.22	12.66
2014	6	22	28	40.73	0.24	18.67
2015	5	15	20	44.30	0.18	25.81
2016	11	38	49	41.75	0.21	10.23
2017	3	9	12	44.30	0.28	22.73
2018	3	25	28	30.01	0.21	21.21
Total/Average	109	445	554	39.10	0.24	15.39

6.5 Discussion

We showed that local people can participate in the voluntary diagnosis of the reproductive status of game species. Although we used the lowland paca as our model species, this method can be used for any hunted tropical forest placental mammal because: i) these share similar internal reproductive morphology; ii) worldwide, local people eviscerate specimens before eating their meat; and iii) pregnancy is a phenomenon that can be easily identified by hunters.

The high score obtained in the first round of interviews shows that most interviewees already possessed ample understanding of the reproductive biology of game species. This traditional ecological knowledge (TEK) probably starts from exposure to animals since childhood (da Cunha 2009). At a very young age, children of both sexes are initiated into hunting practices via storytelling, and during puberty, young teens follow adults to hunts and assist in the butchering and cooking of animals (Bonwitt et al. 2017; MacDonald 2007). This TEK on the reproductive cycles of species play a particularly important role in influencing the younger generation’s capacity to detect and hunt animals, and can be used in local management strategies to avoid overhunting (Berkes et al. 2000). Vieira et al. (2015), in a study in the Brazilian Amazon, indicated that hunters communally agreed not to take pregnant females or hunt during the reproductive season to guarantee the sustainability of game populations. In another example, hunters’ impressions of the body condition of adult female barren-ground caribou (*Rangifer tarandus*) in Canada corresponded to the reproductive status of the animals after dissection (see Lyver and Gunn 2004). Thus, if pregnant animals can be identified during hunting events, it may be possible to develop more effective management strategies that take into account the reproductive biology of the game species.

Several interviewees were unable to identify small conceptuses in pictures of pregnant genitalia. Though we acknowledge that a number of interviewees may have guessed their answers, we argue that they may have classified them as non-pregnant actually believing they were correct, given the difficulty in detecting early pregnancies. This is supported by the rate of correct responses for non-pregnant specimens, which was much higher than expected in a random guessing situation (90% vs. 50%, respectively).

In our study, before the training, younger people were better at diagnosing pregnancy than older people. This could be explained by two factors: hunting frequency decreases with age, and therefore younger people may be more frequently in contact with hunted animals; and older people claimed that their weaker vision impaired them for properly seeing small conceptuses in the pictures, so younger people may have benefited from the method used in the study. Conversely, as exemplified in other citizen scientist studies (e.g., Ratnieks et al. 2016), we showed that after a short training session the difference between these age groups was overcome and we significantly improved our interviewees' ability at diagnosing pregnancy, especially for early pregnancy stages.

Thus, we claim that local peoples' ability at diagnosing pregnancy after training is similar overall, and will be even higher when they are handling the specimens themselves, since they would be able to palpate the uterus in search for any sign of pregnancy, as they do while processing game. A previous training also allows for a direct calculation of pregnancy rates without the need for extensively correcting the data as we did here, considering that only a small proportion of pregnant individuals (around 10% from very early gestations) would be incorrectly diagnosed, which is similar to the proportion of under-detected pregnancies by transabdominal ultrasonography (Mayor et al. 2005). Our claim is supported by the strong match between local and laboratory diagnoses of pregnancy, which shows that citizen scientists in rural communities are able to collect accurate information of the natural cycle of the species in the wild.

Our citizen-science monitoring of annual reproductive rates has also proved to be reliable for assessing density-dependent responses of populations to hunting, which is difficult to obtain in the field. To our knowledge, this technique has not been applied for tropical game species before our study. In addition, the highest pregnancy rate value obtained in our study (64.5%) is similar to that obtained by Mayor et al. (2017) through genitalia collections in the Peruvian Amazon (62.8%), used to refine the intrinsic rate of population increase (r_{max}) in the paca. Mayor et al. (2017) estimated a minimal cost of $2.75 per biological sample obtained through community-based collections. Therefore, in the present study, the citizen-science diagnosis of pregnancy generated savings of US$1,743.50 for the paca alone. Accordingly, we advocate that the method presented here can be useful for faster, easier, low-cost, and accurate assessments of sustainability. Using this method to properly assess hunting impacts would aid more effective strategies to protect wildlife from overexploitation, and decision makers and local leaders can be provided with accurate tools to implement tangible policies aimed at minimizing food insecurity.

Globally, around 45% of the protected areas are fully or co-managed by local people (UNEP-WCMC and IUCN 2016; Garnett et al. 2018), and thus, subjected to direct human use of fauna. We believe that the present method shows great potential to be applied in several contexts around the world, and even improved when integrated into new technologies currently used in participatory monitoring systems, such as smartphones and specific monitoring software (see van Vliet et al. 2017).

Very few studies on life history parameters of tropical species have relied on data obtained in the wild, and even fewer have obtained such data with the collaboration of local people, even though these are the main actors responsible to manage game populations. Here, we provide a tool to overcome the challenge of obtaining reproductive data on game species in the wild, offering a practicable method that improves sample size for wildlife research. We confirmed that the diagnosis of pregnancy in game specimens undertaken by local people integrated in a citizen science program is useful to assess hunting effects and provides accurate data for evaluating hunting sustainability for tropical mammals. Finally, this study offers the opportunity for locally-produced-data to be integrated into educational programs and policies, providing significant information that can be used against food insecurity and wildlife overexploitation worldwide.

6.6 Supporting Information

Appendix S1.

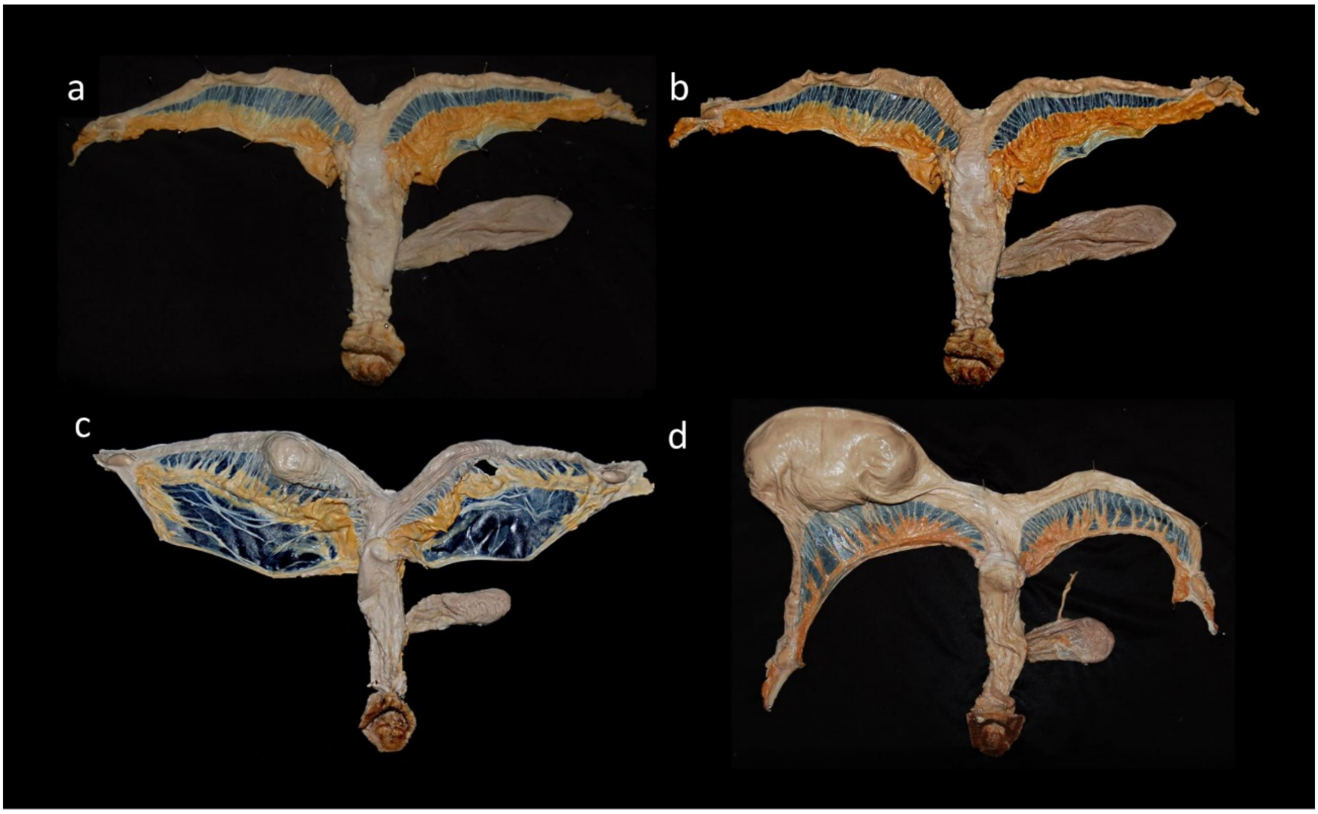


Figure S1. Pictures of *Cuniculus paca* genitalia used in interviews for the diagnosis of pregnancy status by local people. “a” and “b” consist of non-pregnant genitalia, while “c” and “d” consist of pregnant genitalia, with a 3-cm- and a 11-cm-conceptus, respectively.

Appendix S2. Alternative Generalized Linear Mixed Models for the diagnosis of reproductive status of lowland paca (*Cuniculus paca*) by local people in which the difference with the best-fitted model using a likelihood ratio test was non-significant.

Response variables	Predictor variables	Estimate (SE)	z-value	*P*-value	Family of Distribution	Link function	*w*AIC (*k*; df; ΔAIC)	Likelihood ratio test (χ^2; df; *P*-value)
Interview - Pregnant pictures								
First round								
Correct answers	(Intercept)	0.4372 (0.20)	2.217	0.0266*				
	Conceptus size	0.1899 (0.01)	18.012	<0.001*	BI	Logit	0.27 (5; 5; 1.97)	0.0273; 1; 0.87
	Interviewee age	-0.0100 (0.003)	-2.976	0.0029*				
	Interviewee sex	-0.0188 (0.11)	-0.165	0.8688				
Second round – model 1								
Correct answers	(Intercept)	0.3998 (0.17)	2.362	0.0182*				
	Conceptus size	0.5678 (0.05)	11.629	<0.001*	BI	Logit	0.36 (4; 4; 0.75)	2.7539; 1; 0.10
	Interviewee sex	0.2898 (0.18)	1.644	0.1002				
Second round – model 2								
Correct answers	(Intercept)	0.6086 (0.26)	2.317	0.0205*				
	Conceptus size	0.5690 (0.05)	11.632	<0.001*	BI	Logit	0.23 (5; 5; 0.18)	3.8231; 2; 0.15
	Interviewee age	-0.0055 (0.005)	-1.037	0.2998				
	Interviewee sex	0.2848 (0.17)	1.616	0.1062				
Interview - Non-pregnant pictures								
First round								
Correct answers	(Intercept)	3.2405 (0.56)	5.814	<0.001*				
	Interviewee sex	1.8144 (1.05)	1.726	0.0843	BI	Logit	0.29 (4; 4; 0.38)	1.6228; 1; 0.20
	Interviewee age	-0.0156 (0.01)	-1.300	0.1935				
Sencond round								
Correct answers	(Intercept)	2.8350	3.850	<0.001*				
	Interviewee sex	0.1563	0.010	0.9923	BI	Logit	0.19 (4; 4; 1.94)	0.0554; 1; 0.81

	Interviewee age	-0.0038		-0.235	0.8145

Note: *$p<0.05$. BI = Binomial. SE = Standard Error. *w*AIC = Akaike weights; *k* = number of parameters; df = degrees of freedom; ΔAIC null = difference between the AIC of the selected model and the AIC of the null model.

Appendix S3. Calculations of corrected pregnancy rates of lowland paca (*Cuniculus paca*) females from hunting registers, and expected pregnancy rates through genitalia examinations.

Number of adult females hunted according to their reproductive status in the Amazon				
Month	**Non-pregnant**	**Pregnant**	**Total**	**Pregnancy rate (%)**
January	19	6	25	24.00
February	27	10	37	27.03
March	31	16	47	34.04
April	26	10	36	27.78
May	35	6	41	14.63
June	43	12	55	21.82
July	103	15	118	12.71
August	74	10	84	11.90
September	45	8	53	15.09
October	26	8	34	23.53
November	7	7	14	50.00
December	9	1	10	10.00
Total	**445**	**109**	**554**	**22.7**

Concepcion rate (%)	**Correction of the number of pregnant females using the monthly rate of conception with a 2-month time-lag[a]**												
	Month	January	February	March	April	May	June	July	August	September	October	November	December
8.8	January	8.8	8.8	8.8	-	-	-	-	-	-	-	-	-
7.0	February	-	7.0	7.0	7.0	-	-	-	-	-	-	-	-
14.0	March	-	-	14.0	14.0	14.0	-	-	-	-	-	-	-
8.8	April	-	-	-	8.8	8.8	8.8	-	-	-	-	-	-
10.5	May	-	-	-	-	10.5	10.5	10.5	-	-	-	-	-
12.3	June	-	-	-	-	-	12.3	12.3	12.3	-	-	-	-
3.5	July	-	-	-	-	-	-	3.5	3.5	3.5	-	-	-
3.5	August	-	-	-	-	-	-	-	3.5	3.5	3.5	-	-
1.8	September	-	-	-	-	-	-	-	-	1.8	1.8	1.8	-
10.5	October	-	-	-	-	-	-	-	-	-	10.5	10.5	10.5
8.8	November	8.8	-	-	-	-	-	-	-	-	-	8.8	8.8
10.5	December	10.5	10.5	-	-	-	-	-	-	-	-	-	10.5

Results									
Month	**Non-pregnant**	**Pregnant**	**Total**	**Pregnancy rate**	**False negatives**	**Corrected pregnancy rate**	**Monthly percentage of pregnant females[b]**	**Expected pregnancy rate[b]**	**Difference**
January	19	6	25	24.00	5.3	45.33	7.10	35.82	9.5
February	27	10	37	27.03	7.1	46.23	7.95	40.11	6.1
March	31	16	47	34.04	9.2	53.71	9.66	48.71	5.0
April	26	10	36	27.78	7.8	49.32	9.38	47.28	2.0
May	35	6	41	14.63	11.7	43.09	10.23	51.58	-8.5
June	43	12	55	21.82	13.6	46.51	10.51	53.01	-6.5
July	103	15	118	12.71	27.1	35.68	9.94	50.14	-14.5
August	74	10	84	11.90	14.3	28.91	8.52	42.98	-14.1
September	45	8	53	15.09	3.9	22.54	6.53	32.95	-10.4
October	26	8	34	23.53	4.1	35.60	6.82	34.38	1.2
November	7	7	14	50.00	1.5	60.53	7.10	35.82	24.7
December	9	1	10	10.00	2.7	36.84	6.25	31.52	5.3
Total	445	109	554	22.7	108.3	42.02	100	42.02	0.0

[a] The time-lag was calculated using the formula obtained from the first round of interview, through which we estimated that local people would start correctly

diagnosing pregnancies (with 90% probability) for fetuses above 12.6 cm of length, corresponding to around 100 days of age (~ 3 months) (El Bizri et al. 2017). Monthly percentage of conceptions were obtained from El Bizri et al. (2018). [b] These values were obtained from El Bizri et al. (2018), who calculated pregnancy rates from a collection of uterus of lowland pacas in the Amazon. The expected pregnancy rate was calculated based on the expected monthly representativeness of pregnant females among all adult females.

6.7 Acknowledgements

We sincerely thank the people from the Yavarí-Mirín River, Amanã Sustainable Development Reserve, and Juruá River, without whom this work would not be possible. We also thank TQ Morcatty, L Luiselli and an anonymous reviewer for useful comments on the manuscript, and CLB Franco for building the map. This work was supported by the Gordon and Betty Moore Foundation, the National Council for Scientific and Technological Development (CNPq), the IVITA, the Museo de la Universidad Nacional de la Amazonía Peruana, the Earthwatch Institute, and the Fundación Autónoma Solidaria.

6.7 References

Albuquerque, U. P., da Cunha, L. V. F. C., De Lucena, R. F. P., Alves, R. R. N. 2014. *Methods and techniques in ethnobiology and ethnoecology*. Springer New York, USA.

Berkes, F., Colding, J., Folke, C. 2000. Rediscovery of traditional ecological knowledge as adaptive management. *Ecological Applications* 10(5):1251-1262.

Bonney, R., Shirk, J. L., Phillips, T. B., Wiggins, A., Ballard, H. L., Miller-Rushing, A. J., Parrish, J. K. 2014. Next steps for citizen science. *Science* 343(6178):1436-1437.

Bonwitt, J., Kandeh, M., Dawson, M., Ansumana, R., Sahr, F., Kelly, A. H., Brown, H. 2017. Participation of women and children in hunting activities in Sierra Leone and implications for control of zoonotic infections. *PLoS Neglected Tropical Diseases* 11(7):e0005699.

Burnham, K. P., Anderson, D. R. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research* 33(2):261-304.

Coad, L., Fa, J. E., Abernethy, K., van Vliet, N., Santamaria, C., Wilkie, D., El Bizri, H., Ingram, D. J., Cawthorn, D-M., Nasi, R. 2018. Towards a sustainable, participatory and inclusive wild meat sector. CIFOR, Bogor, Indonesia.

da Cunha, M. C. 2009. "Culture" and culture: traditional knowledge and intellectual rights. Prickly Paradigm Press, Chicago, USA.

Danielsen, F., Jensen, P. M., Burgess, N. D., Altamirano, R., Alviola, P. A., Andrianandrasana, H., Brashares, J. S., Burton, A. C., Coronado, I., Corpuz, N., Enghoff, M., Fjeldsa, J., Funder, M., Holt, S., Hubertz, H., Jensen, A. E., Lewis, R., Massao, J., Mendoza, M. M., Ngaga, Y., Pipper, C. B., Poulsen, M. K., Rueda, R. M., Sam, M. K., Skielboe, T., Sorensen, M., Young, R 2014. A multicountry assessment of tropical resource monitoring by local communities. *BioScience*, 64(3):236-251.

Dickinson, J. L., Zuckerberg, B., Bonter, D. N. 2010. Citizen science as an ecological research tool: challenges and benefits. *Annual Review of Ecology, Evolution, and Systematics* 41:149-172.

El Bizri, H. R., Morcatty, T. Q., Lima, J. J., & Valsecchi, J. 2015. The thrill of the chase: uncovering illegal sport hunting in Brazil through YouTube™ posts. *Ecology and Society* 20(3):30.

El Bizri, H. R., Monteiro, F. O. B., de Andrade, R. D. S., Valsecchi, J., de Araújo Guimarães, D. A., Mayor, P. 2017. Embryonic and fetal morphology in the lowland paca (*Cuniculus paca*): a precocial hystricomorph rodent. *Theriogenology* 104:7-17.

El Bizri, H. R., Fa, J. E., Bowler, M., Valsecchi, J., Bodmer, R., Mayor, P. 2018. Breeding seasonality in the lowland paca (*Cuniculus paca*) in Amazonia: interactions with rainfall, fruiting, and sustainable hunting. *Journal of Mammalogy* 99(5):1101-1111.

El Bizri, H. R., Fa, J. E., Valsecchi, J., Bodmer, R., Mayor, P. 2019a. Age at sexual maturity, first parturition and reproductive senescence in wild lowland pacas (*Cuniculus paca*): Implications for harvest sustainability. *Animal Reproduction Science* 205:105-114.

El Bizri, H. R., Morcatty, T. Q., Valsecchi, J., Mayor, P., Ribeiro, J. E., Vasconcelos Neto, C. F., Oliveira, J. S., Furtado, K. M., Ferreira, U. C., Miranda, C. F., Silva, C. H., Lopes, V. L., Lopes, G. P., Florindo, C. C., Chagas, R. C., Nijman, V., Fa, J. E. 2020. Urban wild meat consumption and trade in central Amazonia. *Conservation Biology* 34(2):438-448.

Fragoso, J. M., Levi, T., Oliveira, L. F., Luzar, J. B., Overman, H., Read, J. M., Silvius, K. M. 2016. Line transect surveys underdetect terrestrial mammals: Implications for the sustainability of subsistence hunting. *PloS One* 11(4):e0152659.

Garnett, S. T., Burgess, N. D., Fa, J. E., Fernández-Llamazares, Á., Molnár, Z., Robinson, C. J., Watson, J. E. M., Zander, K. K., Austin, B., Brondizio, E. S., Collier, N. F., Duncan, T., Ellis, E., Geyle, H., Jackson, M. V., Jonas, H., Malmer, P., McGowan, B., Sivongxay, A., Collier, N. F. 2018. A spatial overview of the global importance of Indigenous lands for conservation. *Nature Sustainability* 1(7):369.

Guimarães, D. A., Bastos, L. V., Ferreira, A. C. S., Luz-Ramos, R. S., Ohashi, O. M., Ribeiro, H. L. 2008. Reprodutive characteristics of the female paca (*Agouti paca*) raised in captivity. *Acta Amazonica* 38(3):531-538.

Lima, M., Jaksic, F. M. 1998. Delayed density-dependent and rainfall effects on reproductive parameters of an irruptive rodent in. *Acta Theriologica* 43(3):225-234.

Lyver, P. O. B., Gunn, A. 2004. Calibration of hunters' impressions with female caribou body condition indices to predict probability of pregnancy. *Arctic* 57(3):233-241.

MacDonald, K. 2007. Cross-cultural comparison of learning in human hunting*.* *Human Nature* 18(4):386-402.

Marrocoli, S., Nielsen, M. R., Morgan, D., van Loon, T., Kulik, L., Kühl, H. 2019. Using wildlife indicators to facilitate wildlife monitoring in hunter-self monitoring schemes. *Ecological Indicators* 105:254-263.

Mayor, P., López-Gatius, F., López-Béjar, M. 2005. Integrating ultrasonography within the reproductive management of the collared peccary (*Tayassu tajacu*). *Theriogenology* 63(7):1832-1843.

Mayor, P., Guimarães, D. A., López, C. 2013. Functional morphology of the genital organs in the wild paca (*Cuniculus paca*) female. *Animal Reproduction Science* 140(3-4):206-215.

Mayor, P., El Bizri, H., Bodmer, R. E., Bowler, M. 2017. Assessment of mammal reproduction for hunting sustainability through community-based sampling of species in the wild. *Conservation Biology* 31(4):912-923.

Mendes-Oliveira, A. C., de Maria, S. L., de Lima, R. C. S., Fernandes, A. S., de Almeida, P. C., Montag, L. F., de Carvalho Jr, O. 2012. Testing simple criteria for age estimation of six hunted mammal species in the Brazilian Amazon. *Mastozoología Neotropical* 19(1):105-116.

Milner-Gulland, E. J., Akçakaya, H. R. 2001. Sustainability indices for exploited populations. *Trends in Ecology & Evolution* 16(12):686-692.

Peres, C. A. 2000. Effects of subsistence hunting on vertebrate community structure in Amazonian forests. *Conservation Biology* 14(1):240-253.

Pocock, M. J., Newson, S. E., Henderson, I. G., Peyton, J., Sutherland, W. J., Noble, D. G., Ball, S. G., Beckmann, B. C., Biggs, J., Brereton, T., Bullock, D. J., Buckland, S. T., Edwards, M., Eaton, M. A., Harvey, M. C., Hill, M. O., Horlock, M., Hubble, D. S., Julian, A. M., Mackey, E. C., Mann, D. J., Marshall, M. J., Medlock, J. M., O'Mahony, E. M., Pacheco, M., Porter, K., Prentice, S., Procter, D. A., Roy, H. E., Southway, S. E., Shortall, C. R., Stewart, A. J. A., Wembridge, D. E., Wright, M. A., Roy, D. B. 2015. Developing and enhancing biodiversity monitoring programmes: a collaborative assessment of priorities. *Journal of Applied Ecology* 52(3):686-695.

Ratnieks, F. L., Schrell, F., Sheppard, R. C., Brown, E., Bristow, O. E., Garbuzov, M. 2016. Data reliability in citizen science: learning curve and the effects of training method, volunteer background and experience on identification accuracy of insects visiting ivy flowers. *Methods in Ecology and Evolution* 7(10):1226-1235.

Rist, J., Milner-Gulland, E. J., Cowlishaw, G. U. Y., Rowcliffe, M. 2010. Hunter reporting of catch per unit effort as a monitoring tool in a bushmeat-harvesting system. *Conservation Biology* 24(2):489-499.

Stasinopoulos, D. M., Rigby, R. A. 2007. Generalized additive models for location scale and shape (GAMLSS) in R. *Journal of Statistical Software* 23(7):1-46.

Steger, C., Butt, B., Hooten, M. B. 2017. Safari Science: assessing the reliability of citizen science data for wildlife surveys. *Journal of Applied Ecology* 54(6):2053-2062.

Valsecchi, J., El Bizri, H. R., Figueira, J. E. C. 2014. Subsistence hunting of *Cuniculus paca* in the middle of the Solimões River, Amazonas, Brazil. *Brazilian Journal of Biology*, 74(3):560-568.

van Vliet, N., Sandrin, F., Vanegas, L., L'haridon, L., Fa, J. E., Nasi, R. 2017. High-tech participatory monitoring in aid of adaptive hunting management in the Amazon. *Unasylva* 68(249):53-62.

Vieira, M. A. R. M., von Muhlen, E. M., Shepard Jr, G. H. 2015. Participatory monitoring and management of subsistence hunting in the Piagaçu-Purus reserve, Brazil. *Conservation and Society* 13(3):254-264.

UNEP-WCMC, IUCN. 2016. *Protected Planet Report 2016*. UNEP-WCMC and IUCN, Cambridge, United Kingdom.

Weinbaum, K. Z., Brashares, J. S., Golden, C. D., Getz, W. M. 2013. Searching for sustainability: are assessments of wildlife harvests behind the times? *Ecology Letters* 16(1):99-111.

Zhang, X., Zhu, C., Lin, H., Yang, Q., Ou, Q., Li, Y., Chen, Z., Racey, P., Zhang, S., & Wang, H. 2007). Wild fulvous fruit bats (*Rousettus leschenaulti*) exhibit human-like menstrual cycle. *Biology of Reproduction* 77(2):358-364.

Chapter 7. General Conclusion

In this thesis, I focus on two different but interrelated aspects of wild meat use in the Amazon. At a broader landscape level, I investigated the demand for wild meat in Amazonian cities, and the flow of meat from wild animals from rural communities to urban markets. The information presented here shows that the use of wild meat throughout Amazonia, even in cities, is much more widespread than presumed. The supply of wild meat to cities in Amazonia is propagated by many hunters in rural areas, even from remote communities. Given the importance of understanding the hunted species' life-history and reproduction to ensure sustainable hunting, I also present new data for the lowland paca (*Cuniculus paca*). This rodent is one of the most hunted species in the Amazon. Information gathered on this species can serve as a model for other prey species, useful in the development of better models and management strategies for the sustainable hunting in Amazonia.

In this concluding chapter, I summarise the main results and contributions of the thesis for the general understanding and progress towards the sustainable use of wild meat in Amazonia, and discuss some opportunities for future research on this topic.

7.1 Summary of the thesis main results

Chapter 2. Social and biological correlates of wild meat consumption and trade by rural communities in the Jutaí River basin, central Amazonia

By estimating the consumption rates of wild meat and analyzing the effects of socio-economic and cultural factors at the household level on wild meat consumption and trade in 16 communities in the Jutaí River Extractive Reserve, central Amazonia, I showed that wild meat is important to both diet and income of local people even in considerably remote communities. All interviewees declared consuming wild meat, and two-thirds of the interviewees declared selling wild meat to local communities nearby and in the nearest urban centre. The lowland paca was the most cited species both in terms of consumption and trade, showing the relevance of this species to local people. My results highlighted how important wild meat is for local subsistence and economies of people living in remote Amazonian areas, how some drivers, number of hunters in a household in particular, shape local wild meat use and trade, and the importance of relationships between rural and urban areas through links with people living in the city, who act as intermediaries during wild meat trade. The relevance of wild meat trade to cities in this chapter highlights the need for assessing the urban consumption of wild meat, in which I go deeper in Chapter 3 to understand the scale of consumption and trade of wild meat in large-scales in the urbanized central Amazonia.

Chapter 3. Urban wild meat consumption and trade in central Amazonia

By estimating the frequency of consumption, the means used by local people to obtain wild meat, and the effects of socio-economic factors at municipality-level on wild meat consumption in five cities of central Amazonia, I could elaborate a predictive model to estimate the rates of wild meat across all 62 cities in the region. I estimated that over 10 thousand tonnes of wild meat is consumed in the 62 urban centres in central Amazonia, generating over US$35 million of untaxed revenues to vendors. These results were the first large-scale estimation of the rates of urban consumption and trade in Amazonia. Once again, the lowland paca was a very relevant species, representing the third most consumed species in cities. The relevance of the species to both rural and urban consumers of wild meat made it clear that plans for its sustainable use were urgent. This led to the development of Chapters 4, 5 and 6, in which I present new data on the life-history and reproduction of the lowland paca (*Cuniculus paca*) through participatory methods with support of local Amazonian hunters.

Chapter 4. Breeding seasonality in the lowland paca (Cuniculus paca) in Amazonia: interactions with rainfall, fruiting, and sustainable hunting

By analyzing the genitalia of pregnant paca females donated voluntarily by local hunters living in 6 communities in Amazonia, I showed that although pacas present year-round pregnancies, the majority of pregnancies occurred during periods of greater fruit availability in upland forests, when both river water and rainfall levels were higher. One of my crucial findings was that seasonality in paca pregnancies converged with the seasonality of hunting rates; both were higher during the high river water period. This was the first study showing a consistent relationship between environmental factors and reproduction in lowland pacas, and a strong match between hunting and pregnancies in two distinct sites in Amazonia. This indicates that these patterns may be widespread in the biome. This finding is particularly worrying because pacas are extremely important for local people during the high-water period due to shortage in fish availability, but this convergence may impact its population sustainability in the long-term. The consequent need for better sustainability assessments led me to the development of Chapter 5, in which I refine three of the most important parameters of the life-history of pacas that are invaluable for the development of sustainability models.

Chapter 5. Age at sexual maturity, first parturition and reproductive senescence in wild lowland pacas (Cuniculus paca): implications for harvest sustainability

By analyzing the ovaries and the pregnancy status of genitalia from paca females donated voluntarily by local hunters living in 6 communities in Amazonia, I obtained more realistic measures of age at maturity, first reproduction and reproductive senescence for the species. These three parameters are extremely important for running sustainability models, but most of the information for lowland pacas used in models so far has come from studies in captivity. I found that ovarian functionality was initiated in pacas with 4 months of age, consequently generating a first reproduction at 9 months of age. I did not find any evidence of senescence in lowland pacas, which may indicate that pacas may reproduce along their entire life span in the wild. The age at first reproduction estimated in our study was at least 3 months lower than classical estimates (usally 12 months of age), which consequently determined an increase in the value of r_{max} to 0.6 in regard to the recent figure published by Mayor et al. (2017) of 0.54. This means that paca populations may increase at a higher pace than previously expected, which is a positive sign for its management. However, a better understanding of the density-dependent responses of paca reproduction to hunting is needed to confirm this, as well as for the development of more complex population models, in which age of first reproduction is still important but applied independently from calculations of the r_{max}. This led me to the development of the Chapter 6, in which I validate a citizen-science method to collect reproductive data and assess the hunting impacts on reproductive and population parameters of the lowland paca.

Chapter 6. Involving local communities for effective citizen science: determining game species' reproductive status to assess hunting effects in tropical forests

By comparing the diagnoses of the pregnancy status of genitalia of lowland paca conducted by technicians and people from 15 Amazonian local communities, I was able to confirm that local people are effective at detecting pregnancies in lowland pacas, unmistakenly diagnosing the pregnancy status especially after training and in late pregnancy stages. This result enabled me to correct data from an 18-year citizen science project in 5 communities in central Amazonia, in which hunters diagnosed pregnancy of lowland pacas, to detect hunting impacts and the density-dependent response of paca populations to harvest. Pacas showed higher pregnancy rates in years with lower mean capture-per-unit-effort of hunting trips (as a proxy of paca abundance), and years with higher pregnancy rates matched with years with higher number of juvenile individuals in the population. Such information is challenging to obtain in the field, and this study was one of the first to document the patterns of density-dependent responses to hunting of a tropical game species and provided crucial data to be used in sustainability models. It has also shown how local people can be included in research as citizen scientists to improve our understanding of life-history aspects of game species in the tropics.

7.2 Future directions and opportunities for research

In my first data chapter, I was able to determine that socio-economic and cultural factors were important in determining wild meat consumption rates, including those rarely tested in other research, i.e., number of hunters in the household and meat flavour preferences. However, there are additional drivers of wild meat consumption in local communities not tested in my study that appeared in other researches (see Chapter 1). Drivers such as household income, profession, preference for other activities, age of the hunters, raising of domestic animals, and religious affiliation are known to affect wild meat use (e.g., Knoop et al 2020). In this sense, my study complements other published data, but there is still a need for further researches that investigate the relative importance of all drivers of wild meat consumption in all representative regions throughout the Amazon.

Wild meat consumption and trade in Amazonian urban centres was considered negligible as reflected in publications, such as Rushton et al. (2005) and Nasi et al. (2011). In my two first data chapters, I show very clearly that, despite regulations, wild meat flows freely from forest to urban markets. My investigation for the State of Amazonas, which encompasses ~30% of the Amazon basin, provides the first large-scale estimation of wild meat consumption and trade in Amazonian urban centres. This body of work is important because research on wild meat consumption and trade in the urbanized Amazon is still rare (but see Parry et al. 2014; Morcatty et al. 2015; Mayor et al. 2019). My results are important in highlighting the wild meat trade in a large area of the Amazon and putting wild meat consumption in urban areas within the topics to be considered when developing management strategies for the sustainable use of wild meat in this biome. Further studies that assess the dynamics of the trade within the cities and that includes other Amazon regions are needed.

The large-scale estimation of the amounts of wild meat consumed in Amazonian cities can be seen as a first look of the situation. But I recognise that there were limitations that should be addressed in future studies. The fact that data were gathered during different periods for the various cities and that sample sizes were unequal between surveys may have affected the results. I also use a formula of consumption, specifically derived for this study, which may be limited by using reports on wild meat consumed by Indigenous communities from 25 years ago to determine the amount of daily wild meat consumed per wild-meat based meals. Although these average wild meat consumption rates were useful for the purposes of the study, more up-to-date information of wild meat consumption are required. Another possible limitation of my study may be related to the fact that interviewees may have underreported consumptions rates due to the sensitivity of the topic, especially in larger Amazonian cities, as suggested in Chaves et al. (in review). I was able to show that numbers predicted by our model matched those calculated by other authors in the same cities (i.e., van Vliet et al. 2015, Chaves et al. 2017). Nonetheless, more accurate information on wild meat use, directly obtained from households, indirect methods, or through records of wild meat amounts traded in urban markets will increase our understanding. An example of such studies is Chaves et al. (2020) which focused on turtle and tortoise consumption in central Amazonia. This study, based on a large number of consumer interviews (using indirect methods) simultaneously gathered in 10 cities was able to determine how migration and generation changes affect wild meat consumption in cities; over 1.7

million turtles and tortoise are consumed annually by urban residents. Such studies should be replicated not only within the tropical forest biome in Amazonia but also in others, in particular in those less preserved regions in western and southern Amazonia. Here, deforestation may have more significant impacts on wild meat use.

The sale of wild meat is used by local hunters to generate income that can be used to obtain essential goods, such as gasoline, hygiene items, medicine or even food items. Commonly, it is the wild meat that remains surplus after feeding the family that is traded, and this trade often involves more resilient animals. This is very different from wildlife trafficking, which is highly predatory since actors are motivated by high cash returns, and often biased towards the sale of rare species. Thus, those involved in wild meat trade in cities are often local vendors or the hunters' family members. Accordingly, wild meat trade must be seen as support of the domestic economy that guarantee food and income security to millions of Amazonian people rather than a threatening and criminal activity.

Future research projects should therefore consider the importance of wild meat as food and income in order to support the development of effective policies. This is particularly important since current policies in Amazonian countries often severely restrict or even ban wildlife consumption and trade pushing wild meat use deep underground, making it difficult to monitor, research and, most importantly, to manage (Antunes et al. 2018, van Vliet et al. 2019). To promote a sustainable and inclusive wild meat management in Amazonia, better information on the most hunted wild species are needed to inform hunting and trade policies. However, local stakeholders, who are the first-hand users of the resource, and are the most affected by inefficient policies, must be integrated into research strategies and involved in decision-making. In particular, it is crucial to establish the actual rates of the wild meat extraction and estimate the impact of hunting for trade and subsistence on wild animal prey populations. Studies that refine the population and life-history information on game species, and combine the monitoring of harvests and of the status of wild populations stocks are needed to determine how best to control and regulate the use of a resource that is fundamental to many millions of consumers.

Biological data on game species are an essential information to inform sustainability and guide decision-making on wild meat management; however, such data are lacking for most Amazonian game species. Following a study by Conde et al (2019), which reviewed the available knowledge of life-history parameters of 32,144 tetrapod species contained in 22 data repositories, I examined the data available for Amazonian game species. A total of 222 species (amphibians, reptiles, birds and mammals) are hunted within the Amazon (Antunes et al. unpublished data). Of these 211 (95.0%) are listed in Conde's et al. (2019) demographic database and 206 (97.6%) contained reproductive information for at least one parameter (Table 1). For all groups, information available is mainly on age at first reproduction and litter size, parameters that are more easily obtained from captive animals. Crucial parameters such as proportion of reproductive females and recruitment rates are virtually inexistent for all species and groups. These parameters are crucial for determining variables such as the rate of population increase which are needed in models of sustainable hunting and should ideally be be obtained from studies on wild populations.

Table 1. Number of species among the 211 Amazonian hunted species for which each reproductive parameter is available, by taxonomic class (Amphibia, Aves, Mammalia and Reptilia).

Reproductive parameter	Amphibia (n = 1)	Aves (n = 104)	Mammalia (n = 78)	Reptilia (n = 23)
Age at first reproduction	0 (0%)	20 (19.2%)	65 (82.3%)	14 (60.9%)
Interlitter/interbirth interval	0 (0%)	1 (0.96%)	39 (49.4%)	2 (8.7%)
Litter/clutch size	1 (100%)	104 (100%)	78 (100%)	23 (100%)
Proportion of reproductive females	0 (0%)	1 (0.96%)	0 (0%)	0 (0%)
Recruitment	0 (0%)	1 (0.96%)	0 (0%)	0 (0%)
Age- or stage-specific fertility rates	0 (0%)	1 (0.96%)	6 (7.6%)	2 (8.7%)

Of greater concern is the reliability of the data available on the reproduction of Amazonian game species. As shown in Figure 1, most data are derived from unknown sources, hence it is not possible to infer whether they were from captive or wild populations. As a result, the use of these data on sustainability models can affect the accuracy of the models generating results that are difficult to interpret.

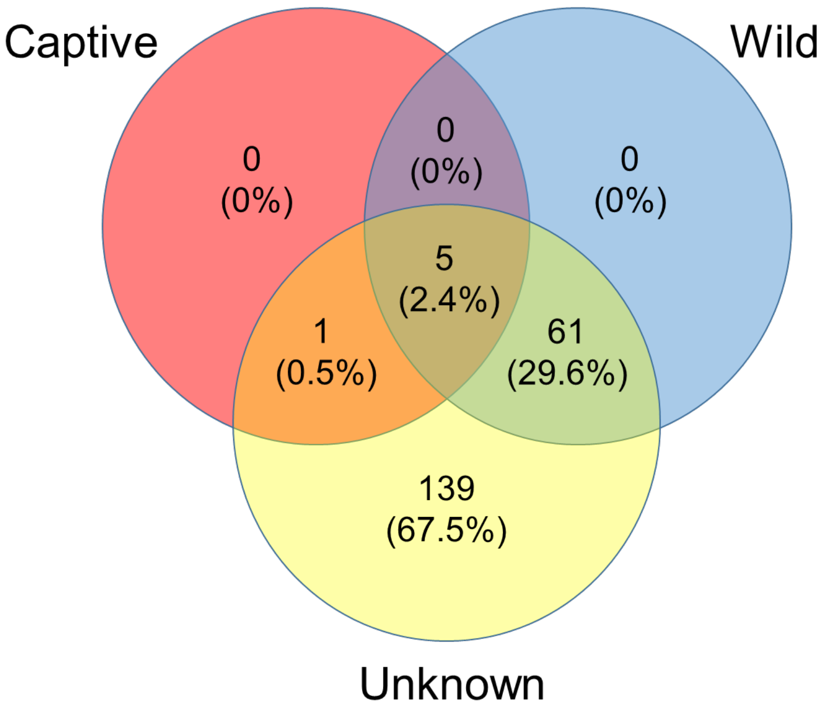


Figure 1. Source of the information across the 22 data repositories analysed and compiled by Conde et al. (2019). Each number in the diagram represents the distribution of the 211 Amazonian game species analysed and whether the sources for reproductive information was from wild, captive or unknown origins, or a combination of these sources.

In my chapters that focussed on the biological aspects of lowland paca, I showed that by increasing stakeholder participation in data collection I was able to refine life-history data on this game species, filling in some critical knowledge gaps such as reproductive and recruitment rates (Mayor et al. 2017). Because local people interact everyday with their environment and in fact handle the animals they hunt, data collection in conjunction with scientists can be easily integrated into their daily lives. This is especially appropriate in tropical forests where data is scarce and data collection by conventional methods can be laborious and resource- and time-consuming (Anadón et al. 2009). In this thesis, I was able to calculate more precise measures of the reproductive rates of the lowland paca, estimate age at maturity and litter size, as well as assess reproductive seasonality and density-dependent effects of hunting, all with the help of local hunters living in remote communities in Amazonia.

Internal organs of game species are often discarded by hunters and neglected by researchers. The examination of male and female reproductive organs in particular, can provide researchers with an invaluable opportunity to improve our knowledge of the reproductive biology of wild animal populations. These materials can be gathered in large numbers and can thus offer faster and more reliable information on game species than captive studies. Community-based data collection schemes that involve the participation of many hunters has shown to be effective in gathering this vital information in a number of Neotropical sites, i.e. in the Peruvian Amazon (Mayor et al. 2017), French Guiana (Dubost et al. 2017), and in Brazilian Amazonia (El Bizri et al. 2020). Such participatory methods can be applied in other parts of the world. For instance, collection of such type of data would improve our understanding of game species biology in Afro- and Asian tropical forests, for which there is still a trying lack of biological information on hunted species (see van Vliet and Nasi, 2019 on the lack of data on blue duikers in Africa).

There are advantages, but also challenges, in applying methods that involve hunters in the collection of biological materials. In Table 2, I summarize the main advantages and difficulties of such method. The main advantage is that hunters have a first-hand access to game species, and of the biological materials needed to improve our scientific knowledge. Often, genitalia are not consumed by hunters, so hunters can be convinced to participate in programmes in which they can donate these materials. The collection of biological materials by hunters is not an onerous chore for them and if properly introduced the local community will benefit from the information gathered, increasing their interest and further their commitment to this approach. Despite the obvious advantages, one of the main difficulties is related to the storage and transportation of samples, especially of larger species. Collection and storage of genitalia of small animals can be done once hunters return to their village but reproductive organs of large animals are usually discarded by hunters in the forest before returning to their villages. As a result, obtaining a large enough sample size of some species, e.g., lowland tapir (*Tapirus terrestris*) can take longer since only occasionally entire animals are brought back to the communities (Mayor et al. 2017). In the last data chapter of this thesis, however, I have shown that a citizen-science project in which hunters not only collect the genitalia, but also diagnose the pregnancy status of hunted specimens in the field, can be an invaluable alternative, especially for large species. This methodological arrangement not only provided reliable data as soon as hunters are properly trained to diagnose the pregnancy status even at very early stages. The participatory diagnosis of pregnancy is somewhat limited compared to the collection of whole genitalia, since the latter can offer the opportunity for further investigations (i.e., foetal development, maturity). Ultimately, both methods can be combined for better results in the field.

Table 2. A summary of advantages and disadvantages of a participatory collection of biological materials with the help of local communities in tropical forests.

Aspect	**Advantages**	**Disadvantages**
Level of participation	It is a voluntary collection inserted within the habitual activity of local, which tends to increase participation and minimize effort of training.	Due to its voluntary nature, it does not allow the continuous and seasonally equivalent collection of wild fauna over a year.
Rate of data collection	It is an indirect, opportunistic and non-invasive strategy that uses the biological material of hunted animals that communities normally discard; therefore, these animals are not collected for the purpose of a specific study, avoiding unnecessary additional deaths.	It is a slow collection, which may involve a long sampling time, especially for less frequently hunted species; therefore, it is important to estimate the collection time for and the number of communities required to be part of each study.
Representation of the system	The collection may reflect the real proportion of species hunted, and species that receive greater anthropic pressure through hunting turn into the priority of studies and best management practices.	On some occasions, when a large animals (e.g. tapirs) are killed, or when animals are hunted in places far from communities, hunters discard their viscera in the forest. Therefore, although these species can be hunted frequently and important to the diet of the residents, it is more difficult to obtain samples of these animals.
Operationalization	Its implementation is relatively simple and cheap and depends to a large extent on the relationship of the technical team with the local community. The main requirement for maintaining this type of collection is to dedicate the necessary time and attention to the residents so they feel motivated to collect the samples, supply them with the few equipments this type of collection requires, and return periodically with the results of the analyses.	Communities are often isolated, which makes coordination and transportation of equipments and samples difficult.

Due to lack of knowledge on life history of game species, most sustainability models implemented over the last 30 years were simplistic and relied on imprecise population parameters (Weinbaum et al. 2013). Although several models that consider complex population dynamics and stochasticity, such as agent-based models (ABMs) have been recently developed, these relied on static indices of population growth (i.e., r_{max}). Reproductive and recruitment rates are therefore simplistic since they do not consider multiple parameters and interactions within the population, including age- and sex-structure, reproductive seasonality, and density-dependent effects. These models have attempted to add complexity to our understanding of hunting dynamics and landscapes, but left species with the same level of inaccuracy as simplistic models used before (see Iwamura et al. 2014).

The results and methods presented in this thesis can generate more appropriate data for inclusion in complex (and more realistic) population dynamics models. Through these models, it is possible to improve the representation of the structure of reproductive dynamics, making the model more effective at representing these phenomena (Weisberg 2006). The advantage of incorporating complexity and realism to reproduction traits is that the final model allows researchers to test a range of management strategies otherwise impossible to conduct relying solely on static indices such as r_{max}. For instance, we have shown that seasonal hunting may pose distinct risks to a hunted species depending on the species' reproductive seasonality, especially in cases when hunting occurs when more females are pregnant. In addition, hunting individuals from different age-classes, sexes and reproductive status can have different outcomes. A complex and realistic model could be used to test a large range of management schemes such as quotas, sex-biased hunting, source-sink dynamics with fixed and rotating no-take areas, and hunting seasonality.

The Amazon rainforest is the largest remnant of tropical forest in the world and contains more than 30 million people that are in direct contact with wildlife, using them as a source of meat and income as part of their culture. Nevertheless, wildlife management in the region is still absent or conducted informally. Therefore, I hope that my findings provide a better understanding of the persistence and drivers of wildlife consumption by rural and urban inhabitants, as well as the importance of refined life-history information needed for calculating sustainable models. Considering the great advance in knowledge obtained for the lowland paca in this thesis, more complex, realistic population dynamics models can now be performed, and, consequently, management strategies can be tested for the species. Ultimately, I hope the approach applied in this thesis could be a role-model for future studies on several other game species in the Amazon and support the development of sustainable management strategies for highly hunted species in the biome and other tropical forests around the globe.

7.3 References

Anadón, J.D., Giménez, A., Ballestar, R., Pérez, I. 2009. Evaluation of local ecological knowledge as a method for collecting extensive data on animal abundance. *Conservation Biology* 23:617–625.

Antunes, A. P., Rebêlo, G. H., Pezzuti, J. C. B., Vieira, M. A. R. M., Constantino, P. D. A. L., Campos-Silva, J. V., Fonseca, R., Durigan, C. C., Ramos, R. M., Amaral, J. V., Pimenta, N. C., Danzi, T. J. R., Lima, N. A. S., Shepard Jr., G. H. 2019. A conspiracy of silence: subsistence hunting rights in the Brazilian Amazon. *Land Use Policy* 84:1-11.

Chaves, W. A., Wilkie, D. S., Monroe, M. C., Sieving, K. E. 2017. Market access and wild meat consumption in the central Amazon, Brazil. Biological Conservation 212:240-248.

Chaves, W. A., Valle, D., Tavares, A. S., Morcatty, T. Q., Wilcove, D. S. 2020. Impacts of rural to urban migration, urbanization, and generational change on consumption of wild animals in the Amazon. *Conservation Biology* Accepted Author Manuscript.

Conde, D. A., Staerk, J., Colchero, F., Silva, R., Schöley, J., Baden, H. M., Jouvet, L., Fa, J. E., Syed, H., Jongejans, E., Meiri, S., Gaillard, J. M., Chamberlain, S., Wilcken, J., Jones, O. R., Dahlgreen, J. P., Steiner, U. K., Bland, L. M., Gomez-Mestre, I., Lebreton, J. D., Vargas, J. G., Flesness, N., Canudas-Romo, V., Salguero-Gómez, R., Byers, O., Berg, T. B., Scheuerlein, A., Devillard, S., Schigel, D. S., Ryder, O. A., Possingham, H. P., Baudisch, A., Vaupel, J. W. (2019). Data gaps and opportunities for comparative and conservation biology. PNAS 116(19): 9658-9664.

Dubost, G., Henry, O. 2017. Seasonal reproduction in Neotropical rainforest mammals. *Zoological Studies* 56:e2.

El Bizri, H. R., Fa, J. E., Lemos, L. P., Campos-Silva, J. V., Vasconcelos Neto, C. F., Valsecchi, J., Mayor, P. 2020. Involving local communities for effective citizen science: Determining game species' reproductive status to assess hunting effects in tropical forests. *Journal of Applied Ecology* DOI: 10.1111/1365-2664.13633.

Iwamura, T., Lambin, E. F., Silvius, K. M., Luzar, J. B., Fragoso, J. M. 2014. Agent-based modeling of hunting and subsistence agriculture on indigenous lands: understanding interactions between social and ecological systems. *Environmental Modelling & Software* 58:109-127.

Knoop, S. B., Morcatty, T. Q., El Bizri, H. R., Cheyne, S. M. 2020. Age, Religion, and Taboos Influence Subsistence Hunting by Indigenous People of the Lower Madeira River, Brazilian Amazon. *Journal of Ethnobiology* 40(2):131-148.

Mayor, P., El Bizri, H. R., Morcatty, T. Q., Moya, K., Solis, S., Bodmer, R. E. 2019. Assessing the minimum sampling effort required to reliably monitor wild meat trade in urban markets. *Frontiers in Ecology and Evolution 7*:180.

Mayor, P., El Bizri, H., Bodmer, R. E., Bowler, M. 2017. Assessment of mammal reproduction for hunting sustainability through community-based sampling of species in the wild. *Conservation Biology 31*(4):912-923.

Morcatty, T., Valsecchi, J. 2015. Social, biological, and environmental drivers of the hunting and trade of the endangered yellow-footed tortoise in the Amazon. *Ecology and Society* 20.

Nasi, R., Taber, A. van Vliet, N. 2011. Empty forests, empty stomachs? Bushmeat and livelihoods in the Congo and Amazon Basins. *International Forestry Review* 13: 355–368.

Rushton, J., Viscarra, R., Viscarra, C., Basset, F., Baptista, R., Brown, D. 2005. *How important is bushmeat consumption in South America: now and in the future*. ODI Wildlife Policy Briefing, Number 11, ODI, United Kingdom.

van Vliet, N., Quiceno-Mesa, M., Cruz-Antia, D., Tellez, L., Martins, C., Haiden, E., Oliveira, M., Adams, C., Morsello, C., Valencia, L., Bonilla, T., Yagüe, B., Nasi, R. 2015*b*. From fish and bushmeat to chicken nuggets: the nutrition transition in a continuum from rural to urban settings in the Tri Frontier Amazon region. *Ethnobiology and Conservation* 4:6.

van Vliet, N., Antunes, A. P., Constantino, P. D. A. L., Gómez, J., Santos-Fita, D., Sartoretto, E. 2019. Frameworks regulating hunting for meat in tropical countries leave the sector in the limbo. *Frontiers in Ecology and Evolution 7*:280.

van Vliet, N., Nasi, R. 2019. What do we know about the life-history traits of widely hunted tropical mammals? *Oryx* 53(4):670-676.

Weinbaum, K. Z., Brashares, J. S., Golden, C. D., Getz, W. M. 2013. Searching for sustainability: are assessments of wildlife harvests behind the times? *Ecology Letters* 16:99-111.

Weisberg, M. 2006. Forty years of ‘the strategy’: Levins on model building and idealization. *Biology and Philosophy* 21:623–645.

Social and Biological Correlates of Wild Meat Consumption and Trade by Rural Communities in the Jutaí River Basin, Central Amazonia

Authors: El Bizri1, Hani R., Morcatty, Thaís Q., Ferreira, José C., Mayor, Pedro, Vasconcelos Neto, Carlos F. A., et al.

Source: Journal of Ethnobiology, 40(2) : 183-201

Published By: Society of Ethnobiology

URL: https://doi.org/10.2993/0278-0771-40.2.183

Journal of
Ethnobiology

2020 40(2): 183–201

Social and Biological Correlates of Wild Meat Consumption and Trade by Rural Communities in the Jutaí River Basin, Central Amazonia

Hani R. El Bizri[1, 2, 3, 4*], Thaís Q. Morcatty[2, 4, 5], José C. Ferreira[2, 6], Pedro Mayor[3, 7, 8, 9], Carlos F. A. Vasconcelos Neto[2, 4], João Valsecchi[2, 3, 4], Vincent Nijman[5], and John E. Fa[1, 10]

Abstract. Wild animals are an important source of food and income throughout the Amazon basin, particularly for forest-dependent communities living in the more remote regions. Through interviews in 51 households within 16 communities in the Jutaí River Extractive Reserve, Amazonas, Brazil, we determined animal taxa consumed and frequency of wild meat consumption, as well as patterns of wild meat trade. We then investigated the influence of social and biological factors on wild meat consumption and trade. People declared consuming wild meat on an average of 3.2 ± 2.8 days/month/household, amounting to 198.85 kg/month consumed by all sampled households. The vast majority of respondents got wild meat by hunting themselves or it was given to them by their neighbors. The most consumed taxa were paca (*Cuniculus paca*) and collared peccary (*Pecari tajacu*). Approximately two-thirds of respondents declared selling wild meat; meat destined for urban markets was more expensive and was primarily sold from houses of relatives living in the city. Wild meat consumption was determined by taste preferences, while prices were related to the body mass of the taxa concerned. Frequency of wild meat consumption and the probability of selling wild meat were positively associated with the number of hunters in the household. We highlight the importance of wild meat for remote communities, and, importantly, the prominent links these communities have with urban markets. These findings are useful in developing strategies to ensure the sustainable use of wildlife in the Amazon.

Keywords: hunting, subsistence, wildlife trade, wild meat, Amazon

Introduction

In tropical forested regions throughout the world, increasing human populations, better access to previously unhunted areas, and improvements in hunting technologies have intensified pressures on wildlife and habitats (Coad et al. 2019). In addition, the integration of local people into the wider market economy in the recent decades has driven the switching of hunting for home consumption to trading and fulfilling city markets' demands for wild meat, exacerbating wildlife harvest in the tropics (Benítez-López et al. 2017; Ripple et al.

[1] Department of Natural Sciences, Manchester Metropolitan University, Oxford Road, M15 6BH, Manchester, U.K.
[2] Instituto de Desenvolvimento Sustentável Mamirauá, Tefé, Brazil.
[3] ComFauna, Comunidad de Manejo de Fauna Silvestre en la Amazonía y en Latinoamérica, Iquitos, Peru.
[4] RedeFauna – Rede de Pesquisa em Diversidade, Conservação e Uso da Fauna da Amazônia, Brazil.
[5] Oxford Wildlife Trade Research Group, Oxford Brookes University, Oxford, U.K.
[6] Programa de Pós-Graduação em Antropologia Social, Universidade Estadual de Campinas, Cidade Universitária Zeferino Vaz, Campinas, Brazil.
[7] Departament de Sanitat i d'Anatomia Animals, Facultat de Veterinària, Universitat Autònoma de Barcelona, Barcelona, Spain.
[8] FUNDAMAZONIA, Iquitos, Loreto, Peru.
[9] Programa de Pós-Graduação em Saúde e Produção Animal na Amazônia (PPGSPAA), Universidade Federal Rural da Amazônia, Belém, Brazil.
[10] Center for International Forestry Research (CIFOR), Jawa Barat, Indonesia.
[*] Corresponding author (hanibiz@gmail.com)

2016). In this context, understanding the livelihood, economic, and cultural values of wild meat (here considered as any wild vertebrate animal used for food, excluding fish) and the drivers of hunting and trade in tropical forests is fundamental to developing strategies for the conservation of game species and to guarantee food sovereignty of local people (Coad et al. 2019).

In the Amazon basin—a region that encompasses c. 4,982,000 km^2 of tropical forests shared by eight countries in South America—wild meat represents important sources of food and income for many forest peoples (Sarti et al. 2015), especially where meat from domestic animals is scarce or expensive (Nunes et al. 2019a). Together with manioc (*Manihot esculenta*) flour and fish, wild meat comprises one of the main components of the diet of rural and Indigenous communities in the Amazon (Adams et al. 2009). In the Brazilian Amazon alone, according to Peres (2000), as many as 23.5 million game vertebrates are hunted for subsistence yearly by rural and Indigenous communities.

As well as consuming wild meat, hunters also sell part of their quarry to nearby communities or in urban centers to complement their income and to enable them to purchase urban goods such as salt, oil, and clothes (Antunes et al. 2019; Morcatty and Valsecchi 2015). The trade in wild meat in Amazonia occurs within and between rural communities and in urban areas (Chaves et al. 2019; van Vliet et al. 2015a, 2015b). Rural communities and urban centers are connected especially by 1) the typical multi-sited household organization, i.e., a network among relatives that connects different localities, with community-based or commercial boats carrying people and goods between localities (Chaves et al. 2019; Padoch et al. 2008), and 2) the riverine trader, or "patron," who acts as an intermediary in commercial relationships, traveling between urban centers and rural communities selling industrialized products and buying forest products, such as manioc flour, fish, and wild meat (Lima 2009). Although households in rural communities regularly exchange fish and wild meat as part of a local reciprocity system (Lima 2009), recent studies show that trade in wild meat also occurs within and between communities (Morcatty and Valsecchi 2015).

Differences in market connectivity, type of habitat, as well as the cultural background of communities, are known to influence patterns of wild meat consumption and trade (Chaves et al. 2019; Morcatty and Valsecchi 2015; van Vliet and Nasi 2008). However, there is still a lack of knowledge of potential drivers of wild meat use in more isolated Amazonian communities. For instance, people's willingness to engage in conservation and land use management depends on their place attachment and how they identify with their surroundings (Walker and Ryan 2008). These bonds are strongly influenced by people's time of residence in an area (Hernández et al. 2007). Although to our knowledge never tested for wildlife exploitation, hunting pressure and frequency of trade in Amazonian communities may differ between long-standing inhabitants and newcomers.

Cooperation among hunters is likely to increase hunting yields (Alvard and Nolin 2002); however, it is unclear whether a larger number of related hunters within a household can increase hunting and trade rates. Additionally, although abundance and body mass influence the species hunters pursue (Peres 2000), there is little data available on how taste preferences affect hunting choice and consumption of game species.

Determining patterns and correlates of wild meat consumption and trade among remote Amazonian communities will allow a more accurate understanding of the use of wildlife resources in the region, and to foster more effective strategies for the sustainable use of Amazonian fauna (Levi et al. 2009). In this study, we measured consumption and trade patterns of wild meat within remote rural communities in the Jutaí River basin, in central Amazonia. We also assessed the social and biological factors that may influence the consumption rates, trade, and pricing of wild meat by these communities.

Materials and Methods

Study Area and Cultural Context

This study was conducted in the Jutaí River Extractive Reserve, in the Jutaí River basin, between the Jutaí and Riozinho Rivers (Figure 1). The Jutaí River Extractive Reserve is 2755 km², mainly covered by upland forests, although other vegetation types occur to a lesser extent (e.g., white-water and black-water flooded forests). Annual precipitation in the reserve averages 883 mm per month in the rainy season (December–March) and 665 mm per month in the dry season (June–September). A total of 1221 riverine people, distributed among 223 families within 24 communities (11 on the Jutaí River and 13 on the Riozinho River), live in the Jutaí River Extractive Reserve (ICMBio 2011). The city of Jutaí, with 17,964 inhabitants, is the closest urban center from the Jutaí River Extractive Reserve, 75–200 km (92.2 ± 54.7 km) from the sampled communities by river.

Extractive reserves are a category of protected areas defined by Brazilian environmental law (Law No. 9985/2000) as a "sustainable use conservation unit," meaning that local populations living within it are allowed to use natural resources. In the past, extractive families lived scattered along Amazon rivers working in rubber tapping. During the 1970s, the Catholic Church brought together extractive families into organized communities (Lima and Peralta 2017). With the support of the progressive branch of the regional Catholic Church, community dwellers in the Jutaí River basin created the Jutaí River Extractive Reserve in 2002. Inhabitants of the Jutaí River Extractive Reserve call themselves *extrativistas* (extractive people), meaning that they are non-Indigenous people, descendants of Amazonia's colonial history (Lima 2009). They are better referred to as "agro-extractive," given their engagement in agriculture, fishing, hunting, logging, and other extractive activities (Fraser et al. 2018).

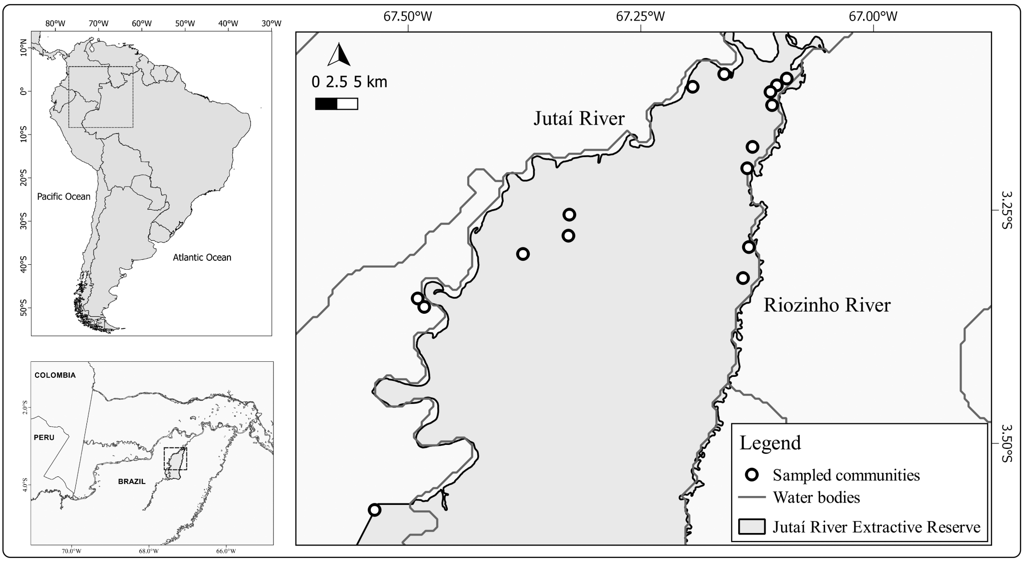


Figure 1. A map showing the location of the Jutaí River Extractive Reserve, central Amazonia, and the 16 sampled communities settled on the Jutaí and Riozinho Rivers.

Data Collection

We interviewed household heads of a total of 51 different families in 16 Jutaí River Extractive Reserve communities from June 9–19, 2014. Within each community, we selected households in which the head was available for interview (i.e., not occupied with other activities). We were able to interview at least one household from each community (average: 3.2 ± 2.8 households/community).

We used a standardized, semi-structured questionnaire (Supplementary Table 1) to ask interviewees the following questions: 1) background information: age of the interviewee, number of residents in the household, number of hunters in the household, whether the household head was born in the community (yes/no, hereafter origin), and residency time in the community (in years); and 2) wild meat consumption and trade patterns: frequency of eating wild meat (in days per month), how wild meat is obtained (i.e., hunting, buying, earning as a gift, or exchanged with other products), the most consumed (open question) and the three most preferred (in terms of meat flavor) taxa, whether wild meat is sold by the household (yes/no), and if sold, where (city or their own/neighboring communities) and what taxa are sold, the sale unit (i.e., entire specimen or in kg), and price it sells for.

Participants were familiarized with our consultation process, as well as the aims of the study prior to the interview. We held a joint meeting with all available residents in each community at the time of the visit, during which we presented the aims of our visit and interviews. We also clarified that respondents were free to participate in the study and to leave the study at any time, and that they were free to refrain from responding to questions they were uncomfortable to answer. All visited households agreed to participate. Interviewees were provided with an Informed Consent Form detailing the project aims and guaranteeing that their identities would remain anonymous. The data collection protocol was approved by the Committee on Research Ethics of the Mamirauá Sustainable Development Institute (Protocol #001-2011).

Data Analysis

We used descriptive statistics to describe the frequency of consumption of wild meat, the means by which wild meat is obtained, most consumed and preferred taxa, and the number of people selling wild meat along with prices. The global threat status of the consumed taxa was classified according to the International Union for Conservation of Nature (IUCN) Red List threat categories (IUCN 2019). If local names provided by informants did not allow us to unequivocally catalog the species, we used genus or family.

The amount of wild meat consumed monthly per household was estimated using the following formula (see El Bizri et al. 2020):

$$B = 0.18\ F_c * N_{people} \qquad (1)$$

where B is the wild meat biomass consumed; 0.18 is a working value of grams of wild meat consumed per person, per day on which wild meat was eaten (obtained from a study of 13 Indigenous communities [Ojasti 1996]); F_c is the declared monthly frequency of wild meat consumption in the household; and N_{people} is the number of people living in the household. The overall monthly biomass consumed in the 51 households was calculated by summing the values for all informants. For those informants who did not declare their frequency of consumption (n = 8 or 15.7% of the total number of informants), we applied the average F_c for all informants. We estimated the amount of meat consumed of each taxon by using the percentage citations of the taxon of the overall biomass (B). The number of individuals consumed was estimated by dividing the biomass consumed of each taxon by the body mass of eviscerated specimens for the taxon (see El Bizri et al. 2020; García et al. 2004).

We used Generalized Additive Models for Location, Scale, and Shape (GAMLSS) to test the effects of social and biological factors on consumption and trade patterns of wild meat. Firstly, we tested whether the frequency of consumption and the probability of selling wild meat varied with the residence time in the community (calculated as percentage of the number of years the interviewees declared they had lived in the community divided by their age), and the number of people and hunters in the household. We then assessed whether the percentage citations of consumed taxa were related to the percentage citations of preferred taxa, as well as the effect of the size of the taxa (body mass) on percentage citations. In addition, we built a model to test whether the price per taxon is related to their body mass and to the locality where sold (whether urban centers or within/among communities), using taxa as a random effect due to differences in the number of citations among them. Body mass of all mentioned taxa was obtained from García et al. (2004) and from Robinson and Redford (1986). Prices per taxon were calculated in USD/kg; when the sale unit was the entire specimen, we divided the price by the eviscerated body mass of the species or taxon (García et al. 2004). We adjusted for inflation and converted the selling price for each taxon by employing the exchange rate for June 15, 2014 to convert Brazilian reals (R$) into US dollars (R$ 2.24 = 1.00 USD), based on the General Price Index for Brazil estimated by the Getúlio Vargas Foundation[1].

To build the models, we tested combinations of predictor variables in linear or non-linear relationships using different distribution families. Firstly, we checked for collinearity among variables. Since the number of people was positively correlated with the number of hunters in the household (Spearman $R = 0.66$), these variables were never included in the same models, but tested separately. Final models were selected based on the Akaike Information Criterion (AIC), considering all models with good support as those with ΔAIC values smaller than two in relation to the model with the smallest AIC. In cases when more than one model was best fitted, we selected the model with the smallest number of parameters (simplest model).

We used R 3.3.3 software and *gamlss* R-package for generalized additive models, and GGally R-package for the collinearity test. For the variables' effects, we assumed significance when $p < 0.05$.

Results

Wild Meat Consumption Patterns

Households were occupied by seven people on average, and the number of hunters in households ranged from none to six people (Table 1). The majority of the respondents were born outside of the sampled communities. All interviewees confirmed that they ate wild meat, with the vast majority of respondents getting wild meat by hunting themselves or receiving it from their neighbors (Table 1). Buying wild meat or exchanging it for other products occurred less frequently (Table 1). Those who exchanged products for wild meat did so for sugar, kitchen oil, soap, petrol, flour, or bananas.

People declared consuming wild meat on an average of 3.2 ± 2.8 days/month/household, resulting in a total of 198.85 kg of wild meat consumed per month by all surveyed households. The declared frequency of wild meat consumption was positively correlated with the number of hunters within the household (Table 2; Figure 2). However, there was no relationship between the number of persons occupying the household or with the percentage time of residency in the community and the frequency of wild meat consumption (Table 2; Figure 2). This suggests that the origin of the family (whether born in the community or not) does not influence wild meat consumption, and that the number of hunters in the

Table 1. Details on the households interviewed and their patterns of consumption and trade of wild meat in the Jutaí River basin.

Characterization of households and patterns of trade and consumption of wild meat	Average	SD
N of inhabitants	7.0	3.5
N of hunters	1.4	1.0
Frequency of wild meat consumption (days/month)	3.2	2.8
Amount of wild meat consumed (kg/month)	3.9	3.8
	N of respondents	**% of respondents**
Origin of the respondents		
Born in the sampled community	11	21.6
Born out of the sampled community	38	74.5
Not declared	2	3.9
Origin of the wild meat consumed		
Hunted	38	86.4
Received from neighbors	34	77.3
Bought from neighbors	23	52.3
Exchanged for household products	12	27.3
Destination of the wild meat sold		
Jutaí city	20	69.0
Neighbors or nearby communities	7	24.1
Both Jutaí city and rural communities	2	6.9

household is more important to define wild meat consumption rates than the amount of people in a family depending on these hunters for food provision.

Most Consumed and Preferred Taxa

Sixteen taxa were mentioned by interviewees in a total of 140 citations of the most consumed wild meat. Mammals were the most cited group, followed by birds and chelonians (Table 3). Six taxa, namely paca (*Cuniculus paca*), collared peccary (*Pecari tajacu*), Razor-billed Curassow (*Mitu tuberosum*), Juruá red howler monkey (*Alouatta juara*), white-lipped peccary (*Tayassu pecari*), and tapir (*Tapirus terrestris*) represented 78.6% of all citations. Overall, an estimated 47 individuals of all taxa were consumed monthly by the 51 households, the most common being curassows and paca. Among the cited taxa for which it was possible to identify the species (n = 14), at a global level, six (42.9% of the taxa) are currently threatened with extinction (Table 3). However, in terms of individuals consumed, threatened taxa represented only 9.8% (n = 4.4 individuals).

As many as 17 different species were cited 117 times as preferred species by the interviewees. Mammals were the most representative group, followed by chelonians, and then birds (Table 3). The top five most preferred taxa were the yellow-spotted river turtle (*Podocnemis unifilis*), curassows, white-lipped peccary, tapir, and paca, together comprising 75.2% of all citations. The percentage number of citations for consumption of each taxon was positively correlated with the percentage number of citations for preference (Table 2; Figure 3). We found no significant effect of species' body mass on the percentage consumed.

Trade in Wild Meat

Regarding the trade of wild meat, from

Table 2. Details of the best-fit generalized additive models for location, scale, and shape (GAMLSS) for the frequency of consumption of wild meat, percentage of consumption per taxon, probability of selling wild meat, and prices applied according to a number of social and biological predictor variables on the Jutaí River basin, central Amazonia. Smoothers were fitted using cubic splines (*cs*) and p-splines (*pb*). AIC is the Akaike Information Criterion for the selected model, while ΔAIC null is the difference between the AIC of the selected model and the AIC of the null model.

Best-fit model						
Response variables	**Predictor variables**	**Estimate**	***P*-value**	**Family of distribution**	**Link function**	**AIC (ΔAIC null)**
Frequency of wild meat consumption	(Intercept) +	0.5427	0.0520	EXP	Log	167.40 (5.15)
	cs (Number of hunters in the household)	0.3780	0.0237*			
Percentage of consumption per taxon	(Intercept) +	1.07035	0.00498*	ZAGA	Log	115.95 (3.7)
	Percentage of preference per taxon	0.10151	0.02590*			
Probability of selling wild meat	(Intercept) +	−1.1980	0.1643	BI	Logit	49.71 (6.56)
	Number of hunters in the household	1.6870	0.0261*			
Price per taxon	(Intercept) +	1.6337	< 0.0001*	BCTo	Log	662.33 (307.08)
	Destination +	−0.2326	< 0.0001*			
	pb(Body mass) +	−0.0027	< 0.0001*			
	random(Taxa)	-	-			

Families of distribution: EXP = Exponential; ZAGA = Zero-adjusted Gamma; BI = Binomial; BCTo = Box-Cox-t original. *Statistically significant variables.

the 48 interviewees that responded to these questions, 30 (62.5%) declared selling wild meat. The trade in wild meat on the Jutaí River basin occurs between neighbors or nearby communities and in the Jutaí city, but most people declared selling exclusively in the city (Table 1). For those selling in the city, most declared selling in only one single place within the city (n = 11), five interviewees declared selling wild meat in two places, five others in three places, and one in four places. Localities where wild meat was sold in urban centers were in most cases houses of relatives in the city (n = 14), followed by direct trade at the Jutaí city quay (n = 9), to intermediaries (n = 7), delivered directly to peoples' houses who pre-order wild meat (n = 7), or directly to consumers in local fairs (n = 3). Similar to the results for the frequency of wild meat consumption, the probability of selling wild meat increased with the number of hunters in the household; households with more than three hunters had ~100% of probability of selling wild meat (Figure 4). However, this probability was not related to the number of people in the household nor with the time of residency in the community.

Wild meat was sold at an average price of 5.6 ± 4.2 USD/kg (6.0 ± 4.4 USD/kg in cities and 4.6 ± 3.5 USD/kg in the communities). Fifteen taxa were recorded as sold; the number of taxa sold in the city being greater than in the communities (14 [n = 134 citations] vs. 10 [n = 69 citations] taxa) (Table 4). The yellow-spotted river turtle was the most cited species sold in the city, while the tapir was the most cited species traded between neighbors and with nearby communities. The most expensive taxa were the yellow-spotted river turtle

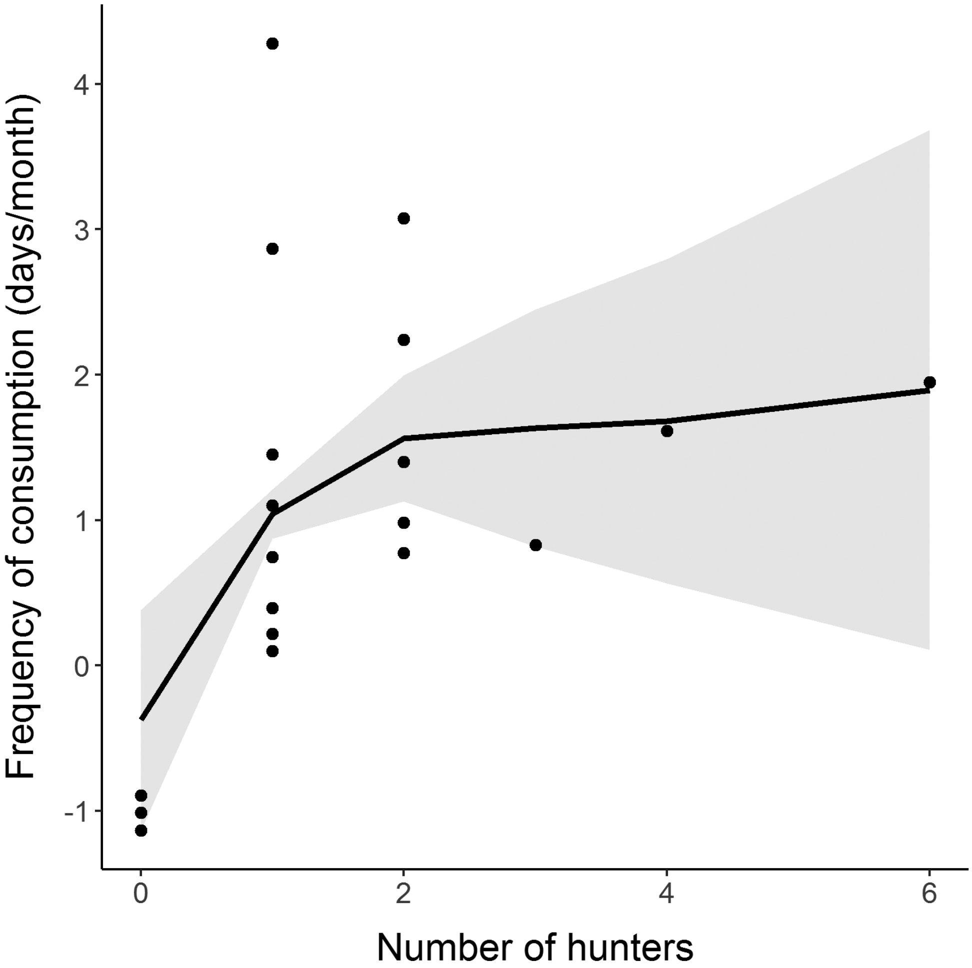


Figure 2. Relationship between the frequency of consumption of wild meat and the number of hunters living in the household on the Jutaí River. Gray shaded area represents the 95% confidence interval. The y-axis is transformed into log (*ln*) scale.

and the curassow, independent of their sale destination (Table 4). Price per kg was higher in the city than in the communities, and a U-shaped trend pattern described the relationship between prices and gross body mass of the sold taxa (Table 2; Figure 5).

Discussion

Our results show that the use of wild meat as food and income in the Jutaí River basin is widespread, and most wild meat was obtained directly by hunters in the families. Amazonian communities further away from urban markets are known to consume larger amounts of wild meat than those having access to other meats in closer city markets (Chaves et al. 2017). Given that the communities in the Jutaí River basin are around 92 km from the nearest urban center, where markets selling domestic meats are found, and are not culturally used to raise domestic animals, access to urban goods, especially domestic meats, is limited. Although we did not quantify this, according to informal reports, inhabitants of the Jutaí River basin travel to the city only once every two to three months. Thus, reliance on timber and non-timber

Table 3. Details of game taxa cited by 51 households of 16 local communities within the Jutaí River Extractive Reserve, central Amazonia, with their gross body mass, net body mass after evisceration, conservation status, percentage of citations as consumed and preferred, and wild meat biomass and number of individuals estimated to be consumed monthly. Taxa names are ordered according to the number of consumption citations.

Taxa	Gross body mass (kg)	Net body mass (kg)	Conservation status (IUCN 2019)	N of consumption citations (%)	N of preference citations (%)	Biomass consumed (kg/month)	Individuals consumed (ind/month)
Lowland paca (*Cuniculus paca*)	8	6	LC	35 (25.0)	11 (9.4)	49.71	8.29
Collared peccary (*Pecari tajacu*)	25	13	LC	25 (17.9)	9 (7.7)	35.51	2.73
Razor-billed Curassow (*Mitu tuberosum*)	3	2.2	LC	20 (14.3)	21 (17.9)	28.41	12.91
Red howler monkey (*Alouatta juara*)	6	4	LC	11 (7.9)	0 (0)	15.62	3.91
White-lipped peccary (*Tayassu pecari*)	35	20	VU	10 (7.1)	19 (16.2)	14.20	0.71
South American tapir (*Tapirus terrestris*)	140	90	VU	9 (6.4)	14 (12.0)	12.78	0.14
Black agouti (*Dasyprocta fuliginosa*)	5	2	LC	7 (5.0)	2 (1.7)	9.94	4.97
Muscovy Duck (*Cairina moschata*)	3	2	LC	6 (4.3)	2 (1.7)	8.52	4.26
Yellow-spotted river turtle (*Podocnemis unifilis*)	8	3.5	VU	5 (3.6)	23 (19.7)	7.10	2.03
Brocket deer (*Mazama* spp.)	18.5	12.5	-	4 (2.9)	6 (5.1)	5.68	0.45
Spix's Guan (*Penelope jacquacu*)	2	1.2	LC	2 (1.4)	1 (0.9)	2.84	2.37
Silvery woolly monkey (*Lagothrix poeppigii*)	11	8	VU	2 (1.4)	1 (0.9)	2.84	0.36
Maguari Stork (*Ciconia maguari*)	4	2	LC	1 (0.7)	0 (0)	1.42	0.71
Six-tubercled river turtle (*Podocnemis sextuberculata*)	3	1.5	VU	1 (0.7)	0 (0)	1.42	0.95
Black-faced black spider monkey (*Ateles chamek*)	9	6.5	VU	1 (0.7)	1 (0.9)	1.42	0.22
Tinamous (Family Tinamidae)	1	0.6	-	1 (0.7)	0 (0)	1.42	2.37
South American giant river turtle (*Podocnemis expansa*)	40	18	LR/CD	0 (0)	2 (1.7)	0.00	0.00
Bald uakari (*Cacajao calvus*)	3.2	2	VU	0 (0)	1 (0.9)	0.00	0.00
Amazonian manatee (*Trichechus inunguis*)	400	256	VU	0 (0)	2 (1.7)	0.00	0.00
Yellow-footed tortoise (*Chelonoidis denticulatus*)	8	3	VU	0 (0)	1 (0.9)	0.00	0.00
Big-headed Amazon river turtle (*Peltocephalus dumerilianus*)	17	6.8	VU	0 (0)	1 (0.9)	0.00	0.00
Total	-	-	-	140 (100)	117 (100)	198.85	47.37

LC = Least Concern; LR/CD = Lower Risk/Conservation Dependent; VU = Vulnerable.

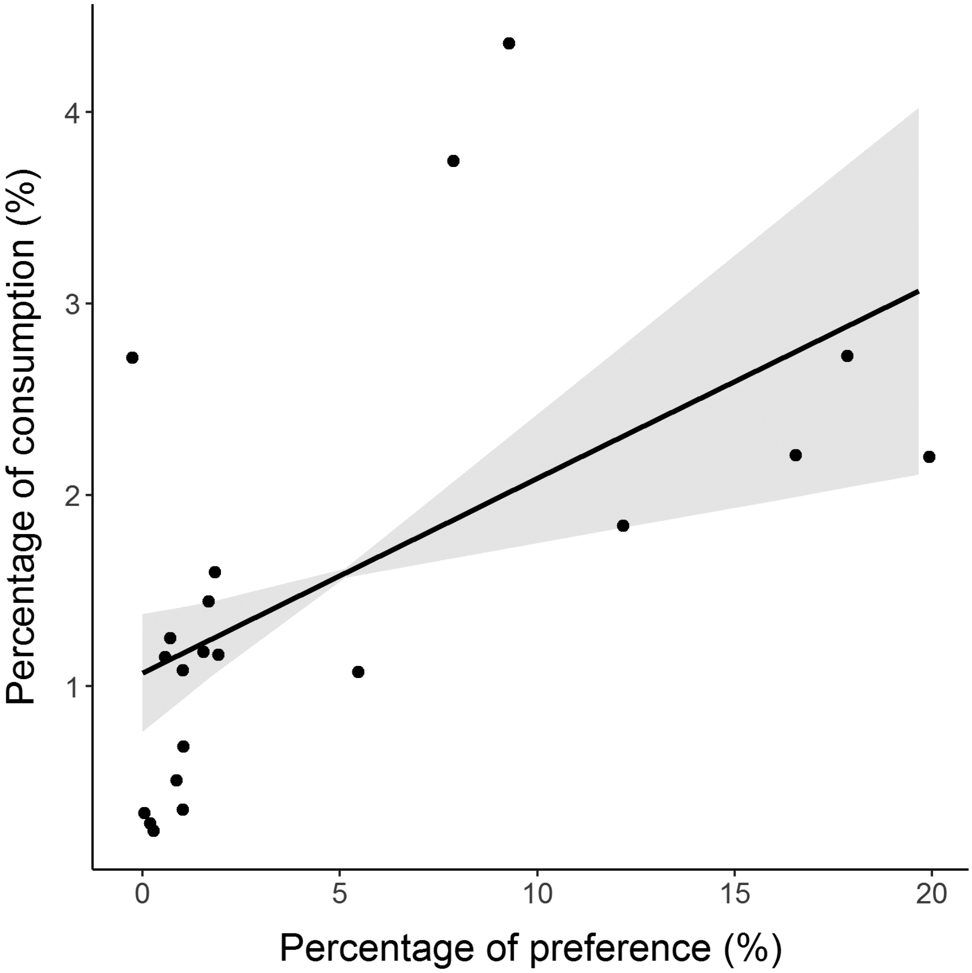


Figure 3. Relationship between the percentages of wild meat consumption per species according to the percentage of preference of meat flavor of the species on the Jutaí River. Gray shaded area represents the 95% confidence interval. The y-axis is transformed into log (*ln*) scale.

forest products is the norm. In addition, the lack of access to reliable electricity supply still does not permit Jutaí River basin inhabitants to refrigerate domestic meat or perishable foods for long periods.

A high proportion of respondents received wild meat as gifts from neighbors. This is not unusual in many rural and traditional societies, reinforcing social bonds and improving food security among closely related people and relatives (see Gurven 2004). In Amazonian communities, there is a term called *vizinhar* that means sharing products with the neighbors, which is frequently used as reference for sharing wild meat (Lima 2009). The rules about *vizinhar*, such as which part or amount of the animal should be donated and to whom they should be donated, vary widely among societies (Almeida et al. 2002). For example, in Riozinho da Liberdade Extractive Reserve, in the Brazilian Amazon, half of all hunted wild meat was given to other village members (Nunes et al. 2019b). In the Ipaú-Anilzinho Extractive Reserve, also in the Brazilian Amazon, the killed animal is divided among the hunters that participated in the hunting event, but the hunter

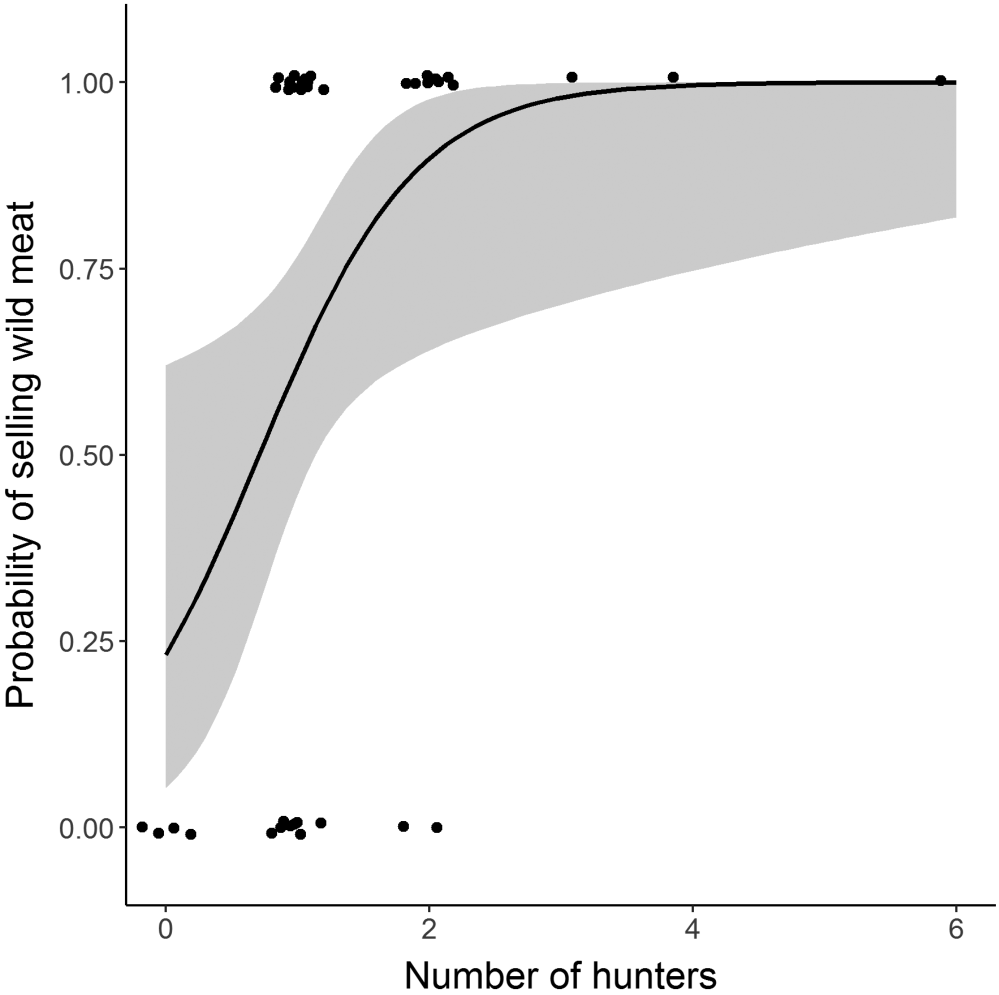


Figure 4. Probability of people selling wild meat on the Jutaí River according to the number of hunters living in the household. Gray shaded area represents the 95% confidence interval.

who shot it has preference over certain parts (Figueiredo and Barros 2016).

Wild meat was traded within and between our study communities. Buying wild meat from neighbors eliminates long periods spent hunting, time that can be dedicated to other income-generating activities, e.g., farming and fishing. In addition, when some communities purchase wild meat from others, it may actually alleviate pressure on game populations in their hunting zones. For wild meat traders, selling the product locally also requires lower investment in transport and meat preservation. Comparative information on the trade of wild meat within and between rural communities in the Amazon and other parts of the tropics is still scarce. However, some studies indicate that the amounts of wild meat sold inside communities can vary significantly. For instance, Coad et al. (2010) estimated that only 8.5% of the overall wild meat offtake in a community in Gabon was sold within it. In another example, Morcatty and Valsecchi (2015) found that 31.4% of tortoises hunted in Amazonia were sold within or between neighboring communities.

Table 4. Details of game species cited as sold and the prices applied in the city and within/between rural communities on the Jutaí River basin, central Amazonia. Taxa names are ordered according to the total number of citations as sold.

Taxa	N of citations as sold in the city (%)	N of citations as sold in the communities (%)	Price in the city (USD/kg ± SD)	Price in the communities (USD/kg ± SD)
Lowland paca (*Cuniculus paca*)	29 (21.6)	10 (14.5)	2.77 (0.63)	2.85 (1.32)
Yellow-spotted river turtle (*Podocnemis unifilis*)	30 (22.4)	6 (8.7)	13.84 (4.84)	9.14 (2.73)
White-lipped peccary (*Tayassu pecari*)	20 (14.9)	15 (21.7)	3.58 (0.68)	2.84 (0.61)
South American tapir (*Tapirus terrestris*)	14 (10.4)	18 (26.1)	3.54 (0.55)	2.77 (0.45)
Collared peccary (*Pecari tajacu*)	11 (8.2)	10 (14.5)	3.35 (0.67)	2.57 (0.66)
Brocket deer (*Mazama* spp.)	3 (2.2)	4 (5.8)	2.9 (1.02)	2.68 (0.48)
Yellow-footed tortoise (*Chelonoidis denticulatus*)	5 (3.7)	1 (1.4)	5.21 (1.66)	3.72 (0)
Razor-billed Curassow (*Mitu tuberosum*)	4 (3.0)	2 (2.9)	14.79 (4.21)	12.83 (0.79)
South American giant river turtle (*Podocnemis expansa*)	6 (4.5)	0 (0)	11.57 (4.41)	-
Big-headed Amazon river turtle (*Peltocephalus dumerilianus*)	3 (2.2)	2 (2.9)	4.71 (1.24)	4.1 (1.16)
Six-tubercled river turtle (*Podocnemis sextuberculata*)	5 (3.7)	0 (0)	4.85 (3.41)	-
Caimans (Family Alligatoridae)	2 (1.5)	0 (0)	1.12 (0)	-
Black agouti (*Dasyprocta fuliginosa*)	0 (0)	1 (1.4)	-	2.23 (0)
Red howler monkey (*Allouata juara*)	1 (0.7)	0 (0)	3.28 (0)	-
Amazonian manatee (*Trichechus inunguis*)	1 (0.7)	0 (0)	8.93 (0)	-
Total/Average	134 (100)	69 (100)	6.03 ± 4.40	4.57 ± 3.53

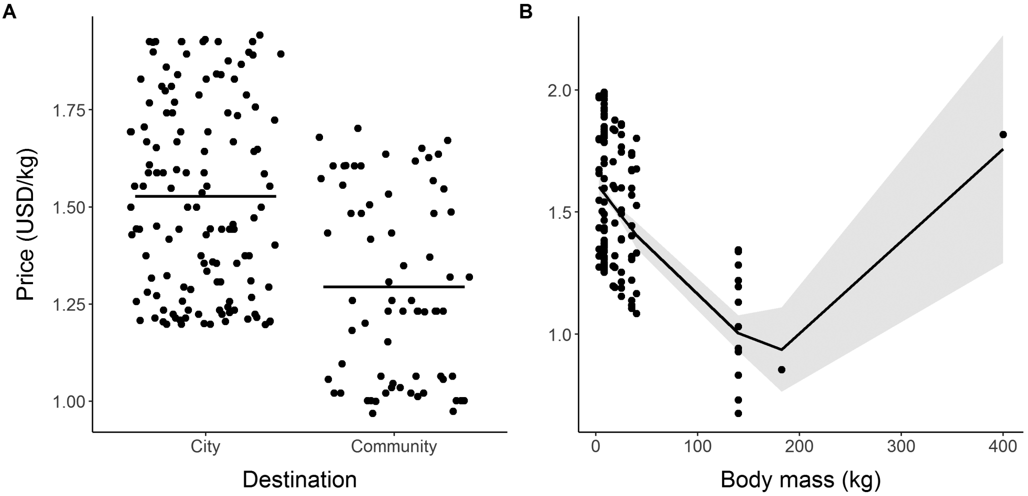


Figure 5. Price of wild meat (in USD/kg) on the Jutaí River according to (A) destination of the product (whether bounded to urban markets or traded within and between rural communities) and (B) body mass of the species. Gray shaded area represents the 95% confidence interval. The y-axes are transformed into log (*ln*) scale.

Van Vliet et al. (2015a) showed that some Amazonian urban hunters may supply urban markets with wild meat directly, but our study revealed that more than half of the interviewees living in rural areas of the Jutaí River basin sold wild meat exclusively to urban centers. This corroborates data from the Peruvian Amazon, which show that 6.5% of the total harvest in rural areas is sold in cities (Bodmer and Lozano 2001). In Amazonian cities, wild meat is commonly traded within local fairs but can also be sold from the hunters' or intermediaries' houses, in the streets, and at docks (Chaves et al. 2019; El Bizri et al. 2020). We showed the importance of hunters having links with people living in the city, since most interviewees declared that wild meat was sold from relatives' houses. This may be a means of avoiding detection and prosecution for selling wild meat. In other cities, strategies for selling wild meat differ in response to law enforcement and surveillance intensity by the authorities. For instance, in the Amazon tri-frontier region between Colombia-Brazil-Peru, hunters already use cell phones to inform their clients about the availability of wild meat and sell the product directly to their consumers, thus avoiding potential controls (van Vliet et al. 2015b). These strategies are so far effective, since information on wild meat trade in cities in Brazilian Amazonia indicates a lucrative wild meat market that, despite being forbidden by law in the country (Law No. 5197/1967), is worth over 35 million USD annually (El Bizri et al. 2020).

One important finding in our study was that the more hunters there were in a household, the higher the household frequency of consumption and amount of wild meat sold was. Cooperation among hunters, often close relatives (e.g., Alvard 2003), led to higher hunting success and return rates (e.g., Alvard and Nolin 2002; Hitchcock et al. 1996). In particular, more hunters in the household also means that large-sized species, such as peccaries and tapirs, which usually require several hunters, can be hunted. In addition, more hunters in a household may mean that the likelihood that at least one household member has ties to outside markets increases. It will likely also lead to increased skills and knowledge sharing about hunting, including those related to pathways and mechanisms for the sale of wild meat, enabling the persistence of the wild meat trade as a culturally acceptable practice in the region.

Since percentage citations of consumed taxa was related to the citations of favored taxa, this suggests that local perceptions on species' flavor is likely to play a crucial role in determining diet breadth in the Jutaí River basin (e.g., Renoux and de Thoisy 2016). For some groups, such as chelonians, however, they may be consumed less frequently despite being highly preferred. Chelonians are highly valued, appearing among the top hunted species throughout the Amazon (Chaves et al. 2019; El Bizri et al. 2020; Peres 2000), but their capture is highly seasonal and most of the yield is frequently traded instead of consumed (Morcatty and Valsecchi 2015; Pantoja-Lima et al. 2014). In addition, Amazonian freshwater turtles have historically been used since the eighteenth century as a food resource and to produce oil for cooking and lighting (Casal et al. 2013), leading to a severe decline in their populations (Johns 1987; Smith 1979). Therefore, the disproportionate percentage of citations of chelonians as consumed (only 4.3%), in comparison to the percentage citations of preference (23.1%), in this study may also reflect depletion in chelonian populations in the Jutaí River basin.

The relationship between price and taxa body mass was very similar to that found by El Bizri et al. (2020) for species sold in urban markets, reflecting that, when pricing species, hunters take into account a balance between prey profitability and yield (Rowcliffe et al. 2004). Smaller species are generally more abundant and easier to capture but are sold at a higher price per kilo because they yield less meat. Conversely, large-bodied species, such as the manatee (*Trichechus inunguis*), although more profitable in terms of meat obtained, are less abundant and difficult to capture, explaining the U-shaped curve in this relationship. Wild meat was less expensive when sold within rural communities than in urban centers. The same difference in prices between urban and rural sectors was observed by Morcatty and Valsecchi (2015) for the trade in yellow-footed tortoise (*Chelonoidis denticulatus*) meat in central Amazonia. However, the observed prices increased only by 24% from rural communities to urban centers, which probably reflects an additional amount to cover travel costs. Considering that urban inhabitants generally have a higher income and greater purchasing power than inhabitants from rural and weakly-monetized communities, the small difference in price might indicate that the wild meat in the Jutaí city is not a luxury item, i.e., only accessed by the wealthier class, as suggested for African cities (e.g., Fa et al. 2009).

Our results show that wild meat still plays a crucial role in communities that are considerably isolated from urban centers on the Jutaí River basin in central Amazonia, being used to guarantee both the subsistence and the economy of local people. A number of social and biological factors seem to be related to the consumption and trade of wild meat in the region, especially the number of hunters in the household, taste preferences, and species' body mass, and should be considered for designing any conservation strategy. Therefore, once we understand the livelihood, economic, and cultural value of wild meat consumption, it is possible to develop management programs that consider local peoples' needs and enhance the sustainable use of wild species.

Rushton et al. (2005) argued that, in rural areas of South America, wild meat could potentially be substituted by domestic meat, especially in Brazil, where there are high rates of livestock production, ultimately reducing the impacts of hunting. However, a complete transition from eating wild meat to exclusively eating beef in Amazonia would require the spending of around 90% of the total wages of local people and the conversion of large portions of Amazonian forests into pasture (Nunes et al. 2019a). Game species represent culturally important elements for Amazonian people, meaning that the depletion of their populations would affect not just their food security but erode the traditional knowledge and practices related to these animals (Tavares de Freitas et al. 2019). Therefore, considering the high level of isolation and dependence on wild meat of communities living in the Jutaí River basin, strategies for sustainably managing wildlife for consumption seems to be a better option than substituting wild meat for domestic meat. The largest-scale wildlife conservation program in the Brazilian Amazon is currently focused on river turtles, and for 30 years, this community-based program has been protecting river turtles' nesting beaches, guaranteeing an increase in the recruitment rate and subsequent population growth for the most historically depleted species, without banning egg consumption by local people (Eisemberg et al. 2019). Since 2007, Jutaí River Extractive Reserve is part of this program, supported by the governmental environmental agency, where the inhabitants released more than 10,000 freshwater turtle hatchlings in 2010 alone, helping to recover these species while guaranteeing the sustenance of local people (ICMBio 2011).

In terms of wild meat trade, a long history of extractive production to the market, under a debt-peonage system called *aviamento*, shaped the patterns of natural resource management and commerce in the Amazon (Almeida 2002; Lima 2009). After the decline of the Amazon rubber production, the domestic and international trade in animal hides replaced it (Antunes et al. 2016). However, during the 1960s, with the advent of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), trade has been more tightly regulated. More recently, the boom and growth of urban agglomerations and intensive migration from rural areas to urban centers increased the demand for wildlife products in Amazonian cities.

There is a consensus that commercial hunting for trade is more impactful to animal populations than subsistence hunting (Coad et al. 2019), but the current prohibition on wildlife commerce in the Amazon has been driving the establishment of hidden markets that hampers control. In urban areas, the replacement of the wild meat with domestic meat at a more affordable price is usually recommended (Rushton et al. 2005), but this strategy has been shown to be ineffective. For instance, a previous experiment conducted in an Amazonian city showed that access to discount coupons to buy chicken had not dissuaded people from consuming wild meat (Chaves et al. 2017). Instead, social marketing with information campaigns and community engagement on activities related to the reduction of wild meat consumption were more effective strategies (Chaves et al. 2017). We argue that this could be applied in the city of Jutaí and other Amazonian cities to reduce the demand for wild meat.

Experiences of wildlife management prove that community-based efforts, if appropriately implemented, provide an effective way to manage natural resources, especially where law enforcement is ineffective (Tavares de Freitas et al. 2019). Our results showed that households with three or more hunters were guaranteed to sell wild meat, so trade is an important source of income for those families. Therefore, regulating wild meat trade and bringing it into the formal economy instead of banning it could improve rural livelihoods, while maintaining the cultural importance of hunting for local people. A major example of this is the community-based management of the giant arapaima fish (*Arapaima gigas*) in the Amazon, which allowed the sustainable commercial exploitation of the species along with the recovery of its previously overharvested populations (Tavares de Freitas et al. 2019). Our results showed that most of the species consumed and traded by local people in the Jutaí River basin are not listed as threatened with extinction on the IUCN Red List. Therefore, this system could be applied for hunted game species that are more resilient, which are also generally more demanded by urban people, such as the paca (*Cuniculus paca*) and the collared peccary (*Pecari tajacu*) (El Bizri et al. 2020). A key first step would be revising national hunting laws in Brazil, since hunting and trade of wild meat still occupies an uncertain status in the legal framework of the country, even for traditional Amazonian populations depending on these activities to live (Antunes et al. 2019). By doing so, game species conservation with the maintenance of their ecosystem services could be aligned with the provision of food and income for local people in the Amazon.

Notes

[1] http://www14.fgv.br/fgvdados20/default.aspx.

Acknowledgments

We thank all local people from the Jutaí River Extractive Reserve for participating in this study and for kindly hosting us during our trip to the reserve. This work was supported by the grant agreement for Instituto de Desenvolvimento Sustentável Mamirauá of the Gordon and Betty Moore Foundation (number 5344) and the National Council for Scientific and Technological Development (CNPq) (grant numbers 300005/2013-0, 452908/2016-7, 201475/2017-0, 300346/2013-1 and 312729/2015-4). T. Q. Morcatty is supported by the WCS Graduate Scholarship Program, a program of the Wildlife Conservation Society and the Christensen Conservation Leaders Scholarship, and by the Wildlife Conservation Network Scholarship Program through the Sidney Byers Scholarship award.

References Cited

Adams, C., R. Murrieta, A. Siqueira, W. Neves, and R. Sanches. 2009. Bread of the Land: The Invisibility of Manioc in the Amazon. In *Amazon Peasant Societies in a Changing Environment: Political Ecology, Invisibility and Modernity in the Rainforest*, edited by C. Adams, R. Murrieta, W. A. Neves, and M. Harris, pp. 281–305. Springer, Dordrecht, Netherlands. DOI:10.1007/978-1-4020-9283-1_13.

Almeida, M. W. B. 2002. The Politics of Amazonian Conservation: The Struggles of Rubber Tappers. *The Journal of Latin American Anthropology* 7:170–219. DOI:10.1525/jlca.2002.7.1.170.

Almeida, M. W. B., E. C. Lima, T. V. Aquino, and M. P. Iglesias. 2002. Parte IV: as atividades: caça. In *A Enciclopédia da Floresta. O Alto Juruá: Práticas e Conhecimentos das Populações*, edited by M. C. Cunha and M. W. B. Almeida, pp. 311–335. Companhia das Letras, São Paulo, Brazil.

Alvard, M. S. 2003. Kinship, Lineage, and an Evolutionary Perspective on Cooperative Hunting Groups in Indonesia. *Human Nature* 14:129–163. DOI:10.1007/s12110-003-1001-5.

Alvard, M. S., and D. A. Nolin. 2002. Rousseau's Whale Hunt? Coordination among Big-Game Hunters. *Current Anthropology* 43:533–559. DOI:10.1086/341653.

Antunes, A. P., R. M. Fewster, E. M. Venticinque, C. A. Peres, T. Levi, F. Rohe, and G. S. Shepard Jr. 2016. Empty Forest or Empty Rivers? A Century of Commercial Hunting in Amazonia. *Science Advances* 2:e1600936. DOI:10.1126/sciadv.1600936.

Antunes, A. P., G. H. Rebêlo, J. C. B. Pezzuti, M. A. R. de Mattos Vieira, P. D. A. L. Constantino, J. V. Campos-Silva, R. Fonseca, C. C. Durigan, R. M. Ramos, J. Valsecchi, N. C. Pimenta, T. J. D. Ranzi, N. A. S. Lima, and G. H. Shepard Jr. 2019. A Conspiracy of Silence: Subsistence Hunting Rights in the Brazilian Amazon. *Land Use Policy* 84:1–11. DOI:10.1016/j.landusepol.2019.02.045.

Benítez-López, A., R. Alkemade, A. M. Schipper, D. J. Ingram, P. A. Verweij, J. A. J. Eikelboom, and M. A. J. Huijbregts. 2017. The Impact of Hunting on Tropical Mammal and Bird Populations. *Science* 356:180–183. DOI:10.1126/science.aaj1891.

Bodmer, R. E., and E. P. Lozano. 2001. Rural Development and Sustainable Wildlife Use in Peru. *Conservation Biology* 15:1163–1170. DOI:10.1046/j.1523-1739.2001.0150041163.x.

Casal, A. C., M. M. Fornelino, M. F. G. Restrepo, M.A. C. Torres, and F. G. Velasco. 2013. Uso Histórico y Actual de las Tortugas Charapa (*Podocnemis expansa*) y Terecay

(*Podocnemis unifilis*) en la Orinoquia y la Amazonia. *Biota Colombiana* 14:45–64. DOI:10.21068/bc.v14i1.275.

Chaves, W. A., D. S. Wilkie, M. C. Monroe, and K. E. Sieving. 2017. Market Access and Wild Meat Consumption in the Central Amazon, Brazil. *Biological Conservation* 212:240–248. DOI:10.1016/j.biocon.2017.06.013.

Chaves, W. A., M. C. Monroe, and K. E. Sieving. 2019. Wild Meat Trade and Consumption in the Central Amazon, Brazil. *Human Ecology* 47:733–746. DOI:10.1007/s10745-019-00107-6.

Coad, L., K. Abernethy, A. Balmford, A. Manica, L. Airey, and E. J. Milner-Gulland. 2010. Distribution and Use of Income from Bushmeat in a Rural Village, Central Gabon. *Conservation Biology* 24:1510–1518. DOI: 10.1111/j.1523-1739.2010.01525.x.

Coad, L., J. E. Fa, K. Abernethy, N. van Vliet, C. Santamaria, D. Wilkie, H. El Bizri, D. Ingram, D.-M. Cawthorn, and R. Nasi. 2019. *Towards a Sustainable, Participatory and Inclusive Wild Meat Sector*. CIFOR, Bogor, Indonesia. DOI:10.17528/cifor/007046.

Eisemberg, C. C., R. C. Vogt, R. A. M. Balestra, S. J. Reynolds, and K. A. Christian. 2019. Don't Put All Your Eggs in One Basket–Lessons Learned from the Largest-Scale and Longest-Term Wildlife Conservation Program in the Amazon Basin. *Biological Conservation* 238:108182. DOI:10.1016/j.biocon.2019.07.027.

El Bizri, H. R., T. Q. Morcatty, J. Valsecchi, P. Mayor, J. E. Ribeiro, C. F. Vasconcelos Neto, J. S. Oliveira, K. M. Furtado, U. C. Ferreira, C. F. Miranda, C. H. Silva, V. L. Lopes, G. P. Lopes, C. C. Florindo, R. C. Chagas, V. Nijman, and J. E. Fa. 2020. Urban Wild Meat Consumption and Trade in Central Amazonia. *Conservation Biology* 34:438–448. DOI:10.1111/cobi.13420.

Fa, J. E., L. Albrechtsen, P. J. Johnson, and D. W. Macdonald. 2009. Linkages Between Household Wealth, Bushmeat and Other Animal Protein Consumption are Not Invariant: Evidence from Rio Muni, Equatorial Guinea. *Animal Conservation* 12:599–610. DOI:10.1111/j.1469-1795.2009.00289.x.

Figueiredo, R. A. A., and F. B. Barros. 2016. Caçar, Preparar e Comer o 'Bicho do Mato': Práticas Alimentares entre os Quilombolas na Reserva Extrativista Ipaú-Anilzinho (Pará). *Boletim do Museu Paraense Emílio Goeldi. Ciências Humanas*, 11:691–713. DOI:10.1590/1981.81222016000300009.

Fraser, J. A., T. Cardoso, A. Steward, and L. Parry. 2018. Amazonian Peasant Livelihood Differentiation as Mutuality-Market Dialectics. *The Journal of Peasant Studies* 45:1382–1409. DOI:10.1080/03066150.2017.1296833.

García, J. B., N. B. Acosta, and L. V. Olivares. 2004. Técnicas de Preservación y Factor de Conversión de Fauna Silvestre en la Región Loreto, Perú. In *Memorias del VI congreso internacional sobre el manejo de fauna silvestre en la Amazonía y Latinoamérica*, edited by R. Bodmer, pp. 427–433. Universidad Nacional de la Amazonía Peruana; Durrell Institute of Conservation and Ecology; and Wildlife Conservation Society, Iquitos, Peru.

Gurven, M. 2004. To Give and to Give Not: The Behavioral Ecology of Human Food Transfers. *Behavioral and Brain Sciences* 27:543–559. DOI:10.1017/S0140525X04000123.

Hernández, B., M. C. Hidalgo, M. E. Salazar-Laplace, and S. Hess. 2007. Place Attachment and Place Identity in Natives and Non-Natives. *Journal of Environmental Psychology* 27:310–319. DOI:10.1016/j.jenvp.2007.06.003.

Hitchcock, R. K., J. E. Yellen, D. J. Gelburd, A. J. Osborn, and A. L. Crowell. 1996. Subsistence Hunting and Resource Management among the Ju/'Hoansi of Northwestern Botswana. *African Study Monographs* 17: 153–220.

ICMBio (Instituto Chico Mendes de Conservação da Biodiversidade). 2011. Plano de Manejo da Reserva Extrativista do Rio Jutaí. Tefé/AM. [online] URL: http://www.icmbio.gov.br/portal/unidades-deconservacao/biomas-brasileiros/amazonia/unidades-de-conservacao-amazonia/512-resex-rio-jutai. Accessed on November 17, 2019.

IUCN. 2019. The IUCN Red List of Threatened Species. Version 2019-2. [online] URL:

http://www.iucnredlist.org. Accessed on November 17, 2019.

Johns, A. D. 1987. Continuing Problems for Amazon River Turtles. *Oryx* 21:25–28. DOI:10.1017/S0030605300020445.

Levi, T., G. H. Shepard Jr, J. Ohl-Schacherer, C. A. Peres, and W. Y. Douglas. 2009. Modelling the Long-Term Sustainability of Indigenous Hunting in Manu National Park, Peru: Landscape-Scale Management Implications for Amazonia. *Journal of Applied Ecology* 46:804–814. DOI:10.1111/j.1365-2664.2009.01661.x.

Lima, D. M. 2009. The Domestic Economy in Mamirauá, Tefé, Amazonas State. In *Amazon Peasant Societies in a Changing Environment: Political Ecology, Invisibility and Modernity in the Rainforest,* edited by C. Adams, R. Murrieta, W. A. Neves, and M. Harris, pp. 131–156. Springer, Dordrecht, Netherlands. DOI:10.1007/978-1-4020-9283-1_7.

Lima, D. M., and N. Peralta. 2017. Developing Sustainability in the Brazilian Amazon: Twenty Years of History in the Mamirauá and Amanã Reserves. *Journal of Latin American Studies* 49:799–827. DOI:10.1017/S0022216X17000414.

Morcatty, T., and J. Valsecchi. 2015. Social, Biological, and Environmental Drivers of the Hunting and Trade of the Endangered Yellow-Footed Tortoise in the Amazon. *Ecology and Society* 20. DOI:10.5751/ES-07701-200303.

Nunes, A. V., C. A. Peres, P. D. A. L Constantino, B. A. Santos, and E. Fischer. 2019a. Irreplaceable Socioeconomic Value of Wild Meat Extraction to Local Food Security in Rural Amazonia. *Biological Conservation* 236:171–179. DOI:10.1016/j.biocon.2019.05.010.

Nunes, A. V., R. D. Guariento, B. A. Santos, and E. Fischer. 2019b. Wild Meat Sharing among Non-Indigenous People in the Southwestern Amazon. *Behavioral Ecology and Sociobiology* 73:26. DOI:10.1007/s00265-018-2628-x.

Ojasti, J. 1996. *Wildlife Utilization in Latin America: Current Situation and Prospects for Sustainable Management*. FAO Conservation Guide 25. Food and Agriculture Organization, Rome, Italy.

Padoch, C., E. Brondizio, S. Costa, M. Pinedo-Vasquez, R. R. Sears, and A. Siqueira. 2008. Urban Forest and Rural Cities: Multi-Sited Households, Consumption Patterns, and Forest Resources in Amazonia. *Ecology and Society* 13:2. [online] URL:http://www.ecologyandsociety.org/vol13/iss2/art2/.

Pantoja-Lima, J., P. H. Aride, A. T. de Oliveira, D. Félix-Silva, J. C. Pezzuti, and G. H. Rebêlo. 2014. Chain of Commercialization of *Podocnemis* spp. Turtles (Testudines: Podocnemididae) in the Purus River, Amazon Basin, Brazil: Current Status and Perspectives. *Journal of Ethnobiology and Ethnomedicine* 10:8. DOI:10.1186/1746-4269-10-8.

Peres, C. A. 2000. Effects of Subsistence Hunting on Vertebrate Community Structure in Amazonian Forests. *Conservation Biology* 14:240–253. DOI:10.1046/j.1523–1739.2000.98485.x.

Renoux, F., and B. de Thoisy. 2016. Hunting Management: The Need to Adjust Predictive Models to Field Observations. *Ethnobiology and Conservation* 5:1–13. DOI:10.15451/ec2016-6-5.1-1-13.

Ripple, W. J., K. Abernethy, M. G. Betts, G. Chapron, R. Dirzo, M. Galetti, T. Levi, P. A. Lindsey, D. W. Macdonald, B. Machovina, T. M. Newsome, C. A. Peres, A. D. Wallach, C. Wolf, and H. Young. 2016. Bushmeat Hunting and Extinction Risk to the World's Mammals. *Royal Society Open Science* 3:160498. DOI:10.1098/rsos.160498.

Robinson, J. G., and K. H. Redford. 1986. Body Size, Diet, and Population Density of Neotropical Forest Mammals. *The American Naturalist* 128:665–680. DOI:10.1086/284596.

Rowcliffe, J. M., E. de Merode, and G. Cowlishaw. 2004. Do Wildlife Laws Work? Species Protection and the Application of a Prey Choice Model to Poaching Decisions. *Proceedings of the Royal Society of London B: Biological Sciences* 271:2631–2636. DOI:10.1098/rspb.2004.2915.

Rushton, J., R. Viscarra, C. Viscarra, F. Basset, R. Baptista, and D. Brown. 2005. *How*

Important is Bushmeat Consumption in South America: Now and in the Future. ODI Wildlife Policy Briefing, Number 11, ODI, United Kingdom.

Sarti, F. M., C. Adams, C. Morsello, N. van Vliet, T. Schor, B. Yagüe, L. Tellez, M. Quiceno-Mesa, and D. Cruz. 2015. Beyond Protein Intake: Bushmeat as Source of Micronutrients in the Amazon. *Ecology and Society* 20:22. DOI:10.5751/ES-07934-200422.

Smith, N. J. 1979. Aquatic Turtles of Amazonia: An Endangered Resource. *Biological Conservation* 16:165–176. DOI:10.1016/0006-3207(79)90019-3.

Tavares de Freitas, C., P. F. Macedo Lopes, J. V. Campos-Silva, M. M., Noble, R. Dyball, and C. A. Peres. 2019. Co-Management of Culturally Important Species: A Tool to Promote Biodiversity Conservation and Human Well-Being. *People and Nature* 2:61–81. DOI:10.1002/pan3.10064.

van Vliet, N., and R. Nasi. 2008. Hunting for Livelihood in Northeast Gabon: Patterns, Evolution, and Sustainability. *Ecology and Society* 13:33. [online] URL: http://www.ecologyandsociety.org/vol13/iss2/art33/.

van Vliet, N., D. Cruz, M. P. Quiceno-Mesa, L. Jonhson Neves de Aquino, J. Moreno, R. Ribeiro, and J. Fa. 2015a. Ride, Shoot, and Call: Wildlife Use among Contemporary Urban Hunters in Três Fronteiras, Brazilian Amazon. *Ecology and Society* 20:8. DOI:10.5751/ES-07506-200308.

van Vliet, N., M. P. Quiceno, D. Cruz, L. J. Neves de Aquino, B. Yagüe, T. Schor, S Hernandez, and R. Nasi. 2015b. Bushmeat Networks Link the Forest to Urban Areas in the Trifrontier Region between Brazil, Colombia, and Peru. *Ecology and Society* 20:21. DOI:10.5751/ES-07782-200321.

Walker, A. J., and R. L. Ryan. 2008. Place Attachment and Landscape Preservation in Rural New England: A Maine Case Study. *Landscape and Urban Planning* 86:141–152. DOI:10.1016/j.landurbplan.2008.02.001.

Conservation Biology

Contributed Paper

Urban wild meat consumption and trade in central Amazonia

Hani R. El Bizri,[1,2,3,4]*† Thaís Q. Morcatty,[2,5] † João Valsecchi,[2,3,4] Pedro Mayor,[3,6,7] Jéssica E. S. Ribeiro,[2] Carlos F. A. Vasconcelos Neto,[2] Jéssica S. Oliveira,[2] Keilla M. Furtado,[2] Urânia C. Ferreira,[2] Carlos F. S. Miranda,[2] Ciclene H. Silva,[2] Valdinei L. Lopes,[2] Gerson P. Lopes,[2,8] Caio C. F. Florindo,[2,9] Romerson C. Chagas,[2] Vincent Nijman,[5] and John E. Fa[1,10]

[1]School of Science and the Environment, Manchester Metropolitan University, Manchester M15 6BH, U.K.
[2]Instituto de Desenvolvimento Sustentável Mamirauá, Estrada do Bexiga, 2584, Tefé, AM, 69553-225, Brazil
[3]ComFauna, Comunidad de Manejo de Fauna Silvestre en la Amazonía y en Latinoamérica, 332 Malecón Tarapacá, Iquitos, Peru
[4]RedeFauna, Rede de Pesquisa em Diversidade, Conservação e Uso da Fauna da Amazônia, Manaus, AM, Brazil
[5]Oxford Wildlife Trade Research Group, Oxford Brookes University, Oxford, OX3 0BP, U.K.
[6]Faculty of Veterinary, Department of Animal Health and Anatomy, Universitat Autònoma de Barcelona (UAB), Barcelona, Spain
[7]FUNDAMAZONIA, Malecón Tarapacá, n°332, Iquitos, Peru
[8]Programa de Pós-Graduação em Zoologia, Universidade Federal do Amazonas, Avenida General Rodrigo Octavio Jordão Ramos, Manaus, AM, 69067-005, Brazil
[9]Departamento de Físico-química, Instituto de Química, Universidade Estadual de Campinas (UNICAMP), Campinas, SP, 13083-970, Brazil
[10]Center for International Forestry Research (CIFOR), Bogor, 16115, Indonesia

Abstract: The switch from hunting wild meat for home consumption to supplying more lucrative city markets in Amazonia can adversely affect some game species. Despite this, information on the amounts of wild meat eaten in Amazonian cities is still limited. We estimated wild meat consumption rates in 5 cities in the State of Amazonas in Brazil through 1046 door-to-door household interviews conducted from 2004 to 2012. With these data, we modeled the relationship between wild meat use and a selection of socioeconomic indices. We then scaled up our model to determine the amounts of wild meat likely to be consumed annually in the 62 urban centers in central Amazonia. A total of 80.3% of all interviewees reported consuming wild meat during an average of 29.3 (CI 11.6) days per year. Most wild meat was reported as bought in local markets (80.1%) or hunted by a family member (14.9%). Twenty-one taxa were cited as consumed, mostly mammals (71.6%), followed by reptiles (23.2%) and then birds (5.2%). The declared frequency of wild meat consumption was positively correlated with the proportion of rural population as well as with the per capita gross domestic product of the municipality (administrative divisions) where the cities were seated. We estimated that as much as 10,691 t of wild meat might be consumed annually in the 62 urban centers within central Amazonia, the equivalent of 6.49 kg per person per year. In monetary terms, this amounts to US$21.72 per person per year or US$35.1 million overall, the latter figure is comparable to fish and timber production in the region. Given this magnitude of wild meat trade in central Amazonia, it is fundamental to integrate this activity into the formal economy and actively develop policies that allow the trade of more resilient taxa and restrict trade in species sensitive to hunting.

Keywords: Amazon, bushmeat, food security, tropical forests, wildlife trade

Mercado y Consumo Urbano de Carne Silvestre en la Amazonia Central

Resumen: El cambio de la caza de animales silvestres para consumo del hogar a caza para surtir mercados urbanos más lucrativos en la Amazonia puede afectar negativamente a algunas especies de caza. A pesar de esto, la

---

**email hanibiz@gmail.com*
†These authors contributed equally to this work.
***Article impact statement**: In central Amazonia, wild meat is widely consumed by urban residents; its trade generates as much as the fish and timber industries.*
Paper submitted October 15, 2018; revised manuscript accepted July 26, 2019.

Conservation Biology, Volume 34, No. 2, 438–448

DOI: 10.1111/cobi.13420

información sobre la cantidad de carne silvestre que se consume en las ciudades de la Amazonia todavía es limitada. Estimamos las tasas de consumo de carne silvestre en cinco ciudades del Estado de Amazonas, Brasil, por medio de 1046 entrevistas presenciales a hogares realizadas entre 2004 y 2012. Con estos datos modelamos la relación entre el uso de la carne silvestre y una selección de índices socioeconómicos. Después aumentamos nuestro modelo para determinar la cantidad de carne silvestre que tal vez se consume anualmente en los 62 centros urbanos de la Amazonia central. Un total de 80.3% de todos los entrevistados reportaron el consumo de carne silvestre durante un promedio de 29.3 (CI 11.6) días por año. La mayoría de la carne silvestre fue reportada como comprada en mercados locales (80.1%) o cazada por algún integrante de la familia (14.9%). Se citaron 21 taxones como parte del consumo, principalmente mamíferos (71.6%), seguidos por reptiles (23.2%) y aves (5.2%). La frecuencia declarada de consumo de carne silvestre estuvo correlacionada positivamente con la proporción de población rural, así como con el producto doméstico bruto per cápita de la municipalidad (divisiones administrativas) en donde se encuentran las ciudades. Estimamos que un máximo de 10,691 toneladas de carne silvestre podrían ser consumidas anualmente en los 62 centros urbanos de la Amazonia central, el equivalente a 6.49 kg/persona/año. En términos monetarios, esto equivale a US$21.72/persona/año o US$35.1 millones en general. Esta última cifra es comparable con la producción de madera y de peces en la región. Dada esta magnitud del mercado de carne silvestre en la Amazonia central, es fundamental la integración de esta actividad en la economía formal y el desarrollo activo de políticas que permitan el mercado de taxones más resilientes y que restrinjan el mercado para las especies sensibles a la caza.

Palabras Clave: Amazonas, bosques tropicales, carne de caza, mercado de fauna, seguridad alimentaria

摘要: 在亚马逊地区, 对野生动物的狩猎从供家庭食用到供应利润更高的城市市场的转变, 可能对一些狩猎物种产生负面影响。尽管如此, 关于亚马逊城市食用野生动物肉类的数量信息仍然很少。我们通过2004-2012年间的1046次上门访问, 估计了巴西亚马逊州五个城市的野生动物肉类食用量, 并利用这些数据分析了野生动物肉类利用与一些社会经济指数的关系。接下来, 我们利用这个模型模拟了亚马逊中部六十二个城市中心区每年的野生动物肉类食用量。结果显示, 总计80.3%的受访者报告每年平均29.3天(CI为11.6天)食用野生动物肉; 大部分肉类购自当地市场(80.1%)或由家庭成员狩猎获得(14.9%); 食用的肉类来自二十一个类群, 主要是哺乳动物(71.6%)、爬行动物(23.2%)和鸟类(5.2%); 野生动物肉类的食用频率与农村人口比例及其城市所在行政区的人均国内生产总值呈正相关。我们估计亚马逊中部地区六十二个城市中心区每年野生动物肉的食用量高达10691吨, 相当于每人每年食用6.49千克。按货币计算, 即每人每年食用21.58美元的野生动物肉, 或每年总计食用3510万美元的肉类, 后者相当于该地区采矿及木材生产总额。鉴于亚马逊中部地区野生动物肉类交易的规模之大, 应将这一活动纳入正式经济活动, 积极制定政策来支持开展那些较强恢复能力物种的交易, 而限制交易对狩猎敏感的物种。**【翻译: 胡怡思; 审校: 聂永刚】**

关键词: 丛林肉, 野生动物贸易, 亚马逊, 热带森林, 食物安全

Introduction

Wild meat contributes to the diet of millions of people worldwide, making up 20–70% of all protein intake, particularly in isolated tropical forest regions, where domestic meat is scarce (Fa et al. 2015). Increased urbanization within the tropics has resulted in a greater demand for wild meat from cities and large towns; these population centers are supplied from the rural areas where wildlife occur. Thus, many rural peoples have shifted from being strictly traditional subsistence hunters to selling wild meat in cities (e.g., Dounias 2016). Although the sale of wild meat provides an important income source for many, uncontrolled trade to large urban markets is a conservation problem in many tropical countries (Nasi et al. 2011).

Until recently, the only published references to urban wild meat consumption in the Amazon were from studies in 1 city, Iquitos, Peru (Bodmer & Lozano 2001). Based on this, urban wild meat consumption in Amazonia was regarded for some time as negligible (Rushton et al. 2005; Nasi et al. 2011). However, recent studies suggest there are significant city markets in the region where a large number of wild animals are sold for human consumption. For example, well-established wild meat markets exist in Abaetuba, Brazilian Amazon (Baía-Júnior et al. 2010), and in 2 prefrontier cities in southern Brazilian Amazonia, where around 80% of interviewed households regularly consumed wild meat (Parry et al. 2014). About 473 t of wild meat were estimated as traded annually in cities in the Amazonian trifrontier (Brazil, Colombia, and Peru) (van Vliet et al. 2014).

Because most of these studies are descriptive, restricted to relatively short sampling periods, and on a local scale, there is still a need to determine the levels of wild meat use and the volumes traded in Amazonian cities in much larger areas. Although factors affecting wild meat consumption and trade in African cities are relatively well known (Fa et al. 2009), these are still largely undescribed for Amazonia. A few studies have been conducted on how the economic and cultural background of consumers in Amazonian cities can affect how much wild meat is eaten

(Morsello et al. 2015; Chaves et al. 2017); however, studies that can predict the volume of wild meat consumed in urban centers at a regional level are still absent.

We estimated wild meat consumption rates in 5 cities in the State of Amazonas in Brazil. From these data, we developed statistical models to determine the relationship between wild meat use and a number of socioeconomic indices obtained from government sources and scaled up our model to estimate the amounts of wild meat likely to be consumed annually in urban centers throughout central Amazonia, an area representing about one-third of the entire Amazon biome. We also calculated the monetary value of the wild meat trade in this region. The results of our study can be useful to understand the extent of urban demand for wild meat in the Amazon as a whole and generate insights that may inform conservation efforts and policies to ensure the sustainable use of wildlife.

Methods

Study Sites

This study was conducted in Amazonas state, the largest state by area in Brazil (1,571,000 km^2). The state is almost entirely covered by moist broadleaf forest and encompasses about 29% of the Amazon Basin.

Brazilian states are divided into administrative municipalities that contain natural areas and urban and rural human settlements. Each municipality has a city that is the seat of the area's administration; these seat cities are not specified in law according to a minimum population size, area, or facilities. Amazonas state contains 62 municipalities with around 3.4 million inhabitants, of which around 2.7 million (79.4%) live in cities (IBGE 2018).

Because most cities in the state are far apart, accessible after long hours of travel by boat or plane, we chose those closest to our main research base in Tefé. Among these more accessible cities, we selected those within municipalities that would be representative of the range of socioeconomic variables we wanted to consider: rural and urban human population, human development index (HDI), and gross domestic product (GDP) (Supporting Information). We sampled households in the seat cities of 5 municipalities: Alvarães (14,080 inhabitants) and Tefé (61,399 inhabitants), at the confluence of the Tefé and Solimões Rivers; Coari (75,909 inhabitants), between the Urucu and Solimões Rivers; Maraã (17,364 inhabitants) on the lower Japurá River; and Fonte Boa (22,659 inhabitants) on the Solimões River (Table 1 & Supporting Information). The economy of these municipalities is based around small-scale industries and farming (IBGE 2018).

Data Collection

Data on wild meat consumption and trade were obtained through household surveys conducted from April 2004 to

Table 1. Details on cities in Amazonas where surveys on wild meat consumption were conducted.

City	*Coordinates*	*Area (km^2)*	*Total inhabitants, urban inhabitants (%)**	*Population density (ind/km^2)**	*Temporal range of interviews*	*Number of urban households*	*Households interviewed (%)*	*No. of neighborhoods (no. interviewed)*
Alvarães	03° 13′ 15″ S, 64° 48′ 15″ W	5,923.46	14,080, 7,878 (55.95)	2.38	Jul–Aug 2007	1,362	153 (11.2)	5 (5)
Coari	04° 05′ 06″ S, 63° 08′ 29″ W	57,970.77	75,909, 49,638 (65.4)	1.31	Oct 2011–May 2012	10,380	60 (0.6)	15 (8)
Fonte Boa	02° 30′ 50″ S, 66° 05′ 30″ W	12,155.43	22,659 (15,039; 66.37)	1.86	Nov 2011	2,791	20 (0.7)	10 (6)
Maraã	01° 51′ 22″ S, 65° 34′ 52″ W	16,830.83	17,364 (8,759; 50.44)	1.03	Oct 2011	1,393	22 (1.6)	8 (8)
Tefé	03° 21′ 15″ S, 64° 42′ 41″ W	23,692.22	61,399 (50,072; 81.55)	2.59	Apr–Nov 2004 Aug 2005–Mar 2006	10,014	791 (7.9)	20 (17)
Total	-	116,572.71	191,411	-	-	25,940	1,046	58 (44)

**Based on the last survey carried out in 2010 by the Brazilian government (IBGE 2018).*

May 2012 (Table 1). Depending on the time available for research in each city, we randomly selected at least 50% of neighborhoods within which we had a minimum of 2 interviews per neighborhood (Table 1). We asked heads of households (women and men) the following questions: is wild meat consumed in the house (*yes* or *no* response), how often is wild meat consumed (number of days per week, month, or year), which species are eaten, how is the consumed wild meat obtained (hunting, buying, or as a gift), if purchased, where is it purchased, and what price is paid for each species and what is the selling unit (e.g., kilograms and entire animal or half the animal specimen).

Although urban consumption and trade of wildlife is forbidden by law in Brazil (Law 5.197/1967) (Antunes et al. 2019), local wildlife management authorities tend to persecute hunters and traders, not consumers. Therefore, consumers do not perceive they are acting illegally and do not fear persecution. Given this, we did not use indirect questioning methods; rather, we applied direct questioning, as used in previous studies of wild meat consumption in the region (e.g., Parry et al. 2014; van Vliet et al. 2015; Chaves et al. 2017). Participants were made comfortable with our interview process by informing them of the study aims prior to the interview. Respondents were free to participate in the study and were informed that we would not disclose their identity. Of a total 1085 visited households, 96.4% (1046 households) agreed to be interviewed, an indication that most people felt comfortable participating (Table 1). We followed the Guidelines for Applying Free, Prior and Informed Consent in Buppert and McKeehan (2013).

Data Analyses

The overall amount of wild meat consumed (B) in each city was estimated using the following formula:

$$B = F_c \times P_c \times D_c, \tag{1}$$

where F_c is the mean frequency of consumption reported by the interviewees expressed as the number of days wild meat was consumed per person per year and P_c is the total potential consumers in the city based on the percentage of informants declaring that they consumed wild meat in our survey multiplied by the number of urban inhabitants. Because actual daily amounts of wild meat consumed by Amazonian urban dwellers are not currently available, we used 0.18 kg per person per day (CI 0.07) (obtained from a study of 13 indigenous communities [Ojasti 1996]) as an average amount of wild meat consumed per person per day (D_c).

For each city, we estimated the amount of meat consumed of each taxon from the percentage of times the taxon was mentioned (hereafter referred to as citations) and the overall amount of wild meat consumed (B). We estimated the number of individuals consumed per taxon per year by dividing the estimated biomass consumed of each taxon by the body mass of eviscerated specimens of the species (García et al. 2004).

All taxa were classified according to the International Union for Conservation of Nature (IUCN) Red List threat categories (vulnerable, endangered, and critically endangered) (IUCN 2019). If the local names provided by informants did not allow an unequivocal classification to species, we used genus or family.

We calculated the average selling price for each taxon by adjusting for the inflation rate for the different years during which each city was sampled based on the General Price Index for Brazil estimated by the Getúlio Vargas Foundation. We used the exchange rate for 1 June 2018 to convert Brazilian reais (R$) into U.S. dollars (R$3.85 = US$1.00). Hereafter all monetary units are U.S. dollars.

We built generalized additive models for location, scale, and shape (GAMLSS) to assess drivers of the 3 response variables: frequency of consumption (reported number of days of wild meat consumption per year), taxa citations, and price per kilogram. As predictor variables, we used socioeconomic indices compiled by the Brazilian Government for each municipality (IBGE 2018): total population (number of inhabitants), percent rural population (rural population/total population), HDI, and the per capita GDP in dollars per individual. Data from 2010 were used as reference for the first 3 variables because no information was available for the specific years when our interview data were collected. Per capita GDP values were available for each sampling year. We considered the gross body mass (noneviscerated weight in kilograms) and habitat type (terrestrial, arboreal, and aquatic) for each taxon as biological drivers for the models in relation to the taxa citations and price per kilogram. We also included taxa as a random factor due to differences in the number of citations among cities and the price per kilogram as a predictor variable for the taxa citations. Gross body mass of all mentioned species was obtained from García et al. (2004) and Robinson and Redford (1986). To avoid overestimating the number of people consuming wild meat due to low sample sizes in some cities, we calculated the potential number of consumers (P_c) by using the same variables of the municipalities as predictors in multiple logistic regressions (Supporting Information).

To build the models, we tested combinations of predictor variables in linear and nonlinear forms with different distribution families. We checked for collinearity among variables. Because the percentage of rural population was negatively correlated with the total population ($r^2 = 0.99$) and HDI ($r^2 = 0.94$), these variables were never included in the same models and were tested separately. Final models were selected based on the Akaike information criteria (AIC); all models with good support were those with ΔAIC values <2

in relation to the model with the smallest AIC. In cases when >1 model was a best fit, we selected the model with the smaller number of parameters.

Based on our best-fit models and variables, we used the function gamlss.predict to predict the current frequency of wild meat consumption, the amount of consumed wild meat (corrected by the percentage of consumers among urban dwellers), and the monetary value generated by wild meat for the entire central Amazonia region by calculating these parameters for all 62 cities in the Amazonas state with the most updated values for the predictor variables available from the government statistics (Supporting Information). We used R version 3.3.3 (http://www.R-project.org/) and the gamlss R-package for generalized linear and additive mixed models and predictions and GGally R-package for the collinearity test. For the variables effects, we assumed significance when $p < 0.05$.

Results

Sampled municipalities were representative of the 62 municipalities in the state of Amazonas. Average per capita GDP ($2835.34 [SD 2540.01]) and average percentage of the rural population (36.06% [SD 11.88]) in our 5 sampled municipalities were not statistically different from the averages for the remaining 57 municipalities (average GDP $2463.56 [SD 1396.36], $t = 0.53$, df $= 60$, $p = 0.65$; rural population $44.95 [SD 14.30], $t = 1.45$, df $= 60$, $p = 0.15$) (Supporting Information).

Consumption and Procurement of Wild Meat

All interviewees in Maraã (20/20) and Fonte Boa (22/22), 90.8% (139/153) in Alvarães, 85.0% in Coari (51/60), and 76.9% (608/791) in Tefé declared consuming wild meat; overall average was 80.3% (Table 2). Respondents declared consuming wild meat during 29.3 (CI 11.6) days per year (Table 2). An average of 80.1% of interviewees reported buying wild meat, and 14.9% of consumers reported hunting wildlife (Table 3). The estimated mean annual wild meat biomass consumed per capita was 4.60 kg per person per year (SD 1.87), a total of 500,497.56 kg (CI 203, 254.42).

Taxa Consumed

Twenty-one taxa were mentioned as eaten by respondents. As many as 40% (6 of 15) of the taxa identified to species are threatened with extinction (Supporting Information). Among the 2067 citations, mammals were the predominant group ($n = 1480$, 71.6%), followed by reptiles ($n = 479$, 23.2%) and birds ($n = 108$, 5.2%). In terms of biomass, white-lipped peccary (*Tayassu pecari*) (127,862.87 kg),

Table 2. Details on the estimated consumption of wild meat in 5 cities in central Amazonia.

City	*No. that consumed wild meat (%)*		*No. of potential consumers (%)*[a]	*Average frequency of consumption, days • person*$^{-1}$ *• year*$^{-1}$ *(CI)*	*Overall wild meat consumption, kg/year (CI range)*[b]	*Per capita urban wild meat consumption, kg • person*$^{-1}$ *• year*$^{-1}$ *(CI range)*
	yes	*no*				
Alvarães	139 (90.8)	14 (8.2)	7,258.81 (92.1)	32.83 (11.07)	41,887 (24,876–58,897)	5.32 (3.16–7.48)
Coari	51 (85.0)	9 (15.0)	43,715.73 (88.1)	29.33 (5.70)	225,546 (133,951–317,141)	4.54 (2.70–6.39)
Fonte Boa	20 (100.0)	0 (0)	13,167.44 (87.6)	24.77 (12.58)	57,383 (34,079–80,686)	3.82 (2.27–5.37)
Maraã	22 (100.0)	0 (0)	8,223.41 (93.9)	42.67 (26.04)	61,713 (36,651–86,775)	7.05 (4.18–9.91)
Tefé	608 (76.9)	183 (23.1)	38,545.36 (77.0)	16.81 (2.51)	113,969 (67,686–160,252)	2.28 (1.35–3.20)
Total	840 (80.3)	206 (19.7)	110,910.75	29.28 (11.58)	500,498 (297,243–703,752)	4.60 (2.73–6.47)

[a] *Calculated with logistic regressions to obtain the likely percentage of people consuming wild meat within the entire population of each city (see Supporting Information).*
[b] *Calculated by summing average wild meat amount.*

Table 3. Declared means by which urban consumers obtained wild meat in 5 cities in central Amazonia.

City	*No. buying (%)*	*No. hunting (%)*	*No. buying or hunting (%)*	*No. receiving gifts (%)*	*Total*
Alvarães	100 (75.8)	18 (13.6)	14 (10.6)	0 (0.0)	132
Coari	42 (82.4)	4 (7.8)	3 (5.9)	2 (3.9)	51
Fonte Boa	16 (80.0)	4 (20.0)	0 (0.0)	0 (0.0)	20
Maraã	19 (86.4)	2 (9.1)	1 (4.5)	0 (0.0)	22
Tefé	463 (75.9)	146 (23.9)	0 (0.0)	1 (0.2)	610
Total (average %)	640 (80.1)	174 (14.9)	18 (4.2)	3 (0.8)	835

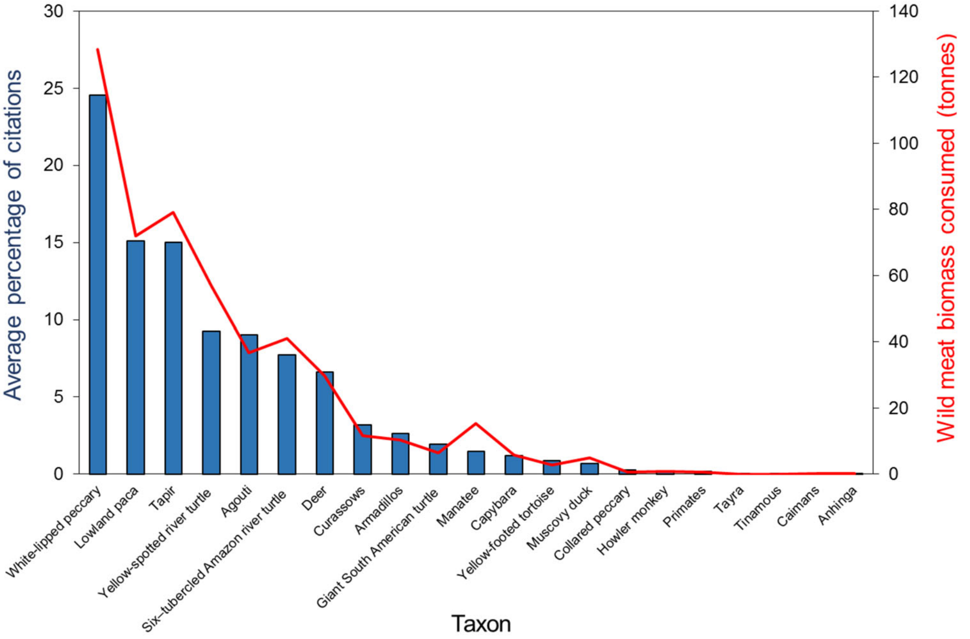


Figure 1. Average percentage of citations (bars) and overall wild meat biomass estimated as consumed (line) per taxon in 5 cities in central Amazonia. Scientific names are in Supporting Information.

tapir (*Tapirus terrestris*) (78,548.01 kg), lowland paca (*Cuniculus paca*) (71,348.85 kg), and yellow-spotted river turtle (*Podocnemis unifilis*) (57,467.75 kg) were the most representative, making up together 67% of the total (Fig. 1). A total of 95,772 (CI 38,893) animals were estimated as consumed annually; 4 species, *Podocnemis sextuberculata*, *Podocnemis unifilis*, agouti (*Dasyprocta fuliginosa*), and *C. paca*, represented 76.7% of this total (Supporting Information).

Traded Biomass

Of the total biomass estimated as consumed, 403,311 kg (80.6%) were estimated as purchased in urban markets. People declared they usually bought wild meat in only 1 place ($n = 605$, 94.4%), although some informants declared buying in 2 ($n = 27$, 4.2%) or 3 different places ($n = 9$, 1.4%). Informants reported that wild meat is mainly obtained at local fairs ($n = 313$, 46.1%), followed by hawkers ($n = 208$, 30.2%), private residences ($n = 69$, 9.2%), directly in rural communities ($n = 63$, 9.3%), and from riverboats ($n = 33$, 5.2%).

Information on prices was reported by informants for 17 taxa: mean price was $3.82/kg (SD 1.60). The sale of these taxa was estimated to generate $1,522,412/year (CI 240,919). The commercialization of 4 taxa alone, 2 chelonians (*P. unifilis* and *P. sextuberculata*) and 2 mammals (*T. pecari* and *T. terrestris*), was responsible for 71.8% of this amount. Curassows (mean price $8.39/kg) and the 3 freshwater turtles (mean prices $7.67/kg for *P. unifilis*, $6.49/kg for *P. sextuberculata*, and $6.01/kg for *Podocnemis expansa*) were the most expensive taxa (Supporting Information).

Drivers of and Overall Wild Meat Consumption in Central Amazonia

The reported frequency of wild meat consumption per person increased significantly relative to the percent rural population in the municipality (2.504×10^{-2} [SE 5.597×10^{-3}], $t = 4.4$, $p < 0.001$) (Fig. 2a) and as per capita GDP increased (1.393×10^{-4} [1.573×10^{-8}], $t = 8855.1$, $p < 0.001$) (Fig. 2b). The gross body mass positively influenced the taxa citations (0.077 [SE 0.007], $t = 10.0$, $p < 0.001$) (Fig. 2c). Prices per kilogram presented a nonlinear relationship with the taxa's gross body mass (−0.001 [SE 0.0001], $t = -10.7$, $p < 0.001$) (Fig. 2d) and increased as the percentage of rural population in the municipality increased (0.005 [0.0005], $t = 8.7$, $p < 0.001$) (Fig. 2e).

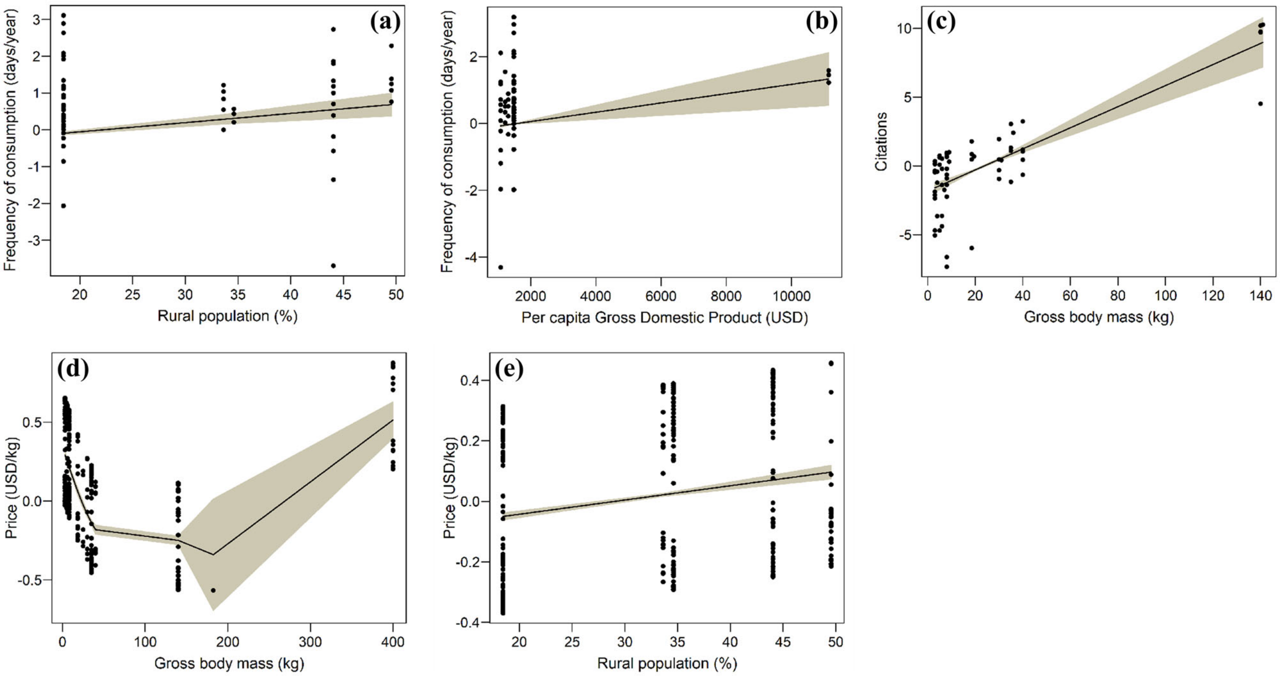


Figure 2. Relationships between (a) percentage of rural population and (b) per capita gross domestic product of the municipalities with the declared frequency of consumption of wild meat: between (c) gross body mass with the percentage of citations of each taxon and between (d) gross body mass and (e) percentage of rural population of the municipalities with the price of each taxon in 5 cities of central Amazonia. Only taxa cited in at least 3 cities were considered for the model (c) gray shading, 95% CI; y-axis values are partial residuals for each variable retained in the models). Model details, such as families of distribution, link functions, and p values, are in Supporting Information.

Using the models obtained from these relationships, we estimated that 10,691,103 kg (CI 4,342,101) of wild meat was consumed annually in the 62 cities (2,755,756 urban inhabitants) within central Amazonia (Supporting Information). This translates to a mean annual per capita consumption of 6.49 kg per person per year and amounts to a total monetary value of $35,112,904/year (CI 14,260,811) (average of $21.72 per person per year) (Supporting Information). The cities with the largest estimated amounts of wild meat consumed per year were along the western part of the state, and few were located in the central part of the Amazon River basin. The cities with a greater estimated per capita wild meat consumption were located along the northwestern portion of the state (Fig. 3).

Discussion

A very large proportion of interviewees in our study reported eating wild meat, corresponding to 1 day of wild meat eaten for every 12.46 days consuming domestic meat in a year. These results correspond with Parry et al.'s (2014) study in the southern Brazilian Amazon, which shows that as many as 80% of the inhabitants consumed wild meat at least once per year.

Data on daily wild meat consumption in Amazonian urban centers are largely unavailable. The average per capita wild meat consumption we used to estimate overall consumption volumes is necessarily a working value only, but it is heuristically useful for estimating the amount of meat consumed in wild meat-based meals and for extrapolating to the entire study region. There is no doubt that more precise information on amounts consumed per individual or household in urban centers is required, and we suggest this should be a priority for future work.

We acknowledge that some respondents could have underreported how much wild meat they consumed. Because we did not apply indirect questioning techniques to determine the level of underreporting, our consumption estimates must be treated as a minimum. We also believe underreporting rates were probably similar among cities because sampled cities are culturally similar and under the same enforcement regimes.

Data collection for the different cities was spread out over 7 years, and data for some socioeconomic indices were not available for the same years of data collection. This may have affected our results because consumption rates and socioeconomic indices may have varied over time. In addition, the most recent values

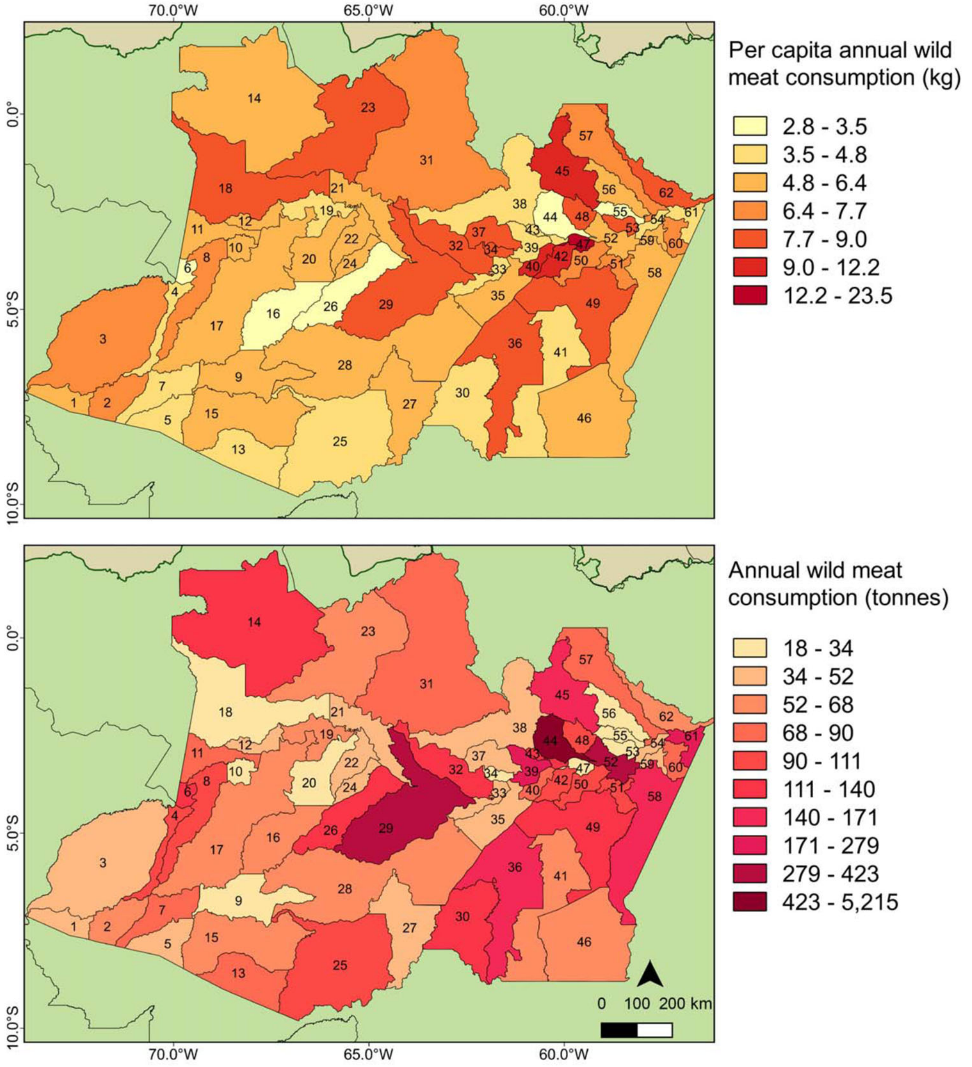


Figure 3. Two maps portraying the predicted per capita wild meat consumption (top) and annual amount of wild meat consumption (bottom) in the cities of 62 municipalities in central Amazonia. The municipalities surveyed for modeling were Alvarães (24), Coari (29), Fonte Boa (19), Maraã (21), and Tefé (26). Names and details of the other municipalities are available in Supporting Information.

of socioeconomic statistics were not obtained at the same time by the government (last available GDP values are from 2016, whereas last census of population was conducted in 2010). However, temporal changes in the 2 variables (rural population and per capita GDP) we used varied differently. The GDP changed substantially over the short term (i.e., some studied municipalities' GDPs more than doubled from 2010 to 2016), whereas the proportion of rural population changed by only −1.0% on average from 2000 to 2010 (IBGE 2001). Despite these shortcomings, our estimation of 3.49 kg per person per year for Tabatinga, a city in the Brazil–Colombia–Peru frontier, was very similar to the 3.40 kg per person per year derived from direct observations at for the same site (van Vliet et al. 2015). In addition, our predicted per capita frequency of wild meat consumption for Tapauá (39.1 days/year) was also comparable to estimates of Chaves et al. (2017) (38.4 days/year) in the same city. We argue that, despite the limitation posed by the lack of some governmental statistics, these observations support the robustness of our model (Supporting Information).

Our results clearly showed that urban wild meat markets are well established in Amazonas state. In all surveyed cities, most interviewed urban dwellers reported buying wild meat, and most of them declared purchasing meat from the same salesmen, vendors in local fairs, and hawkers, an indication of constancy in supply. Parry et al. (2014) show that the poorest urban households hunt to obtain wild meat, whereas wealthier residents buy wild meat. This is because hunting is the cheaper option for poorer people in cities, but also because the lack of formal employment, which is more common among this group, allows them to spend more time in this activity. Although we have not systematically collected data on this, some informants who declared hunting wild meat for consumption in our study informally declared selling part of their quarry. In the Amazonian cities of Benjamin Constant and Atalaia do Norte in Brazil, urban hunters profit from the sale of up to 97% of their game to closed markets (van Vliet et al. 2015). However, the low number of urban people declaring hunting wild meat shows that rural hunters supply city markets. Hunters from rural areas in Amazonia are mainly subsistence hunters, but may sell part of their hunting yields, likely to obtain money to buy urban goods, such as clothes and foods (Antunes et al. 2019). For instance, in the Peruvian Amazon, Bodmer and Lozano (2001) found that rural hunters sell around 7% of mammals hunted, whereas Morcatty and Valsecchi (2015) found that around 21% of yellow-footed tortoises (*Chelonoidis denticulatus*) harvested by rural hunters in Amazonia were traded in urban wild meat markets.

The main groups (mammals and chelonians) and species cited as consumed and traded in our study cities were similar to those traded in other Amazonian localities (Bodmer & Lozano 2001; van Vliet et al. 2014). These species are commonly hunted for subsistence and trade by rural populations throughout Amazonia (e.g., Peres 2000; Lopes et al. 2012) and in other Neotropical regions (El Bizri et al. 2015). In particular, tapir and white-lipped peccary were among the top 3 species cited in our surveys. Both species are listed as vulnerable, following IUCN Red List criteria, and hunting is one of the main threats. Both species are declining in central Amazonia (Parry & Peres 2015). Other highly cited species, such as lowland paca, are also affected by hunting in Amazonia (e.g., Valsecchi et al. 2014; El Bizri et al. 2018), but are listed as least concern by IUCN.

In central Amazonia, governmental statistics for each municipality are useful to predict wild meat consumption at large scales. We found that the proportion of rural inhabitants within a municipality was correlated with the proportion of inhabitants that declared consuming wild meat in cities, the reported frequency of consumption, and the prices per kilogram in the market. This pattern may be a result of the economic connectivity between urban and rural sectors in these municipalities. Thus, in municipalities where the rural population is larger, urban people are able to buy wild meat more frequently from rural people who hunt. Because these small cities are often isolated and only accessible by boat, domestic and processed products become more expensive due to higher transportation costs. As a consequence, wild meat prices are higher in small cities, where rural inhabitants outnumber urban ones, because trading in wild meat is one of the most prevalent and cost-effective activities in localities where the sales of agricultural commodities do not have a large local market and are uncompetitive due to the high costs and long transportation times (Wilkie et al. 2016). Moreover, we argue that the price of the wild meat may also be anchored to the price of domestic meat or other important products for local inhabitants, such as oil.

The relationship between price and species' body mass reflects the fact that smaller species, although more abundant and easier to capture, are sold at a higher price because they yield less meat. Conversely, large-bodied species, although more profitable in terms of meat obtained, are less abundant and therefore more difficult to capture. This explains the U-shaped curve in this relationship and shows that hunters meeting urban demand do not kill prey randomly, but consider prey profitability when choosing which prey to kill and how to price it (Rowcliffe et al. 2004). Our results also indicated that larger species are generally more consumed than smaller species, and this relationship may be caused partially by price differences. However, considering that fewer game taxa were cited as consumed than in rural areas in Amazonia (e.g., 30 species [Vieira et al. 2015], 27 species [Kirkland et al. 2018]), the range of species reaching urban markets may be limited by consumer taste and taboos.

Studies reporting the contribution of wild meat to local economies indicate a large informal sector, often as large as formal sectors, such as timber harvesting or agriculture (Lescuyer & Nasi 2016). Because wild meat trade in Brazil is prohibited, the harvest and selling of this product is excluded from official statistics. Nevertheless, the wild meat market was predicted to generate a great deal of money in central Amazonia ($35.1 million). Compared with other products, it is three times lower than mineral ($102.9 million) production and similar to fish ($40.1 million) and timber production ($39.9 million) in the Amazonas state (SEPLANCTI/DEPI 2018; ANM 2019). However, considering that a large proportion of these economic activities, including the wild meat trade, is carried out illegally, these numbers must be considered an underestimate. Most municipalities in the Amazonas state have >40% of their populations living on less than half minimum wage (IBGE 2018); thus, wild meat represents an important product for the income of several rural and urban families in the region. Hunters are not the only ones who generate income from wild meat; rather, several different actors involved in the commodity chain generate income for themselves (Cowlishaw et al. 2005). In Peru commercial hunters can supply wild meat directly to wholesalers, restaurants, or market traders, who in turn supply meat to the customers; price of the meat increases at each step (Fang et al. 2008). The same has been observed for the trade of tortoise meat in 4 cities in Amazonia, where intermediaries between hunters and urban vendors benefit significantly and obtain high profits (Morcatty & Valsecchi 2015). This highlights the necessity of finding solutions to regulate this sector in Amazonia and to reduce the impacts of wild meat trade in urban centers on Amazonian wildlife.

Our maps provide the first large-scale estimation of the amount of urban wild meat consumption for the Amazon, from which one may determine hotspots of wildlife extraction and where implementation of conservation strategies is more urgent. The high consumption rates of wild meat predicted for large cities, such as Coari and the capital Manaus, where there is an offer of domestic meat, signal that wild meat consumption is not strictly related to dietary necessity or poverty, but possibly a maintenance of the rural heritage and the thrill of local dwellers for diversifying their diet (Wilkie et al. 2016). Many cities in the western Amazon, which are more accessible due to their location downstream on Amazon River, were predicted to have both per capita and total wild meat consumption at relevant levels, likely because of the combination of high GDP and surrounding rural populations. Therefore, the replacement of the wild meat by domestic meat at a more accessible price, which is a very common suggested strategy to reduce wild meat demand in cities (Rushton et al. 2005), may not be sufficient to solve the problem. In addition, law enforcement and surveillance actions face several barriers in the Amazon, especially due to the large extent of the territory and difficult access. Accordingly, the current prohibition on wildlife commerce in most areas of the Amazon has been driving a hidden market that hampers control. Furthermore, captive breeding of wild species, although suggested as an alternative to keep wild meat consumption at sustainable levels (Nogueira & Nogueira-Filho 2011), may not produce enough individuals to supply the demand at an affordable price (Wilkie et al. 2016).

Given the magnitude of the trade of wild meat we found, we suggest the regulation of this unconstrained activity is a fundamental and urgent matter to resolve. Plans that support the sustainable management of wild meat in the surrounding forests should bring regulated wild meat trade into the formal economy and promote the improvement of rural livelihoods. Wildlife trade regulations could include policies designed to allow the trade of more resilient species and to protect or restrict the trade of those more sensitive to hunting. Some of these more resilient species are already among the most consumed taxa in the region, so acceptance of this policy is most likely. This strategy would generate income for those involved in the market chain and adequately control harvests of wildlife species while guaranteeing conservation of threatened species.

Acknowledgments

This work was supported by the grant agreement for Instituto de Desenvolvimento Sustentável Mamirauá of the Gordon and Betty Moore Foundation (number 5344) and the National Council for Scientific and Technological Development (CNPq) (grant numbers 300005/2013-0, 452908/2016-7, 201475/2017-0). The authors thank K. Henle, M. Auliya, and C. Ferreira, from the Helmholtz Centre for Environmental Research (UFZ), for their useful comments on the manuscript. H.R.E.B. thanks the German Federal Ministry of Education and Research (BMBF) for his Green Talents Award, which supported this work. T.Q.M. is supported by the WCS Graduate Scholarship Program, a program of the Wildlife Conservation Society and the Christensen Conservation Leaders Scholarship, and by the Wildlife Conservation Network Scholarship Program through the Sidney Byers Scholarship award.

Supporting Information

A map portraying the location of the sampled cities within central Amazonia (Appendix S1), information on the representativeness and variation of per capita GDP and percentage of rural population values of sampled municipalities (Appendix S2), results of the logistic regression between percentage of rural population of municipalities and probability of wild meat consumption (Appendix S3), details on the game species cited as consumed in 5 cities in central Amazonia (Appendix S4), details on the amount of biomass sold and prices of and annual monetary amount generated by 17 species (cited as traded in the 5 sampled cities in central Amazonia (Appendix S5), statistical results of the relationship between consumption rates, taxa citations, and price with socioeconomic and biological factors (Appendix S6), and results of the modeling of wild meat consumption in the 62 cities of central Amazonia (Appendix S7) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

ANM (Agência Nacional de Mineração). 2019. Anuário Mineral Brasileiro: Principais Substâncias Metálicas. ANM, Brasilia, Brazil.

Antunes AP, et al. 2019. A conspiracy of silence: subsistence hunting rights in the Brazilian Amazon. Land Use Policy **84:**1–11.

Baía-Júnior PC, Guimarães DA, Le Pendu Y. 2010. Non-legalized commerce in game meat in the Brazilian Amazon: a case study. Revista de Biología Tropical **58:**1079–1088.

Bodmer RE, Lozano EP. 2001. Rural development and sustainable wildlife use in Peru. Conservation Biology **15:**1163–1170.

Buppert T, McKeehan A. 2013. Guidelines for applying free, prior and informed consent: a manual for conservation international. Conservation International, Arlington, Virginia.

Chaves WA, Wilkie DS, Monroe MC, Sieving KE. 2017. Market access and wild meat consumption in the central Amazon, Brazil. Biological Conservation **212**:240–248.

Cowlishaw G, Mendelson S, Rowcliffe JM. 2005. Structure and operation of a bushmeat commodity chain in southwestern Ghana. Conservation Biology **19:**139–149.

Dounias E. 2016. From subsistence to commercial hunting: technical shift in cynegetic practices among southern Cameroon forest dwellers during the 20th Century. Ecology and Society **21:**23.

El Bizri HR, Morcatty TQ, Lima JJ, Valsecchi J. 2015. The thrill of the chase: uncovering illegal sport hunting in Brazil through YouTube$^{\text{TM}}$ posts. Ecology and Society **20:**30.

El Bizri HR, Fa JE, Bowler M, Valsecchi J, Bodmer R, Mayor P. 2018. Breeding seasonality in the lowland paca (*Cuniculus paca*) in Amazonia: interactions with rainfall, fruiting, and sustainable hunting. Journal of Mammalogy **99:**1101–1111.

Fa JE, Albrechtsen L, Johnson PJ, Macdonald DW. 2009. Linkages between household wealth, bushmeat and other animal protein consumption are not invariant: evidence from Rio Muni, Equatorial Guinea. Animal Conservation **12:**599–610.

Fa JE, et al. 2015. Disentangling the relative effects of bushmeat availability on human nutrition in central Africa. Scientific Reports **5:**8168.

Fang T, Bodmer R, Puertas P, Mayor P, Perez P, Acero R, Hayman D. 2008. Certificación de pieles de pecaries (*Tayassu tajacu* y *T. pecari*) en la Amazonía peruana: una estrategia para la conservación y manejo de fauna Silvestre en la Amazonia peruana. Wust Editions-Darwin Institute, Lima, Peru.

García JB, Acosta NB, Olivares LV. 2004. Técnicas de preservación y factor de conversión de fauna silvestre en la región Loreto, Perú. Pages 427–433 in Bodmer R, editor. Memorias del VI congreso internacional sobre el manejo de fauna silvestre en la Amazonía y Latinoamérica. Universidad Nacional de la Amazonía Peruana; Durrell Institute of Conservation and Ecology; and Wildlife Conservation Society; Iquitos, Peru.

IBGE (Instituto Brasileiro de Geografia e Estatística). 2001. Sinopse preliminar do Censo Demográfico: 2000. IBGE, Rio de Janeiro, Brazil.

IBGE (Instituto Brasileiro de Geografia e Estatística). 2018. Cidades. IBGE, Rio de Janeiro, Brazil. Available from https://cidades.ibge.gov.br/ (accessed June 2018).

IUCN. 2019. The IUCN Red List of Threatened Species. Version 2019-2. Available from http://www.iucnredlist.org (accessed September 2019).

Kirkland M, Eisenberg C, Bicerra A, Bodmer RE, Mayor P, Axmacher JC. 2018. Sustainable wildlife extraction and the impacts of socio-economic change among the Kukama-Kukamilla people of the Pacaya-Samiria National Reserve, Peru. Oryx. https://doi.org/10.1017/S0030605317001922.

Lescuyer G, Nasi R. 2016. Financial and economic values of bushmeat in rural and urban livelihoods in Cameroon: inputs to the development of public policy. International Forestry Review **18:**93–107.

Lopes GP, Valsecchi J, Vieira TM, Costa EWM. 2012. Hunting and hunters in lowland communities in the region of the middle Solimões, Amazonas, Brazil. Uakari **8:**7–18.

Morcatty TQ, Valsecchi J. 2015. Social, biological, and environmental drivers of the hunting and trade of the endangered yellow-footed tortoise in the Amazon. Ecology and Society **20:**3.

Morsello C, Yagüe B, Beltreschi L, van Vliet N, Adams C, Schor T, Quiceno-Mesa MP, Cruz D. 2015. Cultural attitudes are stronger predictors of bushmeat consumption and preference than economic factors among urban Amazonians from Brazil and Colombia. Ecology and Society **20:**21.

Nasi R, Taber A, van Vliet N. 2011. Empty forests, empty stomachs? Bushmeat and livelihoods in the Congo and Amazon Basins. International Forestry Review **13:**355–368.

Nogueira SSC, Nogueira-Filho SLG. 2011. Wildlife farming: An alternative to unsustainable hunting and deforestation in Neotropical forests? Biodiversity and Conservation **20:**1385-1397.

Ojasti J. 1996. Wildlife Utilization in Latin America: current situation and prospects for sustainable management. FAO conservation guide 25. Food and Agriculture Organisation, Rome, Italy.

Parry L, Peres CA. 2015. Evaluating the use of local ecological knowledge to monitor hunted tropical-forest wildlife over large spatial scales. Ecology and Society **20:**15.

Parry L, Barlow J, Pereira H. 2014. Wildlife harvest and consumption in Amazonia's urbanized wilderness. Conservation Letters **7:** 565–574.

Peres CA. 2000. Effects of subsistence hunting on vertebrate community structure in Amazonian forests. Conservation Biology **14:** 240–253.

Robinson JG, Redford KH.1986. Body size, diet, and population density of Neotropical forest mammals. The American Naturalist **128:** 665–680.

Rowcliffe JM, de Merode E, Cowlishaw G. 2004. Do wildlife laws work? Species protection and the application of a prey choice model to poaching decisions. Proceedings of the Royal Society of London B: Biological Sciences **271:**2631–2636.

Rushton J, Viscarra R, Viscarra C, Basset F, Baptista R, Brown D. 2005. How important is bushmeat consumption in South America: now and in the future. ODI wildlife policy briefing 11. Overseas Development Institute, London.

SEPLANCTI/DEPI. 2018. Anuário Estatístico do Amazonas 2018. Departamento Estadual de Estatística, Manaus, Brazil.

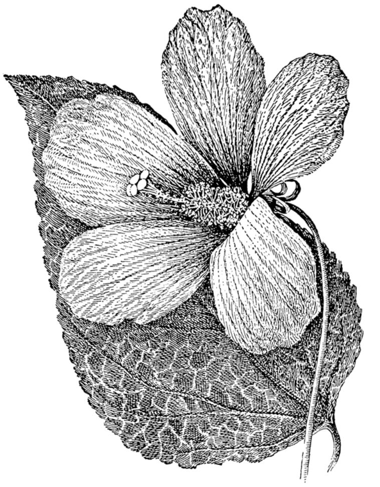
Valsecchi J, El Bizri HR, Figueira JEC. 2014. Subsistence hunting of *Cuniculus paca* in the middle of the Solimões River, Amazonas, Brazil. Brazilian Journal of Biology **74:**560–568.

van Vliet N, Cruz D, Quiceno-Mesa M, Neves de Aquino L, Moreno J, Rairon R, Fa J. 2015. Ride, shoot, and call: wildlife use among contemporary urban hunters in Três Fronteiras, Brazilian Amazon. Ecology and Society **20:**8.

van Vliet N, Mesa MPQ, Cruz-Antia D, de Aquino LJN, Moreno J, Nasi R. 2014. The uncovered volumes of bushmeat commercialized in the Amazonian trifrontier between Colombia, Peru & Brazil. Ethnobiology and Conservation **3:**7.

Vieira M, von Muhlen EM, Shepard Jr GH. 2015. Participatory monitoring and management of subsistence hunting in the Piagaçu-Purus reserve, Brazil. Conservation and Society **13:** 254–264.

Wilkie DS, Wieland M, Boulet H, Le Bel S, van Vliet N, Cornelis D, BriacWarnon V, Nasi R, Fa JE. 2016. Eating and conserving bushmeat in Africa. African Journal of Ecology **54:**402–414.



Journal of Mammalogy, 99(5):1101–1111, 2018
DOI:10.1093/jmammal/gyy102

Breeding seasonality in the lowland paca (*Cuniculus paca*) in Amazonia: interactions with rainfall, fruiting, and sustainable hunting

Hani R. El Bizri,* John E. Fa, Mark Bowler, João Valsecchi, Richard Bodmer, and Pedro Mayor

Grupo de Pesquisa em Ecologia de Vertebrados Terrestres, Instituto de Desenvolvimento Sustentável Mamirauá (IDSM), Estrada do Bexiga 2584, Fonte Boa, CEP 69553-225, Tefé, Amazonas, Brazil (HREB, JV)
ComFauna, Comunidad de Manejo de Fauna Silvestre en la Amazonía y en Latinoamérica, 332 Malecon Tarapaca, Iquitos, Peru (HREB, JV, RB, PM)
School of Science and the Environment, Manchester Metropolitan University, Oxford Road, Manchester M15 6BH, United Kingdom (HREB, JEF)
Center for International Forestry Research (CIFOR), Jalan Cifor Rawajaha, Situ Gede, Bogor Barat, Kota Bogor, Jawa Barat 16115, Indonesia (JEF)
School of Science, Technology and Engineering, University of Suffolk, Waterfront Building, Neptune Quay, Ipswich IP4 1QJ, United Kingdom (MB)
San Diego Zoo Global Institute for Conservation Research, Escondido, California, CA 92027-9614, USA (MB)
FundAmazonia, Malecón Tarapacá nº 332, Iquitos, Loreto, Peru (RB, PM)
Departament de Sanitat i Anatomia Animals, Universitat Autònoma de Barcelona, Bellaterra, E-08193 Barcelona, Spain (PM)
Programa de Pós-Graduação em Saúde e Produção Animal na Amazônia, Universidade Federal Rural da Amazônia, Terra Firme, Postal Code 66077-830, Belém, Pará, Brazil (PM)

* *Correspondent: hanibiz@gmail.com*

The resilience of a given species to hunting is conditioned by the effect of potential threats upon the more sensitive periods in its life history, such as when animals are breeding. We investigated the environmental drivers of breeding seasonality in the lowland paca (*Cuniculus paca*), and the potential impact of hunting on the species. As part of a participative study with hunters in 2 Amazonian sites, we obtained reproductive organs of pacas as well as information on the hunters' daily wild meat extraction. Using data on rainfall, river water level, and fruiting phenology from the 2 study sites, we applied generalized additive models for location, scale, and shape (GAMLSS) to examine the effect of climatic and environmental factors on paca reproduction. Forest fruiting was directly linked to higher pregnancy rates in pacas, and when lactation and weaning of offspring mostly occurred. Hunting was highly seasonal in all studied years and positively correlated with higher levels of river water. The coincidence between hunting patterns and paca reproductive cycles during the wet season resulted in more pregnant females being harvested. In addition to the known slow reproductive rate of pacas, the disproportionate offtake of pregnant females may affect the long-term sustainability of hunting of this species. Reducing hunting during the flooded season may not be feasible because the lowland paca provides most of the wild meat consumed by thousands of rural Amazonians during this period. However, options to offset the negative effects of killing of pregnant females could include the zoning of hunting areas or encouraging hunters to target primarily males. Our results indicate that strategies for the sustainable harvest of pacas and other heavily hunted Amazonian mammals should consider the interaction between the species' reproductive cycles and hunting by local people in order to enhance conservation and management efforts.

A resiliência de uma espécie à caça é condicionada pela sua capacidade reprodutiva intrínseca e pelo efeito de potenciais ameaças durante os períodos mais sensíveis de sua história de vida, como o período reprodutivo. Neste trabalho, nós investigamos os fatores ambientais que determinam a sazonalidade reprodutiva da paca

---

(*Cuniculus paca*) e o potencial impacto da caça sobre a espécie. Em um estudo participativo de 15 anos em duas áreas da Amazônia, obtivemos órgãos reprodutivos de pacas doados voluntariamente por caçadores, bem como informações sobre seus padrões diários de caça. Usando informações sobre precipitação, nível d'água dos rios e fenologia de frutificação, nós aplicamos modelos aditivos generalizados (GAMLSS) para examinar o efeito de fatores climáticos e ambientais na reprodução da paca. A precipitação esteve positivamente ligada a uma maior frutificação, que por sua vez foi correlacionada com maiores taxas de prenhes da paca e com os períodos de lactação e desmame da prole. A caça de paca foi altamente cíclica ao longo dos anos e positivamente associada aos níveis d'água mais elevados. A convergência entre os padrões de caça e os ciclos reprodutivos de paca resulta na extração de um grande número de fêmeas grávidas. Juntamente com a lenta taxa de reprodução da espécie, a captura desproporcional de fêmeas grávidas pode afetar a sustentabilidade do uso da paca. Reduzir a caça durante os períodos de inundação pode não ser viável, pois a paca é a espécie responsável por fornecer grande parte da carne silvestre consumida por milhares de moradores rurais da Amazônia neste período. No entanto, ações para compensar os efeitos negativos da extração de pacas grávidas poderiam incluir o zoneamento de áreas de caça ou o incentivo aos caçadores em abater preferencialmente machos. Nossos resultados indicam que estratégias para a extração sustentável da paca e outras espécies cinegéticas amazônicas devem considerar a interação entre a reprodução e a caça pela população local, a fim de melhorar as ações de conservação e manejo no bioma.

Key words: conception dates, forest phenology, game species, hunter participation, management, pregnancy rates, rainfall patterns, reproduction, Rodentia, wildlife

In high latitudes, where climatic variability between seasons is greatest, most species produce a large number of offspring in a short period of time, most of which do not survive (Bronson 1985). By contrast, in more stable environments with less seasonal variation, such as tropical forest regions, species generally produce a constant, low number of offspring over the year (McNaughton 1975). However, in the Amazon basin, the extreme variation in river levels, caused by seasonal meltwater in the Andes or rainfall, affects food availability (particularly tree fruits) to such an extent that frugivorous mammals may exhibit a greater than expected reproductive seasonality for this environment (Dubost et al. 2005). Furthermore, seasonal patterns in water levels also determine patterns of hunting and fishing by humans (Endo et al. 2016).

Animal populations are regulated by factors that impact mortality and recruitment (Caughley 1977). Understanding the population dynamics of exploited species is essential to determine sustainable harvest rates for wildlife populations. Harvesting individuals can have direct effects on the growth rate of a population by increasing mortality rates. There is increasing evidence that harvesting can also have indirect effects on population growth. For instance, harvest can disrupt the sex and age structure of a population, which can in turn affect fecundity rates (Milner et al. 2007; Bunnefeld et al. 2009). Furthermore, sex-skewed harvesting can have potentially deleterious effects on long-term fecundity (defined as the number of young born) and lead to population collapse, as shown for ungulates (Ginsberg and Milner-Gulland 1994; Freeman et al. 2014). In addition, overhunting of females in seasonally breeding animals, during periods when more females are pregnant, may negatively influence the population dynamics of the species.

In this paper, we evaluate how hunting may affect the population dynamics of the lowland paca (*Cuniculus paca*). The paca is a large, frugivorous caviomorph rodent that occurs throughout the Neotropics, inhabiting primarily broadleaf forests from east-central Mexico to northern Argentina (Collet 1981; Pérez 1992; Aquino et al. 2009). Studies to date, in primary broadleaf forest, suggest that pacas occupy relatively small home ranges (Marcus 1984; Beck-King et al. 1999), and are patchily distributed in mosaic landscapes with scattered resources (Marcus 1984; Beck-King et al. 1999; Ulloa et al. 1999). Pacas feed mostly on fruits and seeds, and occasionally consume leaves and flowers (Beck-King et al. 1999; Dubost 2017).

Pacas are of conservation and management interest throughout their geographic range as a popular game species for people (e.g., Read et al. 2010; El Bizri et al. 2015, 2016; Gutiérrez-Granados 2015; Mayor et al. 2015), an important prey of large carnivores, and as seed dispersers (Dubost and Henry 2006; Aquino et al. 2009). However, there is concern that current levels of hunting may be unsustainable, as observed in several Amazonian sites (e.g., Zapata-Ríos et al. 2009; Valsecchi et al. 2014). Given the importance of the paca as a source of protein to human residents of tropical forests, identifying the factors that may affect paca numbers remains fundamental.

Here, in 2 sites in Amazonian Peru and Brazil, we first assess how environmental factors such as rainfall patterns affect fruit availability, and in turn show how this correlates with the reproductive seasonality of pacas. We then assess the impact of harvest rates during the different phases of the reproductive cycle of pacas using data gathered from a 15-year participatory hunting study for the 2 study sites.

MATERIALS AND METHODS

Study sites.—The Yavarí-Mirín River (YMR; 04°19′53″S, 71°57′33″W) is located in the western Peruvian Amazon, encompassing 107,000 ha of continuous upland forests containing a single indigenous community of 307 inhabitants (Fig. 1). The Amanã Sustainable Development Reserve (ASDR; 01°54′00″S, 64°22′00″W) is a 2,313,000-ha reserve of predominantly upland

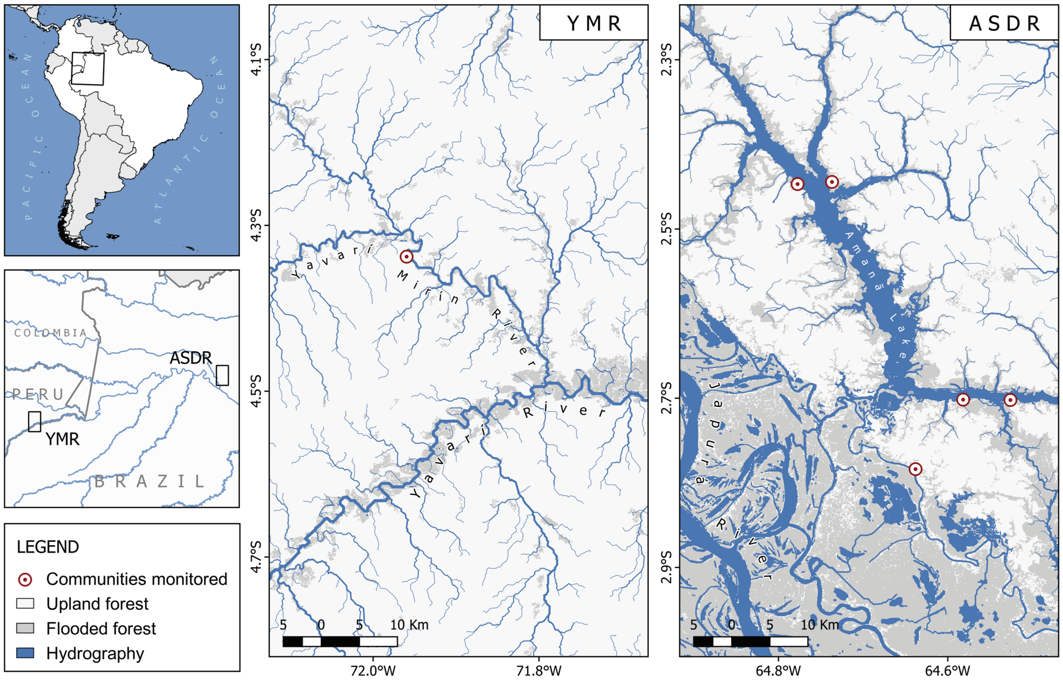


Fig. 1.—Location of the 2 study sites (YMR: Yavarí-Mirín River, ASDR: Amanã Sustainable Development Reserve) in Amazonia and the communities participating in the monitoring of hunting and collection of biological material on lowland pacas (*Cuniculus paca*).

forests in the central Brazilian Amazon, between the Negro and Japurá rivers. Approximately 4,000 riverine people inhabit 23 communities and some isolated settlements within this reserve (Fig. 1). In both study sites, local communities rely on agriculture for income and on hunting and fishing for subsistence. River water levels at both sites change seasonally, varying up to 12 m between the dry and flood peaks (Ramalho et al. 2009). Climate in both study sites is typically equatorial with annual temperatures ranging between 22°C and 36°C, relative humidity of 80%, and an annual rainfall of 1,500–3,000 mm.

Water level and rainfall.—For the YMR, we calculated monthly average river water level (as meters above sea level—m a.s.l.) and rainfall (in mm) on the Yavarí River, from data provided by a Brazilian National Water Agency hydrological station, ca. 50 km from the study site (HidroWeb, Estirão do Repouso station, rainfall: 1962–1999, water level: 1980–2017, http://www.snirh.gov.br/hidroweb/). In the ASDR, we used data on average rainfall (mm) for the Tefé municipality, ca. 90 km from the study area, from information also provided by the Brazilian National Water Agency (HidroWeb, Tefé station, 2005–2017, http://www.snirh.gov.br/hidroweb/). We used data on river water levels from the Mamirauá Sustainable Development Institute for the Amanã Lake station inside the ASDR (1990–2018, https://mamiraua.org.br/pt-br/pesquisa-e-monitoramento/monitoramento/fluviometrico/).

Ripe fruit availability.—We determined annual changes in ripe fruit availability, the main item in the diets of pacas (Dubost et al. 2005), by monitoring tree fruit abundance in 3 transects between March 2004 and February 2005. Two transects, started at random points, were in upland forests in the YMR, and a third transect was located in *aguajal*, upland swamp forest dominated by palms. Two transects were 5 m wide and one in the upland forest was 20 m wide (Pitman et al. 2003). We tagged and identified every tree of a diameter at breast height (DBH) > 10 cm, as well as every vine or liana of DBH > 7 cm (Ayres 1986). We marked plants until the rate of discovery of new species plateaued (Sutherland 2000), which determined the length and area of each transect. Starting mid-month, we observed the canopy of each tagged tree or vine once per month with binoculars and a small telescope, recording the presence or absence of ripe fruits in each sampled individual plant. Because fruits of the moriche palm (*Mauritia flexuosa*) constitute an important part of the diet of pacas (Mendieta-Aguilar et al. 2015), we also obtained more detailed fruiting data from the 38 individuals found within the transects and analyzed it independently.

Paca reproduction and hunting.—We trained local hunters in the YMR community and in 5 ASDR communities to remove all abdominal and pelvic organs from harvested specimens and to store these materials in buffered 4% formaldehyde solution (Mayor et al. 2017). From 2000 to 2015, local hunters collected and voluntarily donated genitalia from 300 female pacas (212 in the YMR and 88 in the ASDR), each labeled with the hunting date. Since hunters do not consume these organs, we avoided encouraging additional mortality to supply our study. In parallel, between 2000 and 2015 in the YMR, and between 2002 and 2015 in the ASDR, hunters recorded all harvested pacas, including sex and hunting date. In each monitored community in YMR and ASDR, local hunters were provided with datasheets in which they voluntarily recorded information on their daily hunting events. To ensure data were accurately collected, we conducted regular workshops and meetings (at least once per year) with all data providers and members of the participating communities. In this study, we only used the data for harvested females.

Data analysis.—We removed the conceptuses from all pregnant females. Using a metal caliper (maximum 300 mm) and a tape measure (1.0 mm accuracy), we measured the crown-rump length and longitudinal length of each embryo or fetus, from rostral edge of nose to distal portion of the tail. Conception dates were determined by backdating the date of collection of each embryo or fetus from their estimated age, using the age formula for paca fetuses in El Bizri et al. (2017). Predicted parturition dates were estimated by summing a standard gestation length of 149 days (Guimarães et al. 2008) to the derived conception dates. We then calculated the monthly number and percentage of conceptions and parturitions during the study period. Hunting data on females collected by local people were also used to calculate the monthly percentage of female pacas harvested in each site within each monitored year (hereafter known as hunting rates). Additionally, we estimated the pregnancy period (from conception to parturition dates) for each paca, and summed the cumulative number of pregnant pacas per month to obtain a monthly percentage of pregnant females among all collected samples in a year (hereafter known as pregnancy rate). We also estimated the monthly percentage of weaned offspring by summing a standard lactation length of 21 days to the parturition dates, which correspond to the period after which the offspring, although still suckling, starts eating solid food (Collett 1981). In addition, we calculated the average longitudinal length of the embryos or fetuses in each locality.

We applied generalized additive models for location, scale, and shape (GAMLSS—Stasinopoulos and Rigby 2007) to assess the relationship between climate, fruiting, paca reproductive events, and hunting. By using GAMLSS, it is possible to test across a wide set of distribution families, ensuring the best fit to the data is selected. Analyses were conducted in 3 sets using a theoretical framework of likely direct relationships between the variables. In set (1), we evaluated the relationship between monthly rainfall (predictor variable) and monthly fruiting percentage in the 3 YMR environments. In set (2), we evaluated the relationship between monthly fruiting percentage in the 3 environments (predictor variables) and paca reproductive events (percentage of conceptions, parturitions, and weaning, and pregnancy rates) for the YMR; in this second set, we also tested rainfall as a predictor variable for conceptions in both areas (YMR and ASDR), since this factor has been reported as a possible cue for conceptions in several mammal species. In set (3), we evaluated the relationship between river water level and paca reproductive events (predictor variables) with hunting rates. For the latter, we calculated the monthly percentage of harvested females in each year in both areas and related these values with the monthly average water level and percentage reproductive events, which were considered constants among months, independently of the year.

We tested all combinations of predictor variables in each set in linear or nonlinear forms using different distribution families. Final models were selected based on ΔAIC values, i.e., the difference between the value of Akaike's information criterion (AIC) for the model being evaluated and the model with the lowest AIC value (Burnham and Anderson 2004); ΔAIC values smaller than 2 indicated models with good support. Among these models, we chose the simplest one as final, i.e., the model with fewest degrees of freedom and with fewest predictor variables in the model. We used R 3.3.3 software (R Core Team 2017) for all statistical analyses. GAMLSS were run using the *gamlss* R-package. Values are expressed as the mean ± standard deviation ($\bar{X} \pm SD$).

Compliance.—All research followed guidelines of the American Society of Mammalogists for the ethical use of wild animals in research (Sikes et al. 2016) and was conducted in compliance with the research protocol approved by the Research Ethics Committee for Experimentation in Wildlife at the Dirección General de Flora y Fauna Silvestre from Peru (License 0229-2011-DGFFS-DGEFFS), by the Instituto Chico Mendes for Biodiversity Conservation from Brazil (License SISBIO No. 29092-1), and by the Committee on Ethics in Research with Animals of the Federal Rural University of the Amazon (UFRA CEUA protocol 007/2016).

Results

Ripe fruit availability.—We sampled 589 trees and vines in 8,970 m^2 of upland forests, and 386 trees and vines in 5,150 m^2 of swamp forests. Fruiting patterns in the YMR varied according to habitat type. In upland forests, fruiting trees were present throughout the year, with peaks in March (6.62% plants fruiting) and December (4.68% plants fruiting; Fig. 2). In swamp forests, fruiting peaked between February and May (6.12 ± 0.83% plants fruiting), with no trees fruiting in September and October. *Mauritia flexuosa* showed marked fruiting during the low rainfall period (May–August), with the highest number of fruiting trees recorded in June (34.21%); no fruits were observed during the remaining months of the year (Fig. 2). Upland forest fruiting was positively correlated with rainfall (Fig. 3; Table 1), but there was no correlation between rainfall and *M. flexuosa* or swamp forest fruiting (Table 1).

Paca reproductive seasonality.—There were 157 (52.3%) pregnant pacas among all sampled females, 100 (47.2%) in the YMR and 57 (64.8%) in ASDR (Fig. 4). Average fetal length was 11.30 ± 10.58 cm in the YMR and 17.43 ± 9.74 cm in the ASDR, with a significant difference between sites ($t_{155} = 3.59$, $P < 0.01$). Paca reproductive events occurred during different periods of the year in the 2 study sites. In YMR, conceptions occurred mainly between October and January (50.0%), while parturitions primarily took place between March and June (49.0%). In ASDR, most conceptions occurred between March and June (45.6%), while most parturitions happened between August and November (42.1%; Fig. 5). Nevertheless, conceptions and parturitions occurred throughout the year in both sites. There was a positive relationship between conceptions and rainfall in both study sites (Figs. 6A and 6B), but there was a negative relationship between conceptions and fruiting in upland forests in the YMR (Fig. 6C; Table 1). Pregnancy rates were positively associated with fruiting in upland forest (Fig. 6D), while the higher weaning rates were

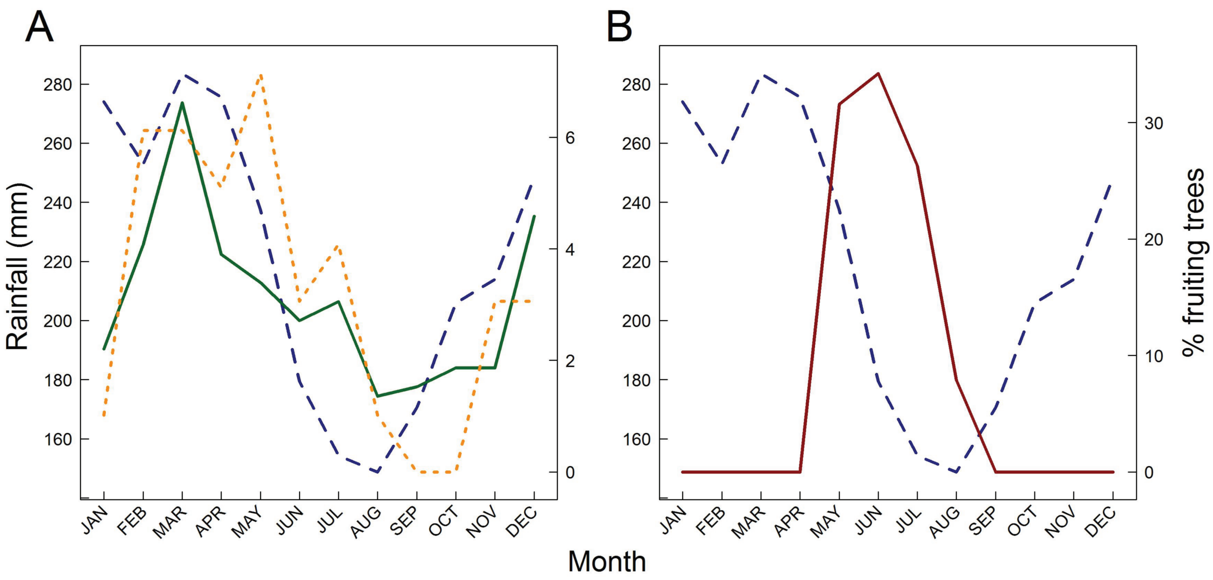


Fig. 2.—Trends in (A) rainfall (dashed line) and percentage of trees bearing fruits in upland forests (solid line) and swamp forest (dotted line); and (B) rainfall (dashed line) and percentage of *Mauritia flexuosa* trees bearing fruits (solid line) along the year in the Yavarí-Mirín River, western Amazonia.

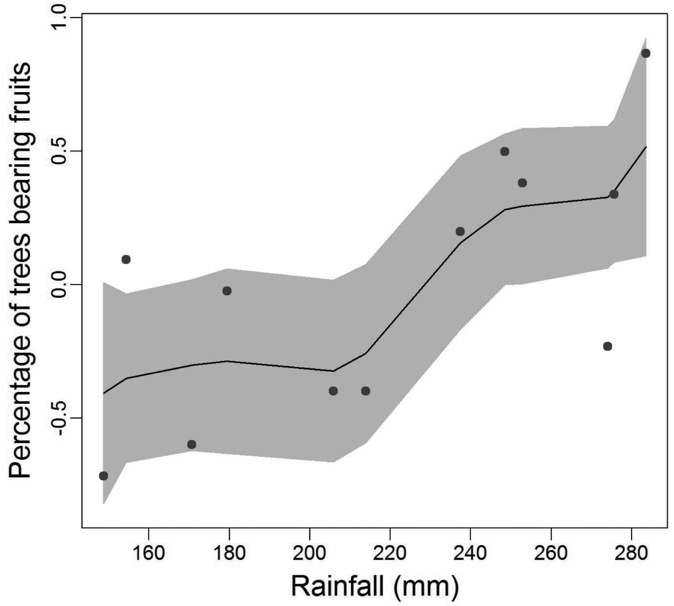


Fig. 3.—Relationship between rainfall (mm) and percentage of trees bearing fruits in upland forests in the Yavarí-Mirín River, western Amazonia. The gray area represents 95% *CI*s. The response variable is plotted on the y-axis in a scale of variation around the mean (μ = 0) calculated from the original data used to build the model.

related to higher fruiting periods in swamp forest (Fig. 6E) and of *M. flexuosa* (Fig. 6F; Table 1). On the other hand, there was no relationship between parturition and fruiting in any environment (Table 1).

Hunting vulnerability of pregnant pacas.—A total of 803 harvested paca females were recorded in the communities, 288 in the YMR and 515 in the ASDR. Hunting rates varied between months, which were cyclical along the years (Figs. 7A and 7B) and showed a positive relationship with the river water level in both study sites (Figs. 7C and 7D; Table 1). A strong positive relationship between hunting rates and pregnancy rates was observed (Figs. 7E and 7F; Table 1). There were no relationships between conceptions, parturitions, and weaned offspring and hunting rates (Table 1).

DISCUSSION

Paca reproductive seasonality and fruit availability.—Although pregnant females were present year-round in our study sites, most pregnancies occurred during periods of greater fruit availability in upland forests, when rainfall was highest. The greater food supply during this period can sustain larger numbers of pregnant females. When most females are in their last third of gestation, a period of greatest absolute fetal growth and when pregnant individuals demand more energy, fruit availability is, in fact, at its peak. A similar pattern has been observed for the ring-tailed coati (*Nasua nasua*) where the gestation period, concentrated between November and March, coincided with greater fruit availability in upland and swamp forests in the YMR (Mayor et al. 2013a). However, mammals with less selective diets are aseasonal breeders, as in the case of the white-lipped peccary (*Tayassu pecari*), collared peccary (*Pecari tajacu*), and the red brocket deer (*Mazama americana*—Mayor et al. 2009, 2010, 2011), because these species consume green leaves, insects, and small vertebrates when fruit is less available (Dubost and Henry 2017). This pattern has also been confirmed by Dubost and Henry (2017) in French Guiana, who showed that mammals that consume more fruits were highly seasonal breeders.

Changing energy demands and seasonality in food supply.—There is evidence from Amazonia that a seasonal increase in rainfall triggers fruit maturation in several habitat types, including nonflooded forests (Haugaasen and Peres 2005). Since rainfall and river water levels vary in different regions of the

Table 1.—Details of the best-fit models using GAMLSS for each response variable, with the family of distribution, ΔAIC in relation to the null model (ΔAIC null), and generalized R^2. Nonlinear effects were fit using cubic spline (*cs*) functions provided by *gamlss* R-package. Families of distributions are represented by log-normal (LOGNO), normal (NO), zero-adjusted gamma (ZAGA), gamma (GA), Box–Cox t (BCTo), inverse Gaussian (IG), Gumbel (GU), inverse gamma (IGAMMA), and reverse Gumbel (RG). Generalized R^2 were calculated using the function Rsq of the *gamlss* package. Null models are indicated by 1. GAMLSS: generalized additive models for location, scale, and shape.

Best-fitted model[a]		Estimate	*P*-value	Family of distribution	ΔAIC null	Generalized R^2
Response variables	Predictor variables					
Yavarí-Mirín River						
Fruiting						
% Plants fruiting U.F.	*cs*(rainfall)	0.0068	0.011	LOGNO	5.45	62.0
% Plants fruiting S.F.	1			NO	0	
% Plants fruiting *M.f.*	1			ZAGA	0	
Paca reproductive events						
% Conceptions	Rainfall	0.0083	0.011	LOGNO	3.97	48.5
	% Plants fruiting U.F.	−0.2147	0.027			
% Parturitions	1			IG	0	
% Weaned offspring	% Plants fruiting S.F.	0.6945	0.009	GU	11.95	73.5
	% Plants fruiting *M.f.*	0.0972	0.041			
Pregnancy rate	*cs*(plants fruiting U.F.)	0.0734	0.007	IGAMMA	5.60	67.0
Paca hunting						
Hunting rates	Water level	0.0541	0.033	ZAGA	6.02	6.7
	Pregnancy rate	0.2239	0.003			
Amanã Reserve						
Paca reproductive events						
% Conceptions	*cs*(rainfall)	0.0333	0.001	RG	3.97	53.6
Paca hunting						
Hunting rates	Water level	0.1020	< 0.001	ZAGA	7.22	29.1
	Pregnancy rate	0.2223	< 0.001			

[a] Abbreviations for plants fruiting—U.F.: upland forest; S.F.: swamp forest; *M.f.*: *Mauritia flexuosa*.

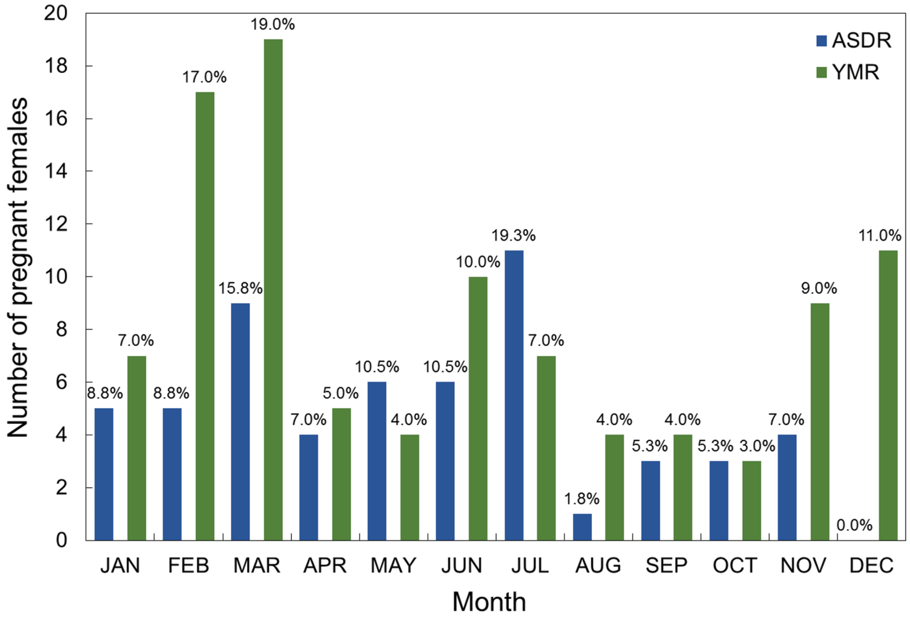


Fig. 4.—Number and percentage of lowland paca (*Cuniculus paca*) samples that included a uterus showing signs of pregnancy, collected in each month over the monitoring years in the Amanã Sustainable Development Reserve (ASDR) and Yavarí-Mirín River (YMR), Amazonia.

Amazon, reproductive events of the paca occur at different phases of the year in each of our studied sites, according to local variations in climate and fruit production. Paca reproduction is therefore plastic and opportunistically seasonal (Mayor et al. 2013b). Thus, for fruit-dependent species, rainfall, in contrast to photoperiod, may drive conceptions to take place some months prior to fruit ripening, and pregnancies and births will coincide with the period of higher fruit abundance. The observation made by Dubost and Henry (2006) that nonpregnant pacas consumed less seeds than pregnant animals also suggests that conceptions occur during periods of low food availability so that pregnancies mostly occur during periods of higher

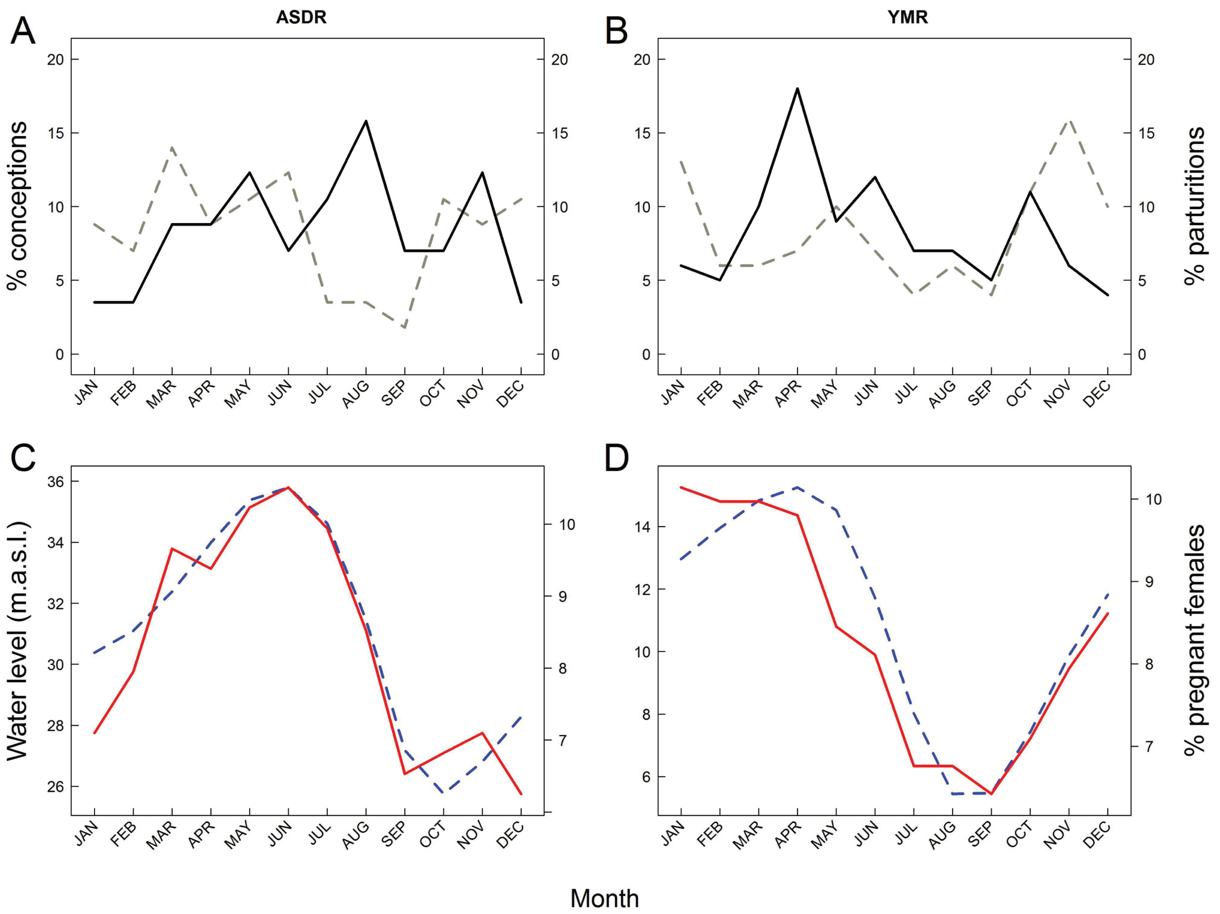


Fig. 5.—Trends in (A and B) the percentage of paca conceptions (dashed gray lines) and parturitions (solid black lines); and (C and D) average river water level (dashed lines) and percentage of pregnant female pacas (solid lines) along the year in the Amanã Sustainable Development Reserve (ASDR) and Yavarí-Mirín River (YMR), Amazonia.

fruit and seed availability. Our results also show that the greatest number of conceptions occurred when fruit availability in upland forests was low; pregnant pacas could take advantage of the subsequent periods of greater food supply. Similarly, in free-ranging, provisioned rhesus macaques (*Macaca mulatta*) on islands in Puerto Rico, more conceptions occurred during the spring rainfall period, just before the main tree-fruiting season (Rawlins and Kessler 1985).

In Amazonia, swamp forest species and *M. flexuosa* in particular (the most important source of food during the drought period) play a major role in sustaining lactating females and their young, which start weaning during the low-water period. Since during lactation females consume up to 5 times more food than before pregnancy (Randolph et al. 1977), the availability of ripe fruits during this period is of extreme importance. For several species of flying foxes (*Pteropus* spp.), O'Brien (1993) showed that lactation and offspring weaning occur during periods when fruit supply is at its peak. In addition, Lee et al. (2017) showed that giraffe (*Giraffa camelopardalis*) calves born during the dry season in Tanzania had a higher survival probability due to the greater energy reserves accumulated by mothers during the rainy season as well as the higher protein concentration of available browse during the late dry-season rains.

Hunting and reproduction in quarry species.—Different prey can cope with human harvest according to their population dynamics and biological capacity (Cardillo et al. 2005), but their patterns of reproduction reflect their response to environmental and human disturbance. Predator–prey systems often co-evolve slowly through generations by the action of natural selection, with the appearance of phenotypical and behavioral traits in prey species that avoid their extinction (Kooijman and Lika 2014). However, the current reproductive strategies in wild species are not adapted to the typically more intensive levels of human predation, especially when hunting is directly impacting pregnant females and affecting the species' recruitment potential.

Water levels and hunting rates were shown to have a similar cyclical pattern over the period of 15 years for which data were available. Other studies in the Amazon basin have also demonstrated that hunters maximize their captures by taking into account seasonal water level changes (Kvist et al. 2001; Endo et al. 2016). This temporal convergence between heavier hunting and pregnancies in pacas is thus likely to adversely impact the species' population dynamics. A probable indication that hunting of pregnant paca females during high-water periods may affect populations of the species is available for the ASDR, where Valsecchi et al. (2014) demonstrated that paca hunting

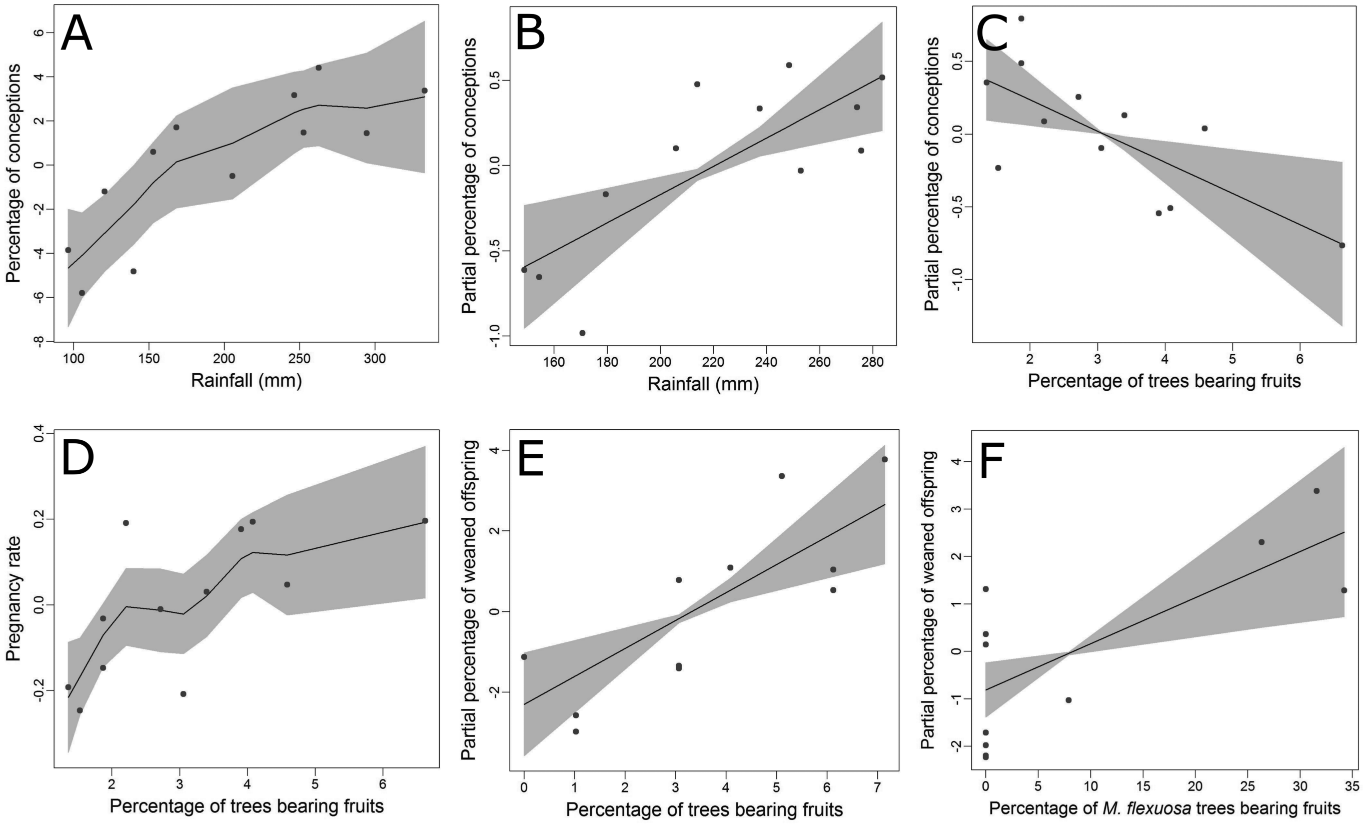


Fig. 6.—Relationship between (A) rainfall and the percentage of paca conceptions in the Amanã Sustainable Development Reserve, central Amazonia; (B) rainfall and percentage of paca conceptions in the Yavarí-Mirín River, western Amazonia; (C) percentage of trees bearing fruits in upland forest and percentage of paca conceptions in the Yavarí-Mirín River, western Amazonia; (D) percentage of trees bearing fruits in upland forest and pregnancy rate in the Yavarí-Mirín River, western Amazonia; (E) percentage of trees bearing fruits in swamp forest and percentage of weaned offspring, and (F) percentage of *Mauritia flexuosa* trees bearing fruits and percentage of weaned offspring in the Yavarí-Mirín River, western Amazonia. The gray area represents 95% *CI*s. Response variables are plotted on the y-axis in a scale of variation around the mean (μ = 0) calculated from the original data for models with a single predictor variable, and from partial residuals for models including more than 1 predictor variable.

is unsustainable and the species' abundance at this site significantly dropped over an 8-year period.

Management implications.—Pacas provide the largest proportion of wild meat consumed by local populations and even urban dwellers in the Amazon (Bodmer and Lozano 2001; Suárez et al. 2009; van Vliet et al. 2015). However, the species has a relatively low reproductive output, in which females only produce 1 young per pregnancy (Mayor et al. 2013b, 2017; El Bizri et al. 2017). The results presented here highlight the necessity for developing sustainable harvest strategies that are compatible with the target species' life history and their reproductive patterns. These strategies could include focusing hunting efforts on males or reducing hunting during the pregnancy season. However, avoiding hunting pacas during high water levels may not be possible for hunters. During the flooded period, fishing becomes difficult and hunting becomes the main source of meat supply during this period (Valsecchi et al. 2014; Endo et al. 2016), thus making it unlikely for a shift away from hunting pacas during the wet season. On the other hand, since male pacas can fertilize several females, hunting males exclusively during the high-water period, when pregnant females are more common, is feasible since rural Amazonian hunters pursue pacas by "spotlighting" (Valsecchi et al. 2014), thus permitting the identification of the sex of the animal and even the pregnancy stage of females (H. R. El Bizri, pers. obs.).

Another strategy to improve the state of hunted paca populations is to encourage the use of rotating hunting areas over the years or to protect areas during the hunting season that could act as refugia for females. This strategy would create a source–sink system where protected grounds would function as sources of individuals to repopulate areas depleted by hunting. This strategy has already been advocated as efficient to conserve species such as the culpeo fox (*Pseudalopex culpaeus*) in the Argentine Patagonia (Novaro et al. 2005) as well as ungulates in the Neotropics (Novaro et al. 2001; Naranjo and Bodmer 2007). A similar approach was effectively applied to recover giant Arapaima (*Arapaima gigas*) populations by encouraging community-based source–sink schemes; this system is now successfully applied throughout the Amazon (Campos-Silva et al. 2017). Here, we argue that source–sink systems could be equally applied for pacas. However, as all systems, these also need to be continuously monitored and adapted especially because the demand for paca meat is likely to increase in line with human population growth. Thus,

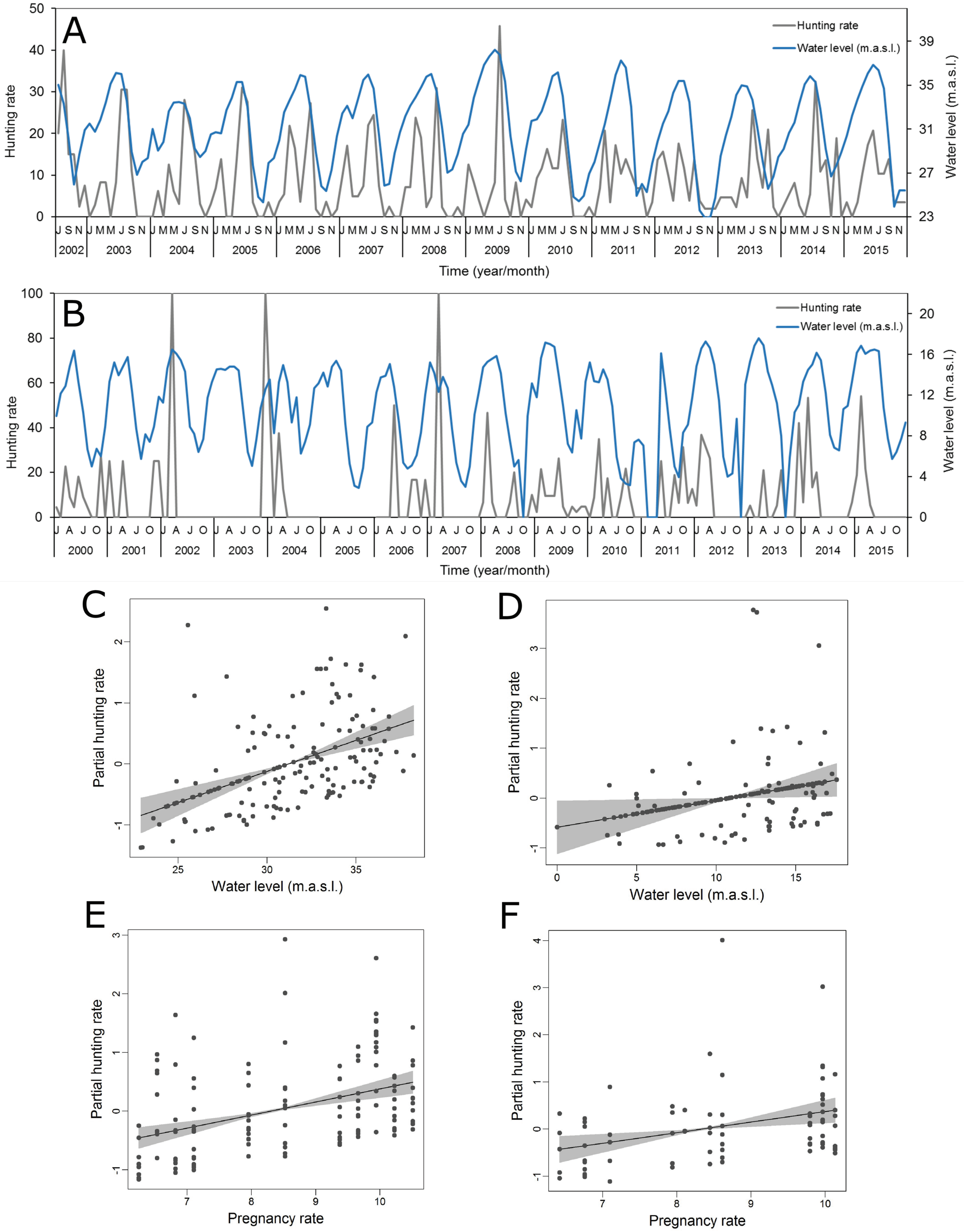


Fig. 7.—Temporal trends of the river water level and hunting rates (monthly percentage of harvested females within each year) in the (A) Amanã Sustainable Development Reserve and (B) Yavarí-Mirín River, in Amazonia. Relationship between river water level and hunting rates in the (C) Amanã Sustainable Development Reserve and (D) Yavarí-Mirín River, in Amazonia. Relationship between pregnancy rate and hunting rates in the (E) Amanã Sustainable Development Reserve and (F) Yavarí-Mirín River, in Amazonia. The gray area represents 95% *CI*s. Response variables are plotted on the y-axis in a scale of variation around the mean (μ = 0) calculated from partial residuals of the models.

additional measures such as setting quotas of the paca population that can be harvested per family, hunter, or community may be needed. Finally, since palm species are essential for pacas, and probably other Amazonian species, to achieve their highest reproductive potential, actions focused on conservation of swamp forest palm species, which are largely exploited by humans (Peters et al. 1989; Rull and Montoya 2014), are also critical.

Due to the fact that most hunting in Amazonia is determined by the annual variation in river water level, we argue that the impact we have observed in pacas could be mirrored in other species, and hence might affect the sustainability of wild meat, so vital for numerous inhabitants. Accordingly, strategies that ensure the sustainability of hunted Amazonian species must be based on reproductive information to minimize the impact on their populations when they are most vulnerable.

Acknowledgments

We sincerely thank the people from the Yavarí-Mirín River and the Amanã Sustainable Development Reserve, without whom this work would not be possible. We also thank J. R. Gonçalves for making the map, and T. Q. Morcatty for aid in the statistical analysis. This work was supported by the Gordon and Betty Moore Foundation, the National Council for Scientific and Technological Development (CNPq) (grant numbers 300005/2013-0; 452908/2016-7; 201475/2017-0), the IVITA (Instituto Veterinario de Investigaciones de Tropico y de Altura), the Museo de la Universidad Nacional de la Amazonía Peruana, the Earthwatch Institute, and the Fundacion Autonoma Solidaria.

Literature Cited

Aquino, R., D. Gil, and E. Pezo. 2009. Aspectos ecológicos y sostenibilidad de la caza del majás (*Cuniculus paca*) en la cuenca del río Itaya, Amazonía peruana. Revista Peruana de Biología 16:67–72.

Ayres, J. M. 1986. The white Uakaris and the Amazonian flooded forests. Ph.D. dissertation, University of Cambridge, Cambridge, United Kingdom.

Beck-King, H., O. Helversen, and R. Beck-King. 1999. Home range, population density, and food resources of *Agouti paca* (Rodentia: Agoutidae) in Costa Rica: a study using alternative methods. Biotropica 31:675–685.

Bodmer, R. E., and E. P. Lozano. 2001. Rural development and sustainable wildlife use in Peru. Conservation Biology 15:1163–1170.

Bronson, F. H. 1985. Mammalian reproduction: an ecological perspective. Biology of Reproduction 32:1–26.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociological Methods & Research 33:261–304.

Bunnefeld, N., D. Baines, D. Newborn, and E. J. Milner-Gulland. 2009. Factors affecting unintentional harvesting selectivity in a monomorphic species. Journal of Animal Ecology 78:485–492.

Campos-Silva, J. V., C. A. Peres, A. P. Antunes, J. Valsecchi, and J. Pezzuti. 2017. Community-based population recovery of overexploited Amazonian wildlife. Perspectives in Ecology and Conservation 15:266–270.

Cardillo, M., et al. 2005. Multiple causes of high extinction risk in large mammal species. Science 309:1239–1241.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley & Sons, London, United Kingdom.

Collet, S. F. 1981. Population characteristics of *Agouti paca* (Rodentia) in Colombia. Michigan State University, East Lansing, USA.

Dubost, G., and O. Henry. 2006. Comparison of diets of the acouchy, agouti and paca, the three largest terrestrial rodents of French Guianan forests. Journal of Tropical Ecology 22:641–651.

Dubost, G., and O. Henry. 2017. Seasonal reproduction in Neotropical rainforest mammals. Zoological Studies 56:2.

Dubost, G., O. Henry, and P. Comizzoli. 2005. Seasonality of reproduction in the three largest terrestrial rodents of French Guiana forest. Mammalian Biology 70:93–109.

El Bizri, H. R., F. O. B. Monteiro, R. S. de Andrade, R. S. Valsecchi, D. A. A. Guimarães, and P. Mayor. 2017. Embryonic and fetal morphology in the lowland paca (*Cuniculus paca*): a precocial hystricomorph rodent. Theriogenology 104:7–17.

El Bizri, H., T. Morcatty, J. Lima, and J. Valsecchi. 2015. The thrill of the chase: uncovering illegal sport hunting in Brazil through YouTube™ posts. Ecology and Society 20:30.

El Bizri, H. R., L. W. da Silva Araújo, W. da Silva Araújo, L. Maranhão, and J. Valsecchi. 2016. Turning the game around for conservation: using traditional hunting knowledge to improve the capture efficiency of Amazon lowland pacas. Wildlife Biology 22:1–6.

Endo, W., C. A. Peres, and T. Haugaasen. 2016. Flood pulse dynamics affects exploitation of both aquatic and terrestrial prey by Amazonian floodplain settlements. Biological Conservation 201:129–136.

Freeman, E. D., R. T. Larsen, M. E. Peterson, C. R. Anderson, Jr., K. R. Hersey, and B. R. McMillan. 2014. Effects of male-biased harvest on mule deer: implications for rates of pregnancy, synchrony, and timing of parturition. Wildlife Society Bulletin 38:806–811.

Ginsberg, J. R., and E. J. Milner-Gulland. 1994. Sex-biased harvesting and population dynamics in ungulates: implications for conservation and sustainable use. Conservation Biology 8:157–166.

Guimarães, D. A. A., L. V. Bastos, A. C. S. Ferreira, R. S. Luz-Ramos, O. M. Ohashi, and H. L. Ribeiro. 2008. Características reprodutivas da paca fêmea (*Agouti paca*) criada em cativeiro. Acta Amazonica 38:531–538.

Gutiérrez-Granados, G. 2015. Assessment on the size-bias in hunting preferences for bush meat consumption in a Mexican tropical rainforest. Global Journal of Advanced Biological Sciences. 1:50–54.

Haugaasen, T., and C. A. Peres. 2005. Primate assemblage structure in Amazonian flooded and unflooded forests. American Journal of Primatology 67:243–258.

Kooijman, S. A., and K. Lika. 2014. Resource allocation to reproduction in animals. Biological Reviews 89:849–859.

Kvist, L. P., S. Gram, and I. Ore. 2001. Socio-economy of flood plain households in the Peruvian Amazon. Forest Ecology and Management 150:175–186.

Lee, D. E., M. L. Bond, and D. T. Bolger. 2017. Season of birth affects juvenile survival of giraffe. Population Ecology 59:45–54.

Marcus, M. J. 1984. Behavioral ecology of paca (*Agouti paca*) on Barro Colorado Island, Panama. Doctoral Dissertation, University of Maine, Orono, USA.

Mayor, P. G., R. E. Bodmer, and M. L. Bejar. 2010. Reproductive performance of the wild collared peccary (*Tayassu tajacu*) female in the Peruvian Amazon. Euopean Journal of Wildlife Research 56:681–684.

Mayor, P., R. E. Bodmer, and M. Lopez-Bejar. 2009. Reproductive performance of the wild white-lipped peccary (*Tayassu pecari*) female in the Peruvian Amazon. European Journal of Wildlife Research 55:631–634.

Mayor, P., R. E. Bodmer, M. Lopez-Bejar, and C. López-Plana. 2011. Reproductive biology of the wild red brocket deer (*Mazama* *americana*) female in the Peruvian Amazon. Animal Reproduction Science 128:123–128.

Mayor, P., H. El Bizri, R. E. Bodmer, and M. Bowler. 2017. Assessment of mammal reproduction for hunting sustainability through community-based sampling of species in the wild. Conservation Biology 31:912–923.

Mayor, P., D. A. Guimarães, and C. López. 2013b. Functional morphology of the genital organs in the wild paca (*Cuniculus paca*) female. Animal Reproduction Science 140:206–215.

Mayor, P., D. Montes, and C. López-Plana. 2013a. Functional morphology of the female genital organs in the wild ring-tailed coati (*Nasua nasua*) in the northeastern Peruvian Amazon. Canadian Journal of Zoology 91:496–504.

Mayor, P., P. Pérez-Peña, M. Bowler, P. Puertas, M. Kirkland, and R. Bodmer. 2015. Effects of selective logging on large mammal populations in a remote indigenous territory in the northern Peruvian Amazon. Ecology and Society 20:36.

McNaughton, S. 1975. r-and K-selection in Typha. The American Naturalist 109:251–261.

Mendieta-Aguilar, G., L. F. Pacheco, and A. I. Roldán. 2015. Dispersión de semillas de *Mauritia flexuosa* (Arecaceae) por frugívoros terrestres en Laguna Azul, Beni, Bolivia. Acta Amazonica 45:45–56.

Milner, J. M., E. B. Nilsen, and H. P. Andreassen. 2007. Demographic side effects of selective hunting in ungulates and carnivores: review. Conservation Biology 21:36–47.

Naranjo, E. J., and R. E. Bodmer. 2007. Source–sink systems and conservation of hunted ungulates in the Lacandon Forest, Mexico. Biological Conservation 138:412–420.

Novaro, A. J., M. C. Funes, and R. S. Walker. 2005. An empirical test of source–sink dynamics induced by hunting. Journal of Applied Ecology 42:910–920.

Novaro, A. J., K. H. Redford, and R. E. Bodmer. 2001. Effect of hunting in source-sink systems in the Neotropics. Conservation Biology 14:713–721.

O'Brien, G. M. 1993. Seasonal reproduction in flying foxes, reviewed in the context of other tropical mammals. Reproduction, Fertility and Development 5:499–521.

Pérez, E. M. 1992. *Agouti paca*. Mammalian Species 404:1–7.

Peters, C. M., M. J. Balick, F. Kahn, and A. B. Anderson. 1989. Oligarchic forests of economic plants in Amazonia: utilization and conservation of an important tropical resource. Conservation Biology 3:341–349.

Pitman, N., C. Vriesendorp, and D. Moskovits. 2003. Peru: Yavari. Rapid biological inventories report 11. The Field Museum, Chicago, Illinois.

Ramalho, E. E., J. Macedo, T. M. Vieira, J. Valsecchi, M. Marmontel, and H. L. Queiroz. 2009. Ciclo hidrológico nos ambientes de várzea da Reserva de Desenvolvimento Sustentável Mamirauá – médio rio Solimões, período de 1990 a 2008. UAKARI 5:61–87.

Randolph, P. A., J. C. Randolph, K. Mattingly, and M. M. Foster. 1977. Energy costs of reproduction in the cotton rat *Sigmodon hispidus*. Ecology 58:31–45.

Rawlins, R. G., and M. J. Kessler. 1985. Climate and seasonal reproduction in the Cayo Santiago macaques. American Journal of Primatology 9:87–99.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Read, J., et al. 2010. Space, place, and hunting patterns among indigenous peoples of the Guyanese Rupununi region. Journal of Latin American Geography 9:213–243.

Rull, V., and E. Montoya. 2014. *Mauritia flexuosa* palm swamp communities: natural or human-made? A palynological study of the Gran Sabana region (northern South America) within a Neotropical context. Quaternary Science Reviews 99:17–33.

Sikes, R. S., and The Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

Stasinopoulos, D. M., and R. A. Rigby. 2007. Generalized additive models for location, scale and 491 shape (GAMLSS) in R. Journal of Statistical Software 23:1–46.

Suárez, E., et al. 2009. Oil industry, wild meat trade and roads: indirect effects of oil extraction activities in a protected area in northeastern Ecuador. Animal Conservation 12:364–373.

Sutherland, W. J. 2000. The conservation handbook: techniques in research, management and policy. Blackwell Science, Oxford, United Kingdom.

Ulloa L., D. Rodriguez, and P. Sanchez. 1999. Movimientos y uso del tiempo y el espacio por una guartinaja (*Agouti paca*) en la Sierra Nevada De Santa Marta, Colombia. Revista de Academia Colombiana de Ciencias. 23:687–694.

Valsecchi, J., H. R. El Bizri, and J. E. C. Figueira. 2014. Subsistence hunting of *Cuniculus paca* in the middle of the Solimões River, Amazonas, Brazil. Brazilian Journal of Biology 74:560–568.

van Vliet, N., et al. 2015. From fish and bushmeat to chicken nuggets: the nutrition transition in a continuum from rural to urban settings in the Tri frontier Amazon region. Ethnobiology and Conservation 4:1–12.

Zapata-Ríos, G., C. Urgilés, and E. Suárez. 2009. Mammal hunting by the Shuar of the Ecuadorian Amazon: is it sustainable? Oryx 43:375–385.

Submitted 21 April 2018. Accepted 13 August 2018.

Associate Editor was Harald Beck.

Animal Reproduction Science 205 (2019) 105–114

Contents lists available at ScienceDirect

Animal Reproduction Science

journal homepage: www.elsevier.com/locate/anireprosci

Age at sexual maturity, first parturition and reproductive senescence in wild lowland pacas (*Cuniculus paca*): Implications for harvest sustainability

Hani Rocha El Bizri[a,b,c,d,*], John E. Fa[a,e], João Valsecchi[b,c,d], Richard Bodmer[c,f], Pedro Mayor[c,f,g]

[a] *School of Science and the Environment, Manchester Metropolitan University, Oxford Road, M15 6BH, Manchester, United Kingdom*
[b] *Instituto de Desenvolvimento Sustentável Mamirauá (IDSM), Tefé, AM, Brazil*
[c] *ComFauna, Comunidad de Manejo de Fauna Silvestre en la Amazonía y en Latinoamérica, 332 Malecon Tarapaca, Iquitos, Peru*
[d] *RedeFauna, Rede de Pesquisa em Diversidade, Conservação e Uso da Fauna da Amazônia, Brazil*
[e] *Center for International Forestry Research (CIFOR), Jalan Cifor Rawajaha, Situ Gede, Bogor Barat, Kota, Bogor, Jawa Barat, 16115, Indonesia*
[f] *FUNDAMAZONIA, Iquitos, Loreto, Peru*
[g] *Universitat Autònoma de Barcelona (UAB), Department of Animal Health and Anatomy, Faculty of Veterinary, Bellaterra, Barcelona, Spain*

ARTICLE INFO

Keywords:
Reproduction
Rodentia
Hunting
Community-based collection
Amazon

ABSTRACT

Generation length (GL) of a mammal, calculated through the age at sexual maturity, first reproduction and reproductive senescence can be used to assess the capacity of a population of a species to withstand differing amounts of hunting pressure by humans without depletion of animal numbers. Due to the lack of reproductive data for wild mammals, the GL is often difficult to determine for most species. In the present study, the GL parameters were assessed for the wild lowland paca (*Cuniculus paca*) from a sample of 119 female genitalia obtained during a 15-year hunter participatory program in the Amazon. The probability of female pacas being sexually active, with observable ovarian functionality or pregnancy, increased as both body and genitalia masses increased. The average body mass at puberty was 5.46 kg. Puberty was estimated to occur at 4 months of age, from which there was estimation when age at first parturition would occur 9 months after birth. Additionally, there was no indication that there was a decrease in parturition rate at more advanced ages. The estimated age of first reproduction for pacas was much less than previous estimates, most from assessments of captive animals. In addition, because there was no evidence of reproductive senescence, it is suggested that the average age of mature hunted pacas should be used to determine optimal harvesting rates of pacas by humans. The present study highlights the importance of in situ studies on reproduction of animals in their natural habitat because these will yield more accurate reproductive variable estimates than those obtained from captive animals. It is suggested that similar methods be used to accurately assess reproductive parameters of other tropical species that are hunted by humans.

---

* Corresponding author at: School of Science and the Environment, Manchester Metropolitan University, Oxford Road, M15 6BH, Manchester, United Kingdom.

E-mail address: hanibiz@gmail.com (H.R. El Bizri).

https://doi.org/10.1016/j.anireprosci.2019.04.009
Received 29 November 2018; Received in revised form 12 April 2019; Accepted 22 April 2019

1. Introduction

Generation length (GL) for mammals has been defined as the “average age of parents of the current cohort” (IUCN, 2001; 2012a), and the “age at which half of total reproductive output is achieved by an individual” (IUCN, 2004); the latter calculated as the average age at which reproduction occurs first and last in an animal’s life. The GL has been used as a reference time-frame in a multitude of ecological analyses to assess a species extinction risk (Gaillard et al., 2005; Perry et al., 2005; Jiguet et al., 2007; Mace et al., 2008; IUCN, 2012b). An accurate estimation of the GL of any species is also important in determining its capacity to withstand additional death losses imposed by humans.

Although GL is often difficult to determine due to the paucity of detailed reproductive data from species in their natural habitat, overall patterns are based on published metrics as well as taxonomic and allometric species relationships (e.g., Di Marco et al., 2012; Pacifici et al., 2013). Long-lived species are usually characterized by having a large body size, relatively lower reproductive rates, slower sexual maturation, greater parental care and a long GL (Clutton-Brock, 1988; de Andrade et al., 2018). Long-lived species are especially vulnerable to hunting pressures; short-lived species of smaller body size, greater reproductive rates, earlier puberty and a shorter GL are generally more resilient to human hunting pressure (Peres, 2000; Jerozolimski and Peres, 2003; Smucny et al., 2004; Nasi et al., 2008; Ripple et al., 2016; 2017).

Reproductive variables, including the GL of game species, are important elements in most mathematical models used for assessing the capacity of a species’ population to withstand hunting by humans at a sustainable level over time (Weinbaum et al., 2013). For example, the intrinsic rate of population increase of a species, *Rmax*, is calculated based on the annual birth rate of female offspring, age at first parturition, and age at last parturition during its lifetime (Cole, 1954), and is useful in predicting how a target species may respond to various harvesting levels (Greene et al., 1998). Gathering empirical data on the reproductive variables of hunted wild species is laborious. This has meant that $R_{\max}$ calculations for most game mammals are based on measures derived from captive animals (Robinson and Redford, 1986).

While data from captive animals are important and can be useful, reproductive variables may differ from populations in their natural habitat due to differences in stress levels, lack of natural predation and diseases, and the constancy of resources, mates and territories. Accordingly, if values for reproductive variables from captive animals are used in hunting assessments, they can under or overestimate the numbers of animals that can be sustainably harvested from populations (Milner-Gulland and Akçakaya, 2001). In a study of ten Amazonian mammals, wild populations of five species had birth rates that were less than those derived from captive animals (Mayor et al., 2017). Furthermore, values for reproductive variables currently used to calculate GL such as age at the time of an animal’s first and last parturition can differ from estimates for captive animals and, therefore, the data are not reliable for population sustainability assessments.

The lowland paca (*Cuniculus paca*) is a large-sized rodent, currently the most hunted Neotropical species (El Bizri et al., 2015, 2016). Paca reproduction has been extensively studied in captivity for about five decades (see Pérez and Hernández, 1979; Matamoros and Pashov, 1984; Smythe, 1991). The paca is a polyestrous species with spontaneous ovulation and an estrous cycle of 32.5 (± 3.69) days that breeds throughout the year in captivity (Guimarães et al., 2008). Additionally, the paca is a uniparous species with rare cases of twin gestations (Pérez and Hernández, 1979; Merrit, 1989; Oliveira et al., 2003, 2007). In the Amazon, the lowland paca in its natural habitat has 1.37–1.48 annual parturitions that are seasonally distributed depending on the amounts of fruitification and river water, with a long estimated farrowing interval of 247–266 days (Mayor et al., 2013; El Bizri et al., 2018).

In contrast to captive studies, little reproductive data are available for wild pacas. For example, the age at first parturition used for *Rmax* calculations, 365 days (Robinson and Redford, 1986; Collett, 1981) is known to vary between 225 and 703 days (Merrit, 1989; Smythe, 1991; Nogueira et al., 2006; Belaunde, 2008; Guimarães et al., 2008). Because most estimates were obtained from captive populations, this variation may be explained by using differing diagnostic methods and environmental conditions in studies that can affect the behaviour and physiology of the animals. In contrast, an analysis of paca female reproduction for animals in their natural habitat was conducted using dental cementum and these animals reached a maximum age of around 12.5 years, and were still reproductively active (Collett, 1981). There is no further detailed information on the decrease of reproduction capacity with aging (i.e., age of reproductive senescence) in pacas and other Neotropical game mammals, and few studies have been conducted to investigate reproductive variables by direct examination of reproductive organs.

In the present study, there was examination of a large sample of genitalia of wild lowland paca females, from which there were calculations of age at sexual maturity and first parturition. From these data, there was also an investigation of whether there was reproductive senescence in the species. These refinements allowed for the discussion of potential effects of using new GL values on the results of models assessing sustainable harvest rates of wild lowland paca populations for human purposes.

2. Materials and methods

2.1. Study sites

Materials used in this study were obtained from two study sites, the Yavarí-Mirín River (YMR, 04°19′53″ S; 71°57′33″ W) and the Amanã Sustainable Development Reserve (ASDR, 01°54′00″ S; 64°22′00″ W). The YMR is located in the Western Amazon, and encompasses 107,000 ha of continuous upland forests with one single indigenous community of 307 inhabitants. The ASDR is a 2,313,000 ha reserve of predominantly upland forests in the Central Amazon, between the Negro and Japurá Rivers. Approximately 4000 riverine people inhabit 23 communities and some isolated settlements within ASDR. In both areas, local residents rely mainly on agriculture for income and on hunting and fishing for subsistence. The climate in both study areas is typically equatorial with annual temperatures ranging from 22 to 36 °C, relative humidity of 80%, and annual rainfall between 1500 and 3000 mm.

2.2. Biological material and data collection

Local hunters from the one community in the YMR and from five communities in the ASDR were trained to remove abdominal and pelvic organs from hunted animals and to store these in buffered 4% formaldehyde solution (v/v). From 2000–2016, local hunters collected and voluntarily donated genitalia from a total of 119 female pacas; 44 in the YMR and 75 in the ASDR. All genitalia were individually labelled with the hunting date and the specimen's body mass.

In addition, between 2002 and 2015, hunters in the ASDR recorded data from all pacas onto datasheets (n = 1027), including sex, body mass and date harvested. Only data related to females (n = 522) were utilized in the present study. All research was conducted in compliance with the research protocol approved by the Research Ethics Committee for Experimentation in Wildlife at the Dirección General de Flora y Fauna Silvestre from Peru (License 0350 – 2012-DGFFS-DGEFFS), by the Instituto Chico Mendes Institute for Biodiversity Conservation from Brazil (License SISBIO No 29092-1), and by the Committee on Ethics in Research with Animals of the Federal Rural University of the Amazon (UFRA CEUA protocol 007/2016).

2.3. Laboratory procedures

Genital organs of females were examined for evidence of conceptuses. In addition, the two ovaries of non-pregnant females were sliced and analyzed using a magnifying glass to evaluate the presence of ovarian structures: corpora lutea (CL) and antral follicles larger than 2 mm. Two classes of sexually active females were defined: i) pregnant females with conceptuses (i.e., pregnant females); and ii) non-pregnant females with at least one CL and/or large antral follicles (i.e., non-pregnant estrous cycling females) (Mayor et al., 2013). In contrast, non-pregnant females without a CL or large antral follicles were considered to be anestrous.

The tubular genital organs (uterine horns, cervix and vagina) of non-pregnant females as well as the conceptuses of pregnant females were weighed using a digital weigh scale (0.1 g accuracy; characterized as genitalia mass). Uterine characteristics of pregnant females were not assessed.

2.4. Data analysis

A one-way ANOVA with a *post-hoc* Tukey test was used to assess whether the average body mass differed among anestrus, estrous cycling-non-pregnant and pregnant females, including the body mass of pregnant females with and without the conceptus mass. A *t*-test was used to compare the uterine mass between anestrus and estrous cycling females. Generalized Additive Models for Location, Scale and Shape (GAMLSS) (Stasinopoulos and Rigby, 2007) with the binomial distribution were used to assess the likelihood of females being sexually active (estrous cycles or pregnancy occurring) based on the body mass for all females in the study and to the genitalia mass for non-pregnant females.

Using the probability curve that was developed, there were calculations of the body mass of individuals with a 75% probability of initiation of estrous cycles as a result of pubertal onset and considered this as the average at which most pacas would become pubertal (i.e., pubertal females). There was also calculation of the body mass at which there was a 50% and 100% probability of puberty occurring, using these as the minimum and maximum range of body mass for puberty to occur in females, respectively. There was a subsequent classification as pubertal females of all female pacas that were harvested in the ASDR that were within this body mass range. There was a cross-correlation of the monthly percentages of births in pacas as reported by El Bizri et al. (2018) with the percentages of harvested females that were pubertal to estimate the best fitted time-lag (in months) corresponding to the onset of puberty. The GAMLSS were then used to assess the relationship between the percentage of harvested pubertal females corrected by the selected time-lag and the percentage of births. The same analysis was used to assess the relationship between conceptus mass and pregnant female mass.

To assess whether there is reproductive senescence or a decrease in reproductive rate with advancing age, the GAMLSS analysis was used to evaluate the relationship between the individual body mass of non-pregnant females and the genitalia mass, both in absolute values and relative percentage in relation to the body mass. The existence of an asymptote or decrease in genitalia mass in females with greater body mass may indicate the cessation of capacity to become pregnant at a certain body mass value.

In all GAMLSS models, linear or non-linear relationships and different families of distribution were tested. Families of distribution and final models were selected based on ΔAIC values (Burnham and Anderson, 2004), in which $\Delta AIC < 2$ indicated best fit models. In addition to the AIC ranking, distribution of the residuals (Q-Q Plot) was also checked for selecting the best-fitted family of distribution. The R 3.3.3 software (http://www.Rproject.org/) was used for all statistical analyses, and GAMLSS models were tested using the *gamlss* R-package.

3. Results

3.1. Ovarian structure determinations, genitalia mass and pregnancy diagnosis

Among the females (n = 111) for which there were ovarian structures detected that indicated there had been onset of estrous cycles and in which there was pregnancy diagnoses, there were nine that were anestrous (8.1%) and 102 (91.9%) that had initiated estrous cycles. Among females that were post-pubertal, 18 (17.6%) were non-pregnant and 84 (82.4%) were pregnant (Fig. 1). Post-

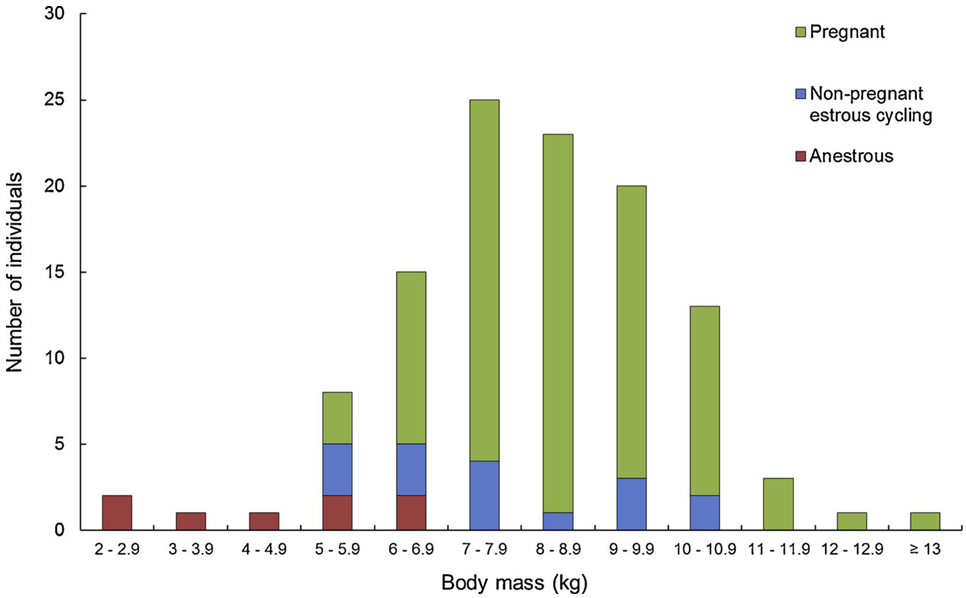


Fig. 1. Distribution of number of lowland paca female genitalia samples characterized by reproductive tract characteristics diagnosed by the presence of ovarian structures and pregnancy (n = 111) as related to the increase in female body mass in Amazonia.

pubertal females had a larger body mass (7.4 ± 1.8) compared to anestrous females (4.2 ± 1.6 kg; $F = 18.36$, df = 3, $P < 0.0001$), however, there was no difference between post-pubertal non-pregnant and pregnant females when assessments were made with or without conceptus mass.

Estrous cycling females had a larger genitalia mass compared to anestrous females ($t = 3.22$, df = 25, $P = 0.0035$; Table 1). Ovarian structures, indicating there had been onset of estrous cycles, were observed in pacas with greater than 5 kg of body mass, and all females with more than 65 g of genitalia mass had ovaries that contained a corpus luteum or large follicles. In addition, the probability of female pacas being estrous cycling increased with an increase in both body and genitalia masses (Fig. 2, Table 2).

3.2. Age at sexual maturity, first parturition and onset of reproductive senescence

Based on the curve between body mass and the probability of females being sexually active (estrous cycling or pregnant) (Sexual activity $= e^{(-11.36+2.28*\text{Body mass})}/1 + e^{(-11.36+2.28*\text{Body mass})}$), there were calculations of the average body mass at the time of puberty to be 5.46 kg (75% of probability), ranging from 4.98 kg (50% of probability) to 6.73 kg (˜100% of probability).

Using the probability curve, there was a determination of the number and percentage of pubertal females among all pacas harvested in the ASDR. Monthly percentage of pubertal females peaked in March (24.0%), August (20.9%) and September (25.8%) (Fig. 3). There was a positive relationship between percentage births and percentage pubertal females with a -4 months time lag ($r^2 = 0.31$; Fig. 4; Table 2). There was also a positive relationship ($r^2 = 0.28$) between conceptus mass and pregnant female body mass (Fig. 5, Table 2). Similarly, in non-pregnant estrous cycling females there was an obvious non-linear positive relationship between body mass and the absolute and relative genitalia mass (Fig. 6, Table 2).

4. Discussion

Reproductive variables such as age at sexual maturity, age at first parturition and decreased reproductive rate as a result of aging

Table 1
Categorization of females based on the presence of pregnancy and ovarian structures that are indicative of the onset of estrous cycles along with number of samples and comparison of mean body mass and mass of tubular genital organs; Distinct letters between values within the same column indicate differences at $P < 0.05$.

Category	Ovarian functionality	n (Number of samples)	Mean body mass (kg) ± SD	Mean genitalia mass (g) ± SD
Non-pregnant	Inactive	9	4.2 ± 1.6^a	20.96 ± 13.16^a
	Active	18	7.4 ± 1.8^b	46.69 ± 21.92^b
Pregnant without conceptus mass	Active	84	8.0 ± 1.5^b	–
Pregnant with conceptus mass	Active	–	8.2 ± 1.5^b	–
Non-pregnant	Unidentified	8	–	–
Overall	–	119	7.6 ± 1.9	40.61 ± 25.68

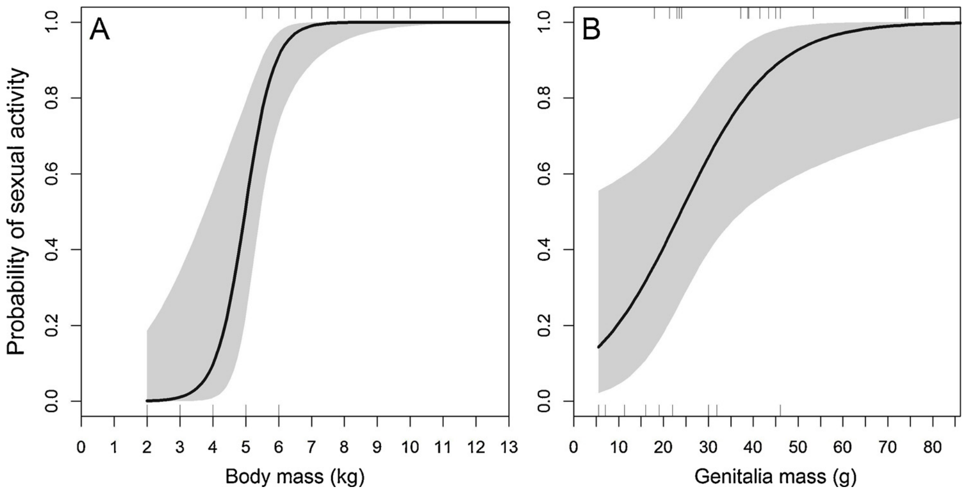


Fig. 2. Probability of reproductive tracts being sexual active (estrous cycling or pregnant) in the lowland paca (*Cuniculus paca*), diagnosed A - by the presence of ovarian structures or pregnancy according to body mass; and B - by the presence of ovarian structures according to genitalia mass.

Table 2

Details of the best-fit models using GAMLSS for each response variable, with the family of distribution, delta AIC in relation to the null model (ΔAIC null) and generalized R^2 Non-linear effects were fit using penalized beta splines (*pb*) and cubic smoothing splines (*cs*) functions provided by gamlss R-package; Families of distributions are represented by Binomial (BI), Gumbel (GU), Weibull (WEI3), Generalized Gamma (GG) and Box-Cox t original (BCTo); Generalized R^2 were calculated using the function *Rsq* of the gamlss package.

Best fitted model		Estimate	*P* (*P*-value)	Family of distribution	ΔAIC null	Generalized R^2
Response variables	Predictor variables					
Sexual activity						
Presence of ovaries' structures/pregnancy	Body mass (kg)	2.281	0.0035	BI	37.71	30.07
Presence of ovaries' structures	Genitalia mass (g)	0.097	0.0286	BI	8.82	33.01
% Hunted pubertal females – 4 months	% Births	0.766	0.0376	GU	2.53	31.42
Pregnancy						
Female body mass (kg)	Conceptus mass (g)	0.00033	< 0.0001	WEI3	19.30	27.58
Reproductive senescence						
Non-pregnant genitalia mass (absolute values)	*pb*(Body mass)	0.283	< 0.0001	GG	46.94	57.07
Non-pregnant genitalia mass (relative values)	*cs*(Body mass)	0.114	< 0.0001	BCTo	18.51	53.11

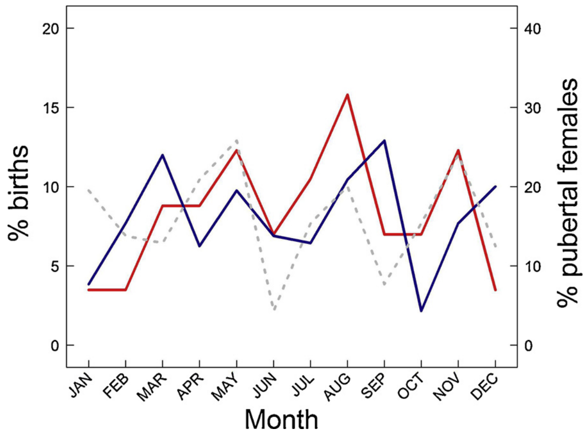


Fig. 3. Temporal trend in the monthly percentage of paca births (solid red line) based on El Bizri et al. (2018) and monthly percentage of hunted pubertal females without time lag (solid blue line) and with a -4 month time lag (dashed gray line) in the Amanã Sustainable Development Reserve, Amazonia (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

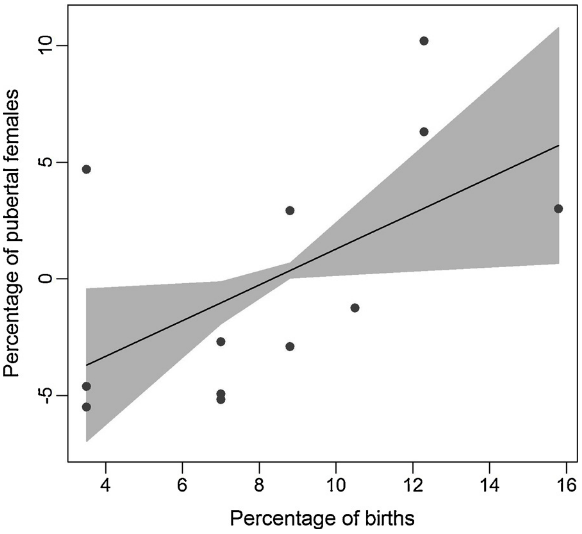


Fig. 4. Association between the percentage of pubertal females and the percentage of births with a -4 month time lag in the Amanã Sustainable Development Reserve; response variable is plotted on the y-axis in a scale of variation around the mean (μ = 0) calculated from the original data used to develop the model.

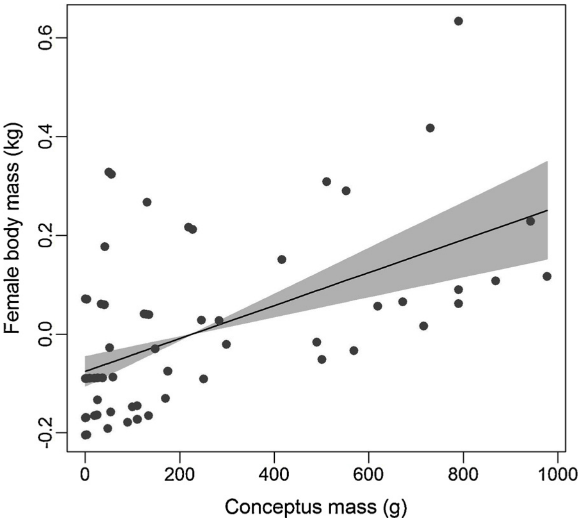


Fig. 5. Relationship between conceptus and body mass of pregnant females; response variable is plotted on the y-axis in a scale of variation around the mean (μ = 0) calculated from the original data used to develop the model.

are important for determining the sustainability of populations of hunted species. In the present study, it was possible to obtain more realistic measures of these variables by using genitalia of animals that were harvested in their natural habitat. Ovarian functionality was initiated in pacas that had about 5.5 kg of body mass. There was determined that these pubertal pacas would have about 4 months of age. In addition, all females larger than 6.5 kg were pregnant or had ovaries that did contained a corpus luteum and/or large follicles indicating there had been onset of estrous cycles, thus all pacas with these ovarian structures or pregnancy were considered to be sexually mature. If a pregnancy length of 149 days is considered (Guimarães et al., 2008), first parturition in the pacas in their natural habitat would occur from 9 months of age onwards. This is much earlier in life than most of these previous estimates for this species where parturition on the average was estimated to occur at about 1 year of age (Collett, 1981; Merrit, 1989; Smythe, 1991; Nogueira et al., 2006; Belaunde, 2008; Guimarães et al., 2008).

Although this estimate indicates that sexual maturity happens earlier in life than was previously thought to occur, this value is validated by body mass growth curves for pacas. Available body mass growth curves indicate that the female paca would weigh 4.54 (Collett, 1981), 4.65 (Rodríguez and Arroyo, 2008), 5.15 (Belaunde, 2008), or 8.35 (Santos et al., 2006) kg at 4 months of age. Realizing that there is a broad range in body weights in these various studies, the average of these values (5.67 kg) is consistent with the estimated average body mass for pubertal females in the present study (5.46 kg, 75% of maturity probability). Furthermore, pacas are considered precocial, having a longer gestation period and a relatively greater intrauterine fetal development than several other

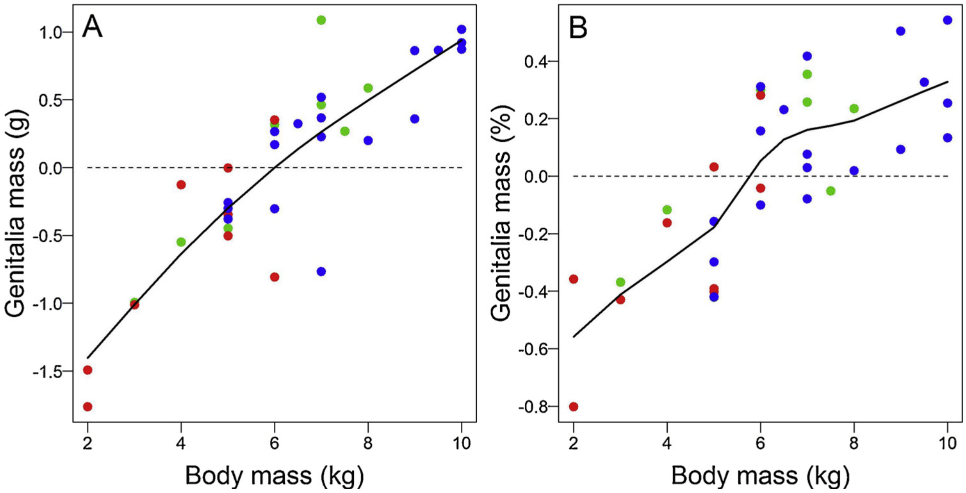


Fig. 6. Relationship between body mass and A - absolute mass of tubular genital organs and B – relative genitalia mass of non-pregnant pacas in Amazonia (n = 35); Red dots: anestrous females (n = 9); blue dots: estrous cycling females (n = 18); green dots: ovarian characteristics unidentified due to lack of ovaries (n = 8); dashed line represents the average absolute genitalia mass (40.61 g) and average relative genitalia mass (0.006%), while the y-axis is in a scale of variation around the mean (μ = 0) calculated from the original data used to develop the model (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

rodent species. This results in pacas giving birth to well-developed neonates that are relatively independent in their extra-uterine life and with a lesser need for parental care (El Bizri et al., 2017). In precocial species, there is a relatively greater metabolic energy utilization during pregnancy with compensation occurring as a result of less time devoted to lactation and offspring care, leading to earlier maturity of the offspring (Derrickson, 1992; Martin et al., 2005). It is, therefore, unlikely that female offspring would require a long maturation period before the time of pubertal onset and ultimately pregnancy occurring.

Previous studies on reproduction of lowland pacas have been conducted using captive animals, so divergences between age at sexual maturity and first parturition in the present and past studies may be related to this difference. For example, although pacas are solitary in the wild, animals have been maintained in large colony groups of males and females in some studies. In these situations, first parturitions have been recorded between 14.9 and 23.4 months of age (Merrit, 1989; Perez-Torres, 1996; Belaunde, 2008). The grouping of animals has been imposed in confinement to enhance the reproductive performance in several hystricomorphs. In colonial hystricomorph rodents, such as the wild cavies, *Cavia aperea*, and domestic guinea-pig, *Cavia aperea* f. *porcellus*, puberty occurs in captive females in the presence of males more than 15 days before those housed without males (Trillmich et al., 2006). Furthermore, maintaining individuals in large groups may also result in suppression of reproductive functions (Wasser and Barash, 1983; Kaplan et al., 1986; Abbott et al., 1988).

In many rodents, reproductive suppression is a consequence of the relatively lesser concentrations of luteinizing hormone (Faulkes et al., 1990), urinary chemo-signals or pheromones (Brown and MacDonald, 1984), or by hierarchical competition where a dominant individual induces stress in subordinates through agonistic behavior. Wild Cape ground squirrel (*Xerus inauris*) females in large groups have a delayed sexual maturation compared to those in smaller groups (Waterman, 2002). This reproductive suppression occurs in both captive and wild colonies and it appears as though naked mole-rat (*Heterocephalus glaber*) females in large group environments are reproductively suppressed for their entire lifespan as a result of relatively lesser concentrations of luteinizing hormone than breeding females (Faulkes et al., 1990). In addition, other factors such as photoperiod, temperature and feeding habits in captivity can affect reproduction and may differ substantially from what occurs in the animal's natural habitat (Trillmich, 2000). Thus, it is likely that these factors contribute to a delayed sexual maturation in the captive lowland paca.

The present study is the first in which there has been an attempt to assess the onset of reproductive senescence of pacas in their natural habitat using characteristics of reproductive organs as the biological markers to do so. There was no indication, based on findings in the present study, of reproductive senescence because there was no asymptote of genitalia mass or absence of structures indicative of onset of estrous cycles in ovaries in large females. There was a consistent positive relationship between body weight and uterine mass of lowland pacas in the present study, thus, there were no indications of uterine involution occurring in the older pacas, at least in hunted populations. The largest females in the present study were pregnant at the time tissues were collected. These findings indicate pacas can reproduce as their age advances, and possibly at a high rate. This interpretation is plausible considering there is not generally a post-reproductive female lifespan in mammals with this being limited to humans and a few species of toothed whales (Ellis et al., 2018). Consistent with findings in the present study there have been estimates of lowland paca age in a previous study through dental enamel analyses. Findings indicated that when there was not hunting of wild pacas by humans in their natural habitat sites in Colombia, these pacas could be 12.5 years of age and still be reproductively active, while the maximum recorded age was 8 years in sites where harvesting of pacas for human purposes occurred (Collett, 1981). This means that senescent paca females are unlikely to exist in hunted populations because larger, and therefore older, individuals are generally harvested for human purposes. These factors can have a substantial effect when considering the effect of paca hunting on population sustainability assessments.

In biological terms, to determine whether there is reproductive senescence in pacas, in-depth studies of pacas in their natural habitat should be conducted because the captive environment may result in an improved fitness and longer lifespan. For example, grey mouse lemur (*Microcebus murinus*) females lived 50% longer in captivity than females in their natural habitat (Hämäläinen et al., 2014). In addition, there needs to be further studies conducted where there is assessment of more precise age data (from skulls) and maturity information from ovaries similar to what occurred in the present study to further ascertain whether there is reproductive senescence in the paca. For paca population sustainability assessments when hunting occurs, the results of the present and a previous study (Collett, 1981) indicate there is no cessation of reproduction, thus, it is suggested that the average age at harvest, as a result of hunting of mature female pacas, be considered the age of the last reproduction event.

The implementation of conservation programs for hunted species is often guided by assessments of their vulnerability to extinction or sustainability of hunting (Bowler et al., 2014). Because previous calculations of reproductive processes of pacas are likely biased, refinements in conservation programs should occur as a result of the enhanced knowledge from the present study regarding the age at sexual maturity. These findings imply that there should be substantial changes to calculations of the GL and, in turn, the calculation of intrinsic rate of population growth (*Rmax*) for this species. Using the most current calculation of birthrate of female offspring (0.71; Mayor et al., 2017), the age of first reproduction calculated in conducting the present study (9 months, or 0.75 years) and the classic measure of age at last reproduction (12.5 years; Collett, 1981), the revised *Rmax* for paca would be 0.60. This is greater than the refined value that was recently published (0.54; Mayor et al., 2017), but still 10.4% less than the established estimate (0.67; Robinson and Redford, 1986). Hence, even when there is consideration of the findings in the present study that pacas sexually mature earlier than what was previously reported, pacas still reproduce less efficiently than expected when calculations were based on data from previous studies. In addition, pacas produce one offspring per gestation and in Amazonia there is an unexpected seasonal pattern of reproduction that converges with periods when there is greater hunting intensity and consequently the harvesting of a large number of pregnant females for human consumption (Oliveira et al., 2007; Mayor et al., 2013, 2017; Valsecchi et al., 2014; El Bizri et al., 2018). When results of the present and previous studies are considered, there needs to be a critical review of previous population sustainability assessments for the species, and calculations of sustainable yields for future in situ management actions (ie., establishment of hunting quotas) should be more conservative.

5. Conclusions

The results of the present study indicate that estrous cycling and pregnant females of lowland paca in their natural habitat have a larger body mass than anestrous females. Ovarian functionality or pregnancy were observed in animals with greater than a 5 kg body mass, and all females with more than 65 g genitalia mass had ovaries containing structures indicative that there had been an onset of estrous cycles before the time of harvest. It is estimated that puberty occurs at about 4 months of age, implying that first parturition occurs at 9 months of age. In addition, there is no evidence that reproductive senescence occurs in the lowland paca. The enhanced information, as a result of the present study, about reproduction of the paca should be considered when conducting population sustainability assessments for the species in areas where hunting occurs.

In addition, results of the present study highlight the importance of in situ studies in understanding the reproduction of species in their natural habitat. These investigations yield more precise information about factors affecting population size of a hunted species in their natural habitat. As ascertained from results of the present study, age at sexual maturity as well as parturition patterns of species in their natural habitat can be obtained and made available to help refine hunting sustainability models. The manner in which the present study was conducted also emphasizes the opportunities to involve local hunter communities in a participatory manner to allow for the collection of large amounts of biological material (see also Mayor et al., 2017). We recommend this method because users of the resource are themselves able to gain directly from the knowledge generated from such studies.

Conflict of interest

The authors declare no conflict of interest.

Funding information

This research was supported by the Gordon and Betty Moore Foundation [Grant Agreement for Instituto de Desenvolvimento Sustentável Mamirauá, #5344], the National Council of Technological and Scientific Development (CNPq) [grant numbers 300005/2013-0; 452908/2016-7; 201475/2017-0], the IVITA (Instituto Veterinario de Investigaciones de Trópico y de Altura), the Museo de la Universidad Nacional de la Amazonía Peruana, the Earthwatch Institute and the Fundación Autónoma Solidaria.

Acknowledgements

We sincerely thank all the people from the communities in the Yavarí-Mirín River and the Amanã Sustainable Development Reserve, without whom this work would not be possible. We also thank T. Q. Morcatty for useful suggestions and comments on the manuscript.

References

Abbott, D.H., Hodges, J.K., George, L.M., 1988. Social status controls LH secretion and ovulation in female marmoset monkeys (*Callithrix jacchus*). J. Endocrinol. 117, 329–339.

Belaunde, S.A., 2008. Determinación de parámetros productivos y reproductivos en la zoocria del "jochi pintado" Cuniculuspaca. Tesis de licenciatura en biología, Universidad Autónoma Gabriel René Moreno. Santa Cruz 95 p.

Bowler, M., Anderson, M., Montes, D., Perez, P., Mayor, P., 2014. Refining reproductive parameters for modelling sustainability and extinction in hunted primate populations in the Amazon. PLoS One 9 (4), e93625.

Brown, R.E., MacDonald, D.W., 1984. Mammalian Social Odours. Oxford University Press, Oxford.

Burnham, K.P., Anderson, D.R., 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociol. Method Res. 33, 261–304.

Clutton-Brock, T.H., 1988. Reproductive Success. University of Chicago Press, Chicago and London.

Cole, L., 1954. The population consequences of life-history phenomena. Q. Rev. Biol. 29, 103–137.

Collett, S.F., 1981. Population characteristics of *Agouti paca* (Rodentia) in Colombia. Publications of the museum, Michigan state university, East Lansing, Michigan. Biol. Ser. 5, 485–602.

de Andrade, R.D.S., Monteiro, F.O.B., El Bizri, H.R., Vicente, W.R.R., de Araujo Guimarães, D.A., Mayor, P., 2018. Fetal development of the Poeppig's woolly monkey (*Lagothrix poeppigii*). Theriogenology 110, 34–43.

Derrickson, E.M., 1992. Comparative reproductive strategies of altricial and precocial eutherian mammals. Funct. Ecol. 6 (1), 57–65.

Di Marco, M., Possingham, H.P., Wilson, K.A., Blomberg, S.P., Boitani, L., Rondinini, C., 2012. A novel approach for global mammal extinction risk reduction. Conserv. Lett. 5 (2), 134–141.

El Bizri, H.R., Morcatty, T.Q., Lima, J.J.S., Valsecchi, J., 2015. The thrill of the chase: uncovering illegal sport hunting in Brazil through YouTube™ posts. Ecol. Soc. 20, 30.

El Bizri, H.R., da Silva Araújo, L.W., da Silva Araújo, W., Maranhão, L., Valsecchi, J., 2016. Turning the game around for conservation: using traditional hunting knowledge to improve the capture efficiency of Amazon lowland pacas. Wildlife Biol. 22, 1–6.

El Bizri, H.R., Monteiro, F.O.B., de Andrade, R.D.S., Valsecchi, J., de Araújo Guimarães, D.A., Mayor, P., 2017. Embryonic and fetal morphology in the lowland paca (*Cuniculus paca*): a precocial hystricomorph rodent. Theriogenology 104, 7–17.

El Bizri, H.R., Fa, J.E., Bowler, M., Valsecchi, J., Bodmer, R., Mayor, P., 2018. Breeding seasonality in the lowland paca (*Cuniculus paca*) in Amazonia: interactions with rainfall, fruiting, and sustainable hunting. J. Mammal. 99, 1101–1111.

Ellis, S., Franks, D.W., Nattrass, S., Cant, M.A., Bradley, D.L., Giles, D., Balcomb, K.C., Croft, D.P., 2018. Postreproductive lifespans are rare in mammals. Ecol. Evol. 8, 2482–2494.

Faulkes, C.G., Abbott, D.H., Jarvis, J.U.M., 1990. Social suppression of ovarian cyclicity in captive and wild colonies of naked mole-rats, *Heterocephalus glaber*. J. Reprod. Fertil. 88, 559–568.

Gaillard, J.M., Yoccoz, N.G., Lebreton, J.D., Bonenfant, C., Devillard, S., Loison, A., Pontier, D., Allaine, D., 2005. Generation time: a reliable metric to measure life-history variation among mammalian populations. Am. Nat. 166, 119–123.

Greene, C., Umbanhowar, J., Mangel, M., Caro, T., 1998. Animal breeding systems, hunter selectivity, and consumptive use in wildlife conservation. In: Caro, T. (Ed.), Behavioral Ecology and Conservation Biology. Oxford University Press, Oxford, pp. 271–305.

Guimarães, D.A., Bastos, L.V., Ferreira, A.C.S., Luz-Ramos, R.S., Ohashi, O.M., Ribeiro, H.L., 2008. Características reprodutivas da paca fêmea (*Agouti paca*) criada em cativeiro. Acta Amazon. 38, 531–538.

Hämäläinen, A., Dammhahn, M., Aujard, F., Eberle, M., Hardy, I., Kappeler, P.M., Perret, M., Schliehe-Diecks, S., Kraus, C., 2014. Senescence or selective disappearance? Age trajectories of body mass in wild and captive populations of a small-bodied primate. Proc. R. Soc. B. 281, 20140830.

IUCN, 2001. IUCNRed List Categories and Criteria: Version 3.1. IUCNSpecies Survival Commission. IUCN, Gland, Switzerland and Cambridge, U.K.

IUCN, 2004. Guidelines for Using the IUCNRed List Categories and Criteria. Standards and Petitions Subcommittee. [accessed 2018-9-11]. http://www.globaltrees.org/downloads/RedListGuidelines.pdf.

IUCN, 2012a. The IUCNRed List of Threatened Species. Version 2012.2. [accessed 2018-9-11]. http://www.iucnredlist.org.

IUCN, 2012b. IUCNRed List Categories and Criteria: Version 3.1, second edition. IUCN, Gland, Switzerland and Cambridge, UK [accessed 2018-9-11]. http://www.iucnredlist.org/technical-documents/categories-and-criteria.

Jerozolimski, A., Peres, C.A., 2003. Bringing home the biggest bacon: a cross-site analysis of the structure of hunter–kill profiles in Neotropical forests. Biol. Conserv. 111, 415–425.

Jiguet, F., Gadot, A.S., Julliard, R., Newson, S.E., Couvet, D., 2007. Climate envelope, life history traits and the resilience of birds facing global change. Glob. Change Biol. Bioenergy 13, 1672–1684.

Kaplan, J.R., Adams, M.R., Koritnik, D.R., Rose, J.C., Manuk, S.B., 1986. Adrenal responsiveness and social status in intact and ovariectomized *Macaca fascicutaris*. Am. J. Primatol. 11, 181–193.

Mace, G.M., Collar, N.J., Gaston, K.J., Hilton-Taylor, C., Akçakaya, H.R., Leader-Williams, N., Millner-Gulland, E.J., Stuart, S.N., 2008. Quantification of extinction risk: IUCN's system for classifying threatened species. Conserv. Biol. 22, 1424–1442.

Martin, R.D., Genoud, M., Hemelrijk, C.K., 2005. Problems of allometric scaling analysis: examples from mammalian reproductive biology. J. Exp. Biol. 208, 1731–1747.

Matamoros, Y., Pashov, B., 1984. Ciclo estral del tepezcuinte (*Cuniculus paca*, Brisson), en cautiverio. Brenesia 22, 249–260.

Mayor, P., Guimaraes, D.A., Lopez, C., 2013. Functional morphology of the genital organs in the wild paca (*Cuniculus paca*) female. Anim. Reprod. Sci. 140, 206–215.

Mayor, P., El Bizri, H., Bodmer, R., Bowler, M., 2017. Assessment of mammal reproduction for hunting sustainability through community-based sampling of species in the wild. Conserv. Biol. 31, 912–923.

Merrit, D., 1989. The husbandry and management of the Paca (*Cuniculus paca*) at Lincoln Park Zoo, Chicago. Int. Zoo Yearb. 28, 264–267.

Milner-Gulland, E.J., Akçakaya, H.R., 2001. Sustainability indices for exploited populations. Trends Ecol. Evol. (Amst.) 16, 686–692.

Nasi, R., Brown, D., Wilkie, D., Bennett, E., Tutin, C., van Tol, G., Christophersen, T., 2008. Conservation and use of wildlife-based resources: the bushmeat crisis. Secretariat of the Convention on Biological Diversity, Montreal, and Center for International Forestry Research (CIFOR), Bogor. Technical Series no. 33. 50 pages.. .

Nogueira, T., Giannoni, M., Toniollo, G., 2006. Observações preliminares sobre a reprodução de uma colônia de pacas *Agouti paca* Linnaeus, 1766 em cativeiro. Cadernos do CEAM-Núcleo de Estudios Agrários 6, 83–95.

Oliveira, F.S., Machado, M.R.F., Canola, J.C., 2003. Real time B-mode ultrasound in pacas pregnancy (Agouti paca, L.1766). Braz. J. Vet. Res. Anim. Sci. 40, 73–78.

Oliveira, F.S., Machado, M.R.F., Canola, J.C., Camargo, M.H.B., 2007. Uniparidade em pacas criadas em cativeiro (Agouti paca, Linnaeus, 1766). Arq. Bras. Med. Vet. Zoo. 59, 387–389.

Pacifici, M., Santini, L., Di Marco, M., Baisero, D., Francucci, L., Grottolo Marasini, G., Visconti, P., Rondinini, C., 2013. Database on Generation Length of Mammals. 5427 Data Records. Online at http://doi.org/10.5061/dryad.gd0m3, version 1.0 (last updated on 2013-08-27), Resource ID: 10.5061/dryad.gd0m3, Data Paper ID:. https://doi.org/10.3897/natureconservation.5.5734.

Peres, C.A., 2000. Effects of subsistence hunting on vertebrate community structure in Amazonian forests. Conserv. Biol. 14, 240–253.

Pérez, H.C., Hernández, F.Z., 1979. Comportamiento reproductivo y datos de la alimentación de Agouti paca. Acta Zool. Lilloana 35, 283–385.

Perez-Torres, J., 1996. Guía para el manejo y cría de la "Paca" Agouti paca. Convenio Andrés Bello, Bogotá, Colombia.

Perry, A.L., Low, P.J., Ellis, J.R., Reynolds, J.D., 2005. Climate change and distribution shifts in marine fishes. Science 308, 1912–1915.

Ripple, W.J., Abernethy, K., Betts, M.G., Chapron, G., Dirzo, R., Galetti, M., Levi, T., Lindsey, P.A., Macdonald, D.W., Machovina, B., Newsome, T.M., Peres, C.A., Wallach, A.D., Wolf, C., Young, H., 2016. Bushmeat hunting and extinction risk to the world's mammals. Roy. Soc. Open Sci. 3, 160498.

Ripple, W.J., Wolf, C., Newsome, T.M., Hoffmann, M., Wirsing, A.J., McCauley, D.J., 2017. Extinction risk is most acute for the world's largest and smallest vertebrates.

PNAS 114, 10678–10683.

Robinson, J.G., Redford, K.H., 1986. Body size, diet, and population density of Neotropical forest mammals. Am. Nat. 128, 665–680.

Rodríguez, M.A.B., Arroyo, M.D.B., 2008. Efecto de la dieta sobre la ganancia de peso en individuos de *Agouti paca* (Rodentia: Agoutidae) en cautiverio. Rev. Mex. Mastozool. 12, 6–16.

Santos, R., Lima, A.L., Barbosa, W.A., Vargas Junior, J.G., 2006. Determinação da curva de crescimento em pacas (*Agouti paca* L.) criadas em cativeiro do nascimento ao desmame. IX Encontro Latino Americano de Iniciação Científica e V Encontro Latino Americano de Pós-graduação. Universidade do Vale do Paraíba, Vale do Paraíba: Univap.

Smucny, D.A., Abbott, D.H., Mansfield, K.G., Schultz-Darken, N.J., Yamamoto, M.E., Alencar, A.I., Tardif, S.D., 2004. Reproductive output, maternal age, and survivorship in captive common marmoset females (*Callithrix jacchus*). Am. J. Primatol. 64, 107–121.

Smythe, N., 1991. Steps toward domesticating the paca (*Agouti* = *Cuniculus paca*) and prospects for the future. In: Robinson, J.G., Redford, K.H. (Eds.), Neotropical Wildlife Use and Conservation. University of Chicago Press, Chicago, Illinois, pp. 202–216.

Stasinopoulos, D.M., Rigby, R.A., 2007. Generalized additive models for location, scale and shape (GAMLSS). R. J. Stat. Softw. 23, 1–46.

Trillmich, F., 2000. Effects of low temperature and photoperiod on reproduction in the female wild guinea pig (*Cavia aperea*). J. Mammal. 81, 586–594.

Trillmich, F., Laurien-Kehnen, C., Adrian, A., Linke, S., 2006. Age at maturity in cavies and guinea-pigs (*Cavia aperea* and *Cavia aperea f. porcellus*): influence of social factors. J. Zool. 268, 285–294.

Valsecchi, J., El Bizri, H.R., Figueira, J.E.C., 2014. Subsistence hunting of *Cuniculus paca* in the middle of the Solimões River, Amazonas, Brazil. Braz. J. Biol. 74, 560–568.

Wasser, S.K., Barash, D.P., 1983. Reproductive suppression among female mammals: implications for biomedicine and sexual selection theory. Q. Rev. Biol. 58, 513–538.

Waterman, J.M., 2002. Delayed maturity, group fission and the limits of group size in female Cape ground squirrels (Sciuridae: *Xerus inauris*). J. Zool. 256, 113–120.

Weinbaum, K.Z., Brashares, J.S., Golden, C.D., Getz, W.M., 2013. Searching for sustainability: are assessments of wildlife harvests behind the times? Ecol. Lett. 16, 99–111.

Received: 11 September 2019 | Accepted: 24 March 2020

DOI: 10.1111/1365-2664.13633

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

CITIZEN SCIENCE

Research Article

Involving local communities for effective citizen science: Determining game species' reproductive status to assess hunting effects in tropical forests

Hani R. El Bizri[1,2,3,4] | **John E. Fa**[1,5] | **Lísley P. Lemos**[2,3] | **João V. Campos-Silva**[3,6,7] | **Carlos F. A. Vasconcelos Neto**[2,3] | **João Valsecchi**[2,3,4] | **Pedro Mayor**[4,8,9,10]

[1]Department of Natural Sciences, Manchester Metropolitan University, Manchester, UK; [2]Mamirauá Sustainable Development Institute, Tefé, Amazonas, Brazil; [3]Rede de Pesquisa para Estudos sobre Diversidade, Conservação e Uso da Fauna na Amazônia (RedeFauna), Manaus, Amazonas, Brazil; [4]ComFauna, Comunidad de Manejo de Fauna Silvestre en la Amazonía y en Latinoamérica, Iquitos, Peru; [5]Center for International Forestry Research (CIFOR), Situ Gede, Kota Bogor, Jawa Barat, Indonesia; [6]Institute of Biological Sciences and Health, Federal University of Alagoas, Maceió, Brazil; [7]Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway; [8]Museo de Culturas Indígenas Amazónicas, Iquitos, Loreto, Peru; [9]Departament de Sanitat i Anatomia Animals, Universitat Autònoma de Barcelona, Bellaterra, Barcelona, Spain and [10]Programa de Pós-Graduação em Saúde e Produção Animal na Amazônia, Universidade Federal Rural da Amazônia (UFRA), Belém, Pará, Brazil

Correspondence
Hani R. El Bizri
Email: hanibiz@gmail.com

Funding information
Gordon and Betty Moore Foundation, Grant/Award Number: 5344; Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: 201475/2017-0, 300005/2013-0, 300504/2019-5 and 452908/2016-7; Earthwatch Institute; Instituto Veterinario de Investigaciones de Tropico y de Altura; Museo de la Universidad Nacional de la Amazonía Peruana; Fundación Autónoma Solidaria

Handling Editor: Fernanda Michalski

Abstract

1. Involving communities in sustainable wildlife management in tropical forests can ensure food security and livelihoods of millions of forest dwellers that depend on wild meat, and also safeguard hunted species. Mathematical models have been developed to assess hunting sustainability; but these require empirical information on reproductive parameters of the prey species, often challenging to obtain.
2. Here, we suggest that if local people can accurately identify the reproductive status of hunted animals in the field, these data could fill the existing knowledge gap regarding species' life-history traits and enable better assessments of hunting impacts.
3. We first tested whether local people in 15 rural communities in three Amazonian sites could accurately diagnose, before and after training, the pregnancy status of hunted pacas *Cuniculus paca*, which we use as our model. We then applied the results from these tests to correct reproductive status data of hunted specimens, voluntarily collected over 17 years (2002–2018) as part of a citizen-science project in one of our study sites. We ran generalized additive models to contrast these corrected reproductive rates with those obtained from the direct analysis of genitalia by researchers, and with indices describing game extraction levels (catch-per-unit-effort, CPUE, and age structure of hunted individuals).
4. Before training, interviewees correctly diagnosed pregnancy in 72.5% of tests, but after training, interviewees accurately diagnosed pregnancy in 88.2% of tests, with high improvements especially for earlier pregnancy stages. Monthly pregnancy rates determined by hunters and by researchers were similar. Reported annual pregnancy rates were negatively correlated with CPUE, and positively

correlated with the percentage of immatures in the hunted population, in accordance with an expected density-dependent response to variations in hunting levels.

5. *Synthesis and applications*. We show that the voluntary diagnosis of game species' reproductive status by local people is a feasible method to obtain accurate life-history parameters for hunted tropical species, and to assess hunting effects on game populations. Given that almost half of the protected areas in the world are co-managed by local people, our results confirm the potential of integrating local communities in citizen-science initiatives to ensure faster, low-cost and more accurate data collection for wildlife management.

KEYWORDS

Amazon, citizen science, hunting, protected areas, reproduction, sustainability, tropical forests, wild meat

1 | INTRODUCTION

Ensuring the sustainability of wildlife hunting in tropical forests is crucial to guarantee the conservation of game species and safeguard the food security and livelihoods of millions of forest dwellers (Coad et al., 2019). Since the early 1990s, a wide range of mathematical models have been developed to assess hunting sustainability (Weinbaum, Brashares, Golden, & Getz, 2013). These models require accurate information on population abundance, reproductive and mortality patterns of the hunted species (Weinbaum et al., 2013).

Reproductive performance of wild vertebrates is usually studied by directly examining animals after capture and restrain, or from direct field observations of births (e.g. Zhang et al., 2007). Because both methods are challenging, especially for tropical forest animals (Fragoso et al., 2016), researchers are limited by the lack of basic information on age of first reproduction, breeding cycles and pregnancy rates of hunted species (Milner-Gulland & Akçakaya, 2001). Moreover, such information is also essential for the development of complex demographic models, such as how reproductive rates change in response to the removal of individuals by hunting. These models are rarely applied due to the lack of data; thus, researchers employ simpler ones that perform with much higher uncertainty levels (Weinbaum et al., 2013).

A cost-effective option for gathering large amounts of biological and ecological evidence in the field is via citizen scientists (Dickinson, Zuckerberg, & Bonter, 2010). By involving non-professionals it is possible to obtain vital information on a variety of subjects (Bonney et al., 2014; Steger, Butt, & Hooten, 2017). In the tropics, Indigenous and rural people have been involved in citizen-science projects, providing information on animal populations and trends, just as accurately as trained scientists (e.g. Danielsen et al., 2014). Since local communities in tropical forests have extensive knowledge of the environment and are the main direct users of natural resources, their participation in scientific monitoring is central (Pocock et al., 2015).

Mayor, El Bizri, Bodmer, and Bowler (2017) have demonstrated the effectiveness of citizen science through a community-based collection of organs of Amazonian forest mammals to determine reproductive parameters. In this study, local hunters collected and voluntarily donated complete visceras of hunted specimens over an uninterrupted 15-year period. Using this material, Mayor et al. (2017) were able to estimate annual birth rates of female offspring. These estimates differed significantly from those obtained in sustainability assessments that often use data from captive populations.

As shown by Mayor et al. (2017) it is possible to collect accurate reproductive parameters of some hunted species over the long-term through the examination of biological materials brought back to researchers. This is possible for small-bodied animals but not for large species since their viscera are often not brought back from the forest due to their heavy weight (see Mayor et al., 2017). In the current system, local people are only responsible for sample collection, since the determination of the reproductive status of animals is done by technicians in laboratories, thus increasing survey costs, and does not involve locals in data processing and analysis, and arguably in using the collected data in decision-making. Conversely, if local people could accurately categorize the reproductive status of hunted specimens where they are hunted, data collection becomes cheaper, easier to implement and more frequent, therefore substantially increasing sample sizes. Beyond providing more precise estimates of reproductive rates, larger sample sizes would also permit the better understanding of hunting impacts, for example by determining how variation in reproductive rates over time relates to density-dependent responses of populations to hunting.

In this study, we used the lowland paca *Cuniculus paca* as our model species, because it is among the top three most hunted species in the Neotropics (e.g. El Bizri, Morcatty, Lima, & Valsecchi, 2015; El Bizri et al., 2020; Peres, 2000), allowing us to acquire a large number of samples. Using photographs of genitalia of paca females donated by hunter families, we tested whether an effective method could be implemented for citizen scientists to accurately diagnose the reproductive status of hunted specimens. We first established the local peoples' capacity to determine the reproductive status of female pacas in three Amazonian sites, before and after a period of training. We then used these results to correct the pregnancy rates estimated for the species from data collected by local people on hunted specimens' reproductive status over a 17-year period (2002–2018) in one study site. For this study site, we compared the corrected pregnancy rates with those determined from genitalia samples by trained researchers, and with hunting indices to describe the effects of hunting on the studied game populations.

2 | MATERIALS AND METHODS

2.1 | Study sites

We conducted our study in three Amazonian sites (Figure 1). The Yavarí-Mirín River (YMR, 04°19′53″S; 71°57′33″W) is located in the northeastern Peruvian Amazon, and encompasses 107,000 ha of continuous upland forests where a single Indigenous community of 307 inhabitants live (Figure 1). The Amanã Sustainable Development Reserve (ASDR, 01°54′00″S; 64°22′00″W) is a 2,350,000 ha reserve of predominantly upland forests in the central Brazilian Amazon, between the Negro and Japurá Rivers. Approximately 4,000 riverine people inhabit 80 communities and some isolated settlements within this reserve. The middle Juruá River (MJR) region in southern Brazilian Amazonia (5°40′26″S, 67°30′25″W) comprises two protected areas of sustainable natural resources use (Middle Juruá Extractive Reserve and Uacari Sustainable Development Reserve) with 886,175 ha of lowland and upland forests. These two reserves are occupied by *c.* 3,200 people in 57 settlements. In all three areas, local communities rely mainly on agriculture for income and on hunting and fishing for subsistence.

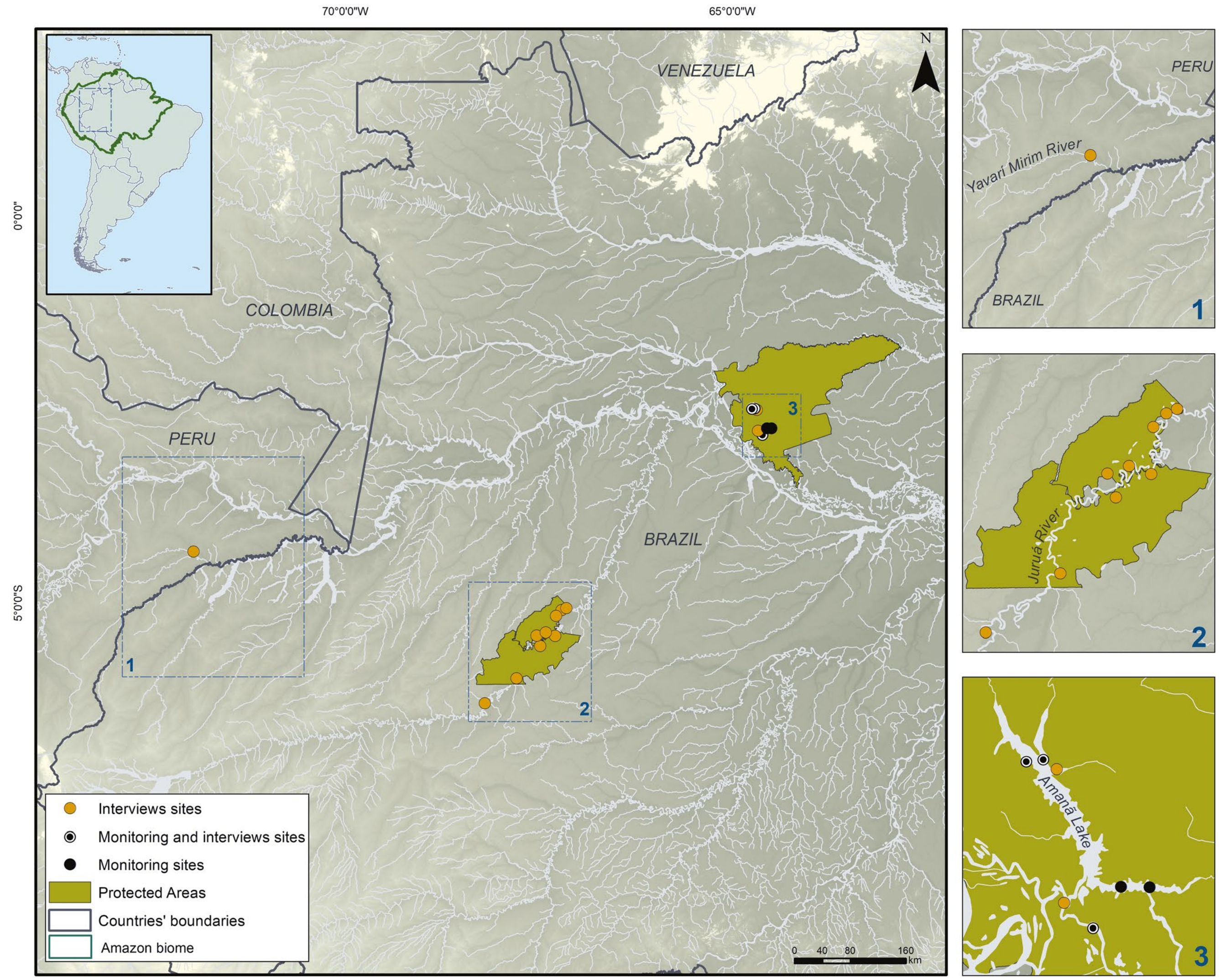


FIGURE 1 A map showing the three sampled sites with locations of the 15 communities within Amazonia where interviews on the reproductive status of game species were performed (interview sites), between 2017 and 2019, and of the five communities where hunting and reproductive data were provided by local people in a citizen-science project between 2002 and 2018 (monitoring sites). Note that three communities in the Amanã Sustainable Development Reserve participated in both interviews and monitoring collections, and thus are classified as 'monitoring and interviews sites'

2.2 | Local people interviews

Photographs were taken of all paca female genitalia collected (n = 300) from animals donated for research by local people in the YMR and ASDR (see El Bizri et al., 2018; Mayor et al., 2017; Mayor, Guimarães, & López, 2013; see Figure S1). For pregnant genitalia, we removed the conceptuses and measured their crown-rump length using a metal vernier calliper (maximum 300 mm).

From the pool of photographs, we selected a total of 42 showing complete genitalia, being seven (16.7%) photographs of non-pregnant females and 35 (83.3%) from pregnant females with conceptuses ranging from 0.5 to 26 cm in length (M = 7.51 cm; SD = 7.28 cm), depicting the increasing range in conceptus size along gestation. Using these photographs, we asked interviewees to answer whether they thought the specimen was pregnant or not. If they considered the specimen to be pregnant, the interviewee was requested to point out where he/she believed the conceptus was implanted within the uterus.

Considering the time available for the study, we used simple random sampling (Albuquerque, Cunha, De Lucena, & Alves, 2014) to select the maximum number of young and adults to interview within each sampled community. We interviewed a total of 104 people, 81 men (77.9%) and 23 (22.1%) women. The average age of the men was 38.7 ± 13.9 *SD* (17–72 years old), and of women 41.3 ± 14.1 *SD* (24–75 years old). Interviews were conducted in August 2017 in the single YMR community, in May and October 2018, and in January and June 2019 in five ASDR communities, and in November 2018 in nine communities in the MJR.

We held two rounds of interviews for each person during a single interview day. In the first round, we showed the pictures randomly and asked people to determine the reproductive status of each specimen without giving them any clues or guidance on the reproductive biology of the species. In the second round, we used three of the pictures to train interviewees on how pregnancy occurs, explaining where the conceptuses would normally be found in the uterus, and how to determine their presence. We then shuffled the photographs and randomly presented these again for their second diagnosis.

2.3 | Hunting registers

In the ASDR, a citizen-science hunting monitoring system has been active since 2002 and is ongoing. In this site, we trained five local hunters within five separate communities to assemble a wide range of data on the daily hunting activity of community members, including time spent hunting and number of hunters involved, as well as collect data on each specimen hunted: sex and the body mass of hunted individuals, and reproductive status of females (pregnant or non-pregnant). Hunters voluntarily provided information to collectors after returning from their hunts. By the end of 2018, collectors had recorded data for a total of 1,236 hunted pacas.

All research were conducted in compliance with the research protocol approved by the Research Ethics Committee for Experimentation in Wildlife at the Dirección General de Flora y Fauna Silvestre from Peru (License 0350-2012-DGFFS-DGEFFS) and by the Instituto Chico Mendes for Biodiversity Conservation from Brazil (License SISBIO No 29092-1).

2.4 | Data analysis

2.4.1 | Interview responses

For each interview, responses were scored as 1 if correct and 0 if incorrect. We considered an incorrect answer when the interviewee identified a non-pregnant paca as pregnant (false positive) and a pregnant paca as non-pregnant (false negative), also when the interviewee incorrectly indicated the location where the conceptus was implanted in the uterus.

We analysed all responses using GLMM with a binomial distribution to obtain logistic regressions of the probability of interviewees giving correct answers according to a set of predictor variables. We generated separate models for non-pregnant and pregnant females. For non-pregnant specimens, we considered the number of correct and incorrect responses (scores: 0—incorrect and 1—correct) as the dependent variables, and the interviewees' sex (man/woman) and age (continuous) as predictor variables. For pregnant specimens, we considered the number of correct and incorrect responses (scores: 0—incorrect and 1—correct) as dependent variables, and the interviewees' sex and age and the length of the conceptuses (continuous) as predictor variables. We built a null model (no effect of predictor variables) and models with different combinations of predictor variables, from simple ones (only one predictor variable) to a more complex one (all variables in the model). We independently tested each interview round. Interviews from the same community may not be independent since there were a different number of interviewees for each community, and because we consider that the learning process and sharing of information on the biological traits of game species among local people may be nested at the community level. As a result of these two issues, the communities sampled were included as a random categorical factor.

Final models from GLMMs were compared based on Akaike information criterion (AIC) values, and all models with the ΔAIC < 2 in relation to the model with lowest AIC were considered as with strong support (see Burnham & Anderson, 2004). To avoid selecting a model that was overfitting due to a large sample size, we also used a likelihood ratio test to compare the significance of these models; if two models were similar ($p > 0.05$), we considered the best-fitted model the one with lowest number of parameters, that is fewest degrees of freedom. However, we present all models with ΔAIC < 2 in Table S1. GLMMs were conducted using the R package LME4.

Finally, we assessed the effect of training on the probability of giving more correct answers in the second interview. For both non-pregnant and pregnant specimens, we calculated the difference between the percentages of correct and incorrect responses in the two interview rounds using a chi-squared test. In addition, for pregnant specimens, we calculated the difference between the average logistic regression formulas produced in the GLMMs for each round of interview.

2.4.2 | Corrections of reproductive status and density dependence effects

Interview results were then used to correct the data on the reproductive status of hunted females collected over the 17-year (2002–2018) monitoring period in the ASDR. Since no systematic training on pregnancy diagnosis was conducted with local people during the monitoring period, we considered they could be categorizing pregnant females as non-pregnant at a similar rate as obtained in the first interview round. On this basis, we therefore applied a correction factor based on two steps. First, we used the formula of the relationship between conceptus length and gestational age in El Bizri et al. (2017; Crown-rump length = 0.179*Age − 5.28) to obtain the proximate number of pregnancy days up to which hunters would be mistakenly diagnosing pregnant pacas as non-pregnant. For this, we considered the threshold for an accurate diagnosis to be at a conceptus length in which the probability of giving a correct answer was 90%. Second, we used the monthly percentage of paca conceptions presented by El Bizri et al. (2018) as a proxy for the percentage of pacas that would be in the early days of pregnancy, not detectable as pregnant by the hunters. Based on the number of pregnancy days calculated from our first step, we calculated a retroactive monthly percentage of false negatives for each month, thus correcting the number of pregnant and non-pregnant females (see Table S2). The gestation length of 149 days for the paca was based on the study by Guimarães et al. (2008).

We used these corrected reproductive data to validate the effectiveness of a long-term citizen-science collection of reproductive performance data to: (1) provide reliable information on the reproductive rates for the species; and (2) understand hunting effects. For the first aim (1), we selected females with a body mass ≥5.5 kg, which we considered as mature, following El Bizri, Fa, Valsecchi, Bodmer, and Mayor (2019). We then calculated the monthly percentage of pregnant specimens among the mature females sampled each month (hereafter monthly pregnancy rate), independently for each year and assessed the relationship between monthly pregnancy rate and the expected monthly pregnancy rate of pacas. For this purpose, we considered the published metrics of pregnancy rates in El Bizri et al. (2018), calculated from pregnancy diagnoses from genitalia collected in the ASDR by researchers and examined in the laboratory, as the expected monthly pregnancy rates (see Table S2). In this analysis, the month was treated as a fixed factor, while the year of collection was treated as a random factor.

For our second aim (2), we hypothesized that any hunting impact on any animal population would lead to an increase in pregnancy rates over time as a density-dependent response to lower population abundance (e.g. Lima & Jaksic, 1998). This increase in pregnancy rate would then be related to an increase in immature individuals in the population due to higher birth rates. We tested for all these relationships by calculating the yearly pregnancy rates of hunted specimens, correlating these with the mean annual catch-per-unit-effort (CPUE, in ind hunter^{-1} hr^{-1}) of hunting events as a proxy of paca abundance (see Marrocoli et al., 2019; Rist, Milner-Gulland, Cowlishaw, & Rowcliffe, 2010; Valsecchi, Bizri, & Figueira, 2014). Then, we correlated the yearly pregnancy rates with the annual percentage of immature individuals (number of individuals < 5.5 kg/total number of individuals hunted; see El Bizri, Fa, Valsecchi, et al., 2019; Mendes-Oliveira et al., 2012). Although 848 paca hunting events were recorded, we calculated CPUE for only nocturnal hunts using the ‘spotlighting’ method (n = 519), since paca is strictly nocturnal and spotlighting is a technique that is specifically used to hunt this and no other species, therefore guaranteeing that this index indeed reflected the species' abundance in the study area (see Valsecchi et al., 2014).

To assess the relationship between the monthly pregnancy rate and the expected monthly pregnancy rate of pacas, as well as density-dependent effects, we used a generalized additive model (GAM), which consists of univariate regression analysis that allows each regression variable to have a linear or nonlinear relationship with the dependent variable. The type of nonlinearity is tested through the use of several smoothers/additive terms in the modelling process. These terms normally adds penalizations in the model to prevent overfitting. For the conduction of GAMs, we first tested the best family of distribution fitted to the response variable, comparing these based on QQ-plots of the residuals, and on the difference between AIC values among them. After selecting the best-fitted distribution, we built a null model (no relationship with the predictor variable), and models with the predictor variables in linear and nonlinear forms, testing penalized splines and cubic splines as additive terms. The final model, both in terms of retention of predictor variables and the type of relationship (whether linear or nonlinear), was selected based on AIC values (Burnham & Anderson, 2004), in which the model with the lowest AIC was selected. For these analyses, the R package GAMLSS was used (Stasinopoulos & Rigby, 2007). An advantage of using the GAMLSS package is its flexibility in terms of families of distribution (over 100 continuous, discrete and mixed distributions for modelling the response variable are available), and the various additive terms available compared to other packages. We used R 3.3.3 software for all statistical procedures, and a p-value < 0.05 was considered significant.

3 | RESULTS

3.1 | The diagnosis of the reproductive status by local people

For non-pregnant females, there was a proportion of 92.6% and 90.4% of correct responses in the first and second round of interviews, respectively, with no significant difference between rounds

(χ^2 = 0.17; p = 0.68); no significant effect was observed for any of the predictor variables on the probability of giving correct responses (Table 1).

For pregnant females, the proportion of correct responses was 72.5% for the first interview round. The probability of correctly diagnosing pregnancy varied according to the conceptus size, with lower probabilities for smaller conceptuses (Table 1; Figure 2a). This probability also varied according to the age of the interviewee, with youngers answering correctly more often than older individuals; this difference being greater for small-sized conceptuses

TABLE 1 Details of the best-fit GLMMs for the diagnoses of mature paca *Cuniculus paca* females by local people through genitalia pictures, and generalized additive models (GAMs) for the relationship between the corrected monthly pregnancy rate from hunting registers with the expected pregnancy rate from genitalia, the trend in annual pregnancy rates along the hunting monitoring period (2002–2018), and between annual pregnancy rates with the catch-per-unit-effort (CPUE, ind hunter^{-1} hr^{-1}) and proportion of immature individuals in the Amanã Sustainable Development Reserve (ASDR). The interviewees' communities were included as a random categorical factor in the GLMMs

Best-fit model							
Response variables	**Predictor variables**	**Estimate (*SE*)**	***z*-value/ *t*-value**	***p*-value**	**Family of distribution**	**Link function**	***w*AIC (*k*; *df*; ΔAIC null)**
Interview—Pregnant pictures							
First round							
Correct answers							
	(Intercept)	0.433 (0.20)	2.21	0.0272*			
	Conceptus size	0.190 (0.01)	18.01	<0.001*	BI	Logit	0.71 (4; 4; 576.19)
	Interviewee age	−0.001 (0.003)	−2.98	0.0029*			
Second round							
Correct answers	(Intercept)	0.452 (0.16)	2.85	0.0044*	BI	Logit	0.25 (3; 3; 457.06)
	Conceptus size	0.569 (0.05)	11.64	<0.001*			
Interview—Non-pregnant pictures							
First round							
Correct answers	(Intercept)	2.640 (0.30)	8.90	<0.001*	BI	Logit	0.35 (3; 3; 2.53)
	Interviewee sex	1.788 (1.04)	1.72	0.086			
Second round							
Correct answers	(Intercept)	2.687 (0.37)	7.28	<0.001*	BI	Logit	0.50 (3; 3; 2.17)
	Interviewee sex	15.774 (17.42)	0.01	0.993			
Monthly pregnancy rate							
From hunting registers	(Intercept)	−9.910 (4.83)	−2.05	0.042			
	From genitalia	1.042 (0.15)	6.79	<0.001*	BCCGo	Identity	0.65 (14; 15.5; 31.80)
Temporal trends							
Annual pregnancy rate	(Intercept)	−0.002 (0.16)	−146.00	<0.001*	IG	Identity	0.99 (3; 4.9; 15.86)
	pb (year)	1.169 (0.008)	148.10	<0.001*			
Density-dependent responses							
Annual pregnancy rate	(Intercept)	67.83 (11.56)	5.87	<0.001*	GA	Identity	0.86 (2; 3; 3.58)
	CPUE	−118.95 (44.37)	−2.68	0.018*			
Proportion of immatures	(Intercept)	8.00 (4.11)	1.95	0.072	GU	Identity	0.87 (2; 3; 3.79)
	Annual pregnancy rate	0.26 (0.10)	2.65	0.019*			

Note: Smoothers were fitted using p-splines (*pb*).

Abbreviations: BI, binomial, BCCGo, Box Cox Cole Green Original, GA, gamma, GU, Gumbel; *df*, degrees of freedom; IG, Inverse Gaussian; *k*, number of parameters; *w*AIC, Akaike weights; ΔAIC null, difference between the AIC of the selected model and the AIC of the null model.

*$p < 0.05$.

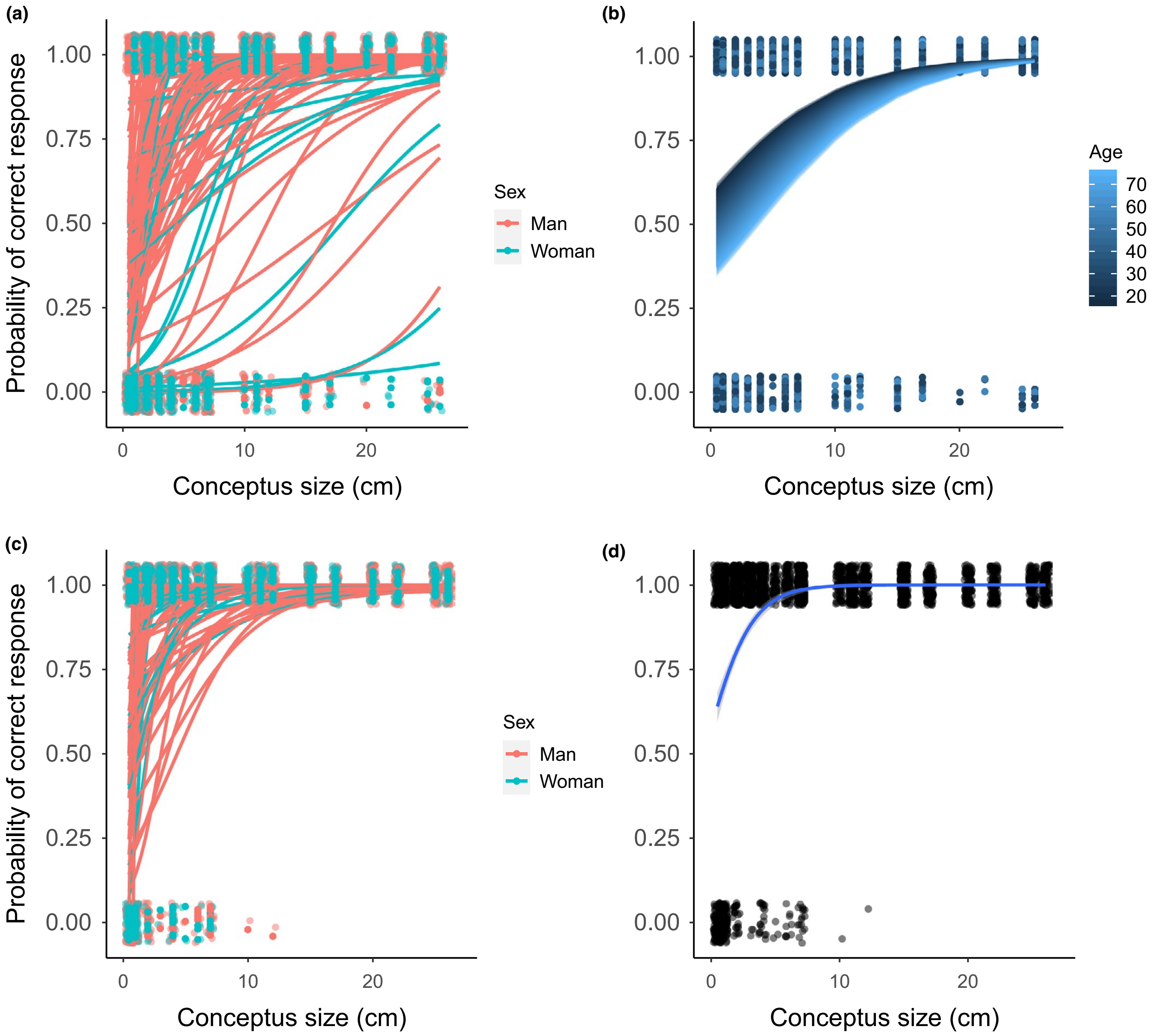


FIGURE 2 Probability of local people at correctly diagnosing pregnancy in pictures of genitalia of lowland pacas *Cuniculus paca* before (a and b) and after training (c and d), according to sex and age of the interviewee along the increase in conceptus size in pregnancy. Each line of graphs *a* and *c* represents one of the 104 people interviewed in this study

(Table 1; Figure 2b). The average probability formula calculated according to conceptus size is given by: Probability of Correct Responses = $1/1 + e^{-(0.19^{*}\text{Foetal size}-0.08)}$.

In the second round of interviews, after training, we recorded a total of 88.2% correct answers. The size of the conceptus still influenced the probability of giving correct answers (Table 1; Figure 2c,d). The average probability formula calculated according to conceptus size in the second round is given by: Probability of Correct Responses = $1/1 + e^{-(0.57^{*}\text{Foetal size}+0.45)}$, changing substantially from the first round of interviews due to significant improvements in the diagnosis of pregnancy after training ($\chi^2 = 236.65$; $p < 0.0001$). This improvement occurred for all conceptus sizes, but was higher for pregnant females with smaller conceptuses, between 0.5 and 10 cm (32–85 gestation days, 21.5%–57.0% of total gestation length respectively), with peak at around 5 cm (57 gestation days, 38.3% of total gestation length), for which diagnoses improved by around 25% (Figure 3).

3.2 | Estimates of reproductive rates of game species and hunting effects

Out of the total number of hunted individuals recorded in our monitoring program (n = 1,236 pacas), 634 were females out of which 554 were mature (87.4%, ≥5.5 kg). Among these, local dwellers classified 445 as non-pregnant and 109 as pregnant. Without any correction, the average monthly pregnancy rate from hunting registers was 22.7% (Table 2). Using the formula obtained from the first round of interviews, we estimated that hunters would start diagnosing pregnancies with ≥90% accuracy for conceptuses larger than 12.6 cm in length. This length corresponds to around 100 days gestational age (El Bizri et al., 2017). Thus, by including a retroactive 3-month time-lag (~90 days) to the percentage of conceptions provided by El Bizri et al. (2018), the average monthly pregnancy rate increased by 19.3%, reaching 42.0% with the inclusion of 108 females that were in fact pregnant but incorrectly diagnosed as non-pregnant (Table 2).

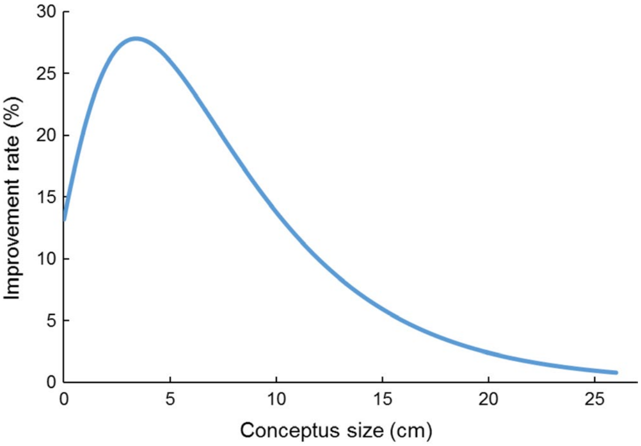


FIGURE 3 Improvement rate, in percentage, of the probability of local people in Amazonia at correctly diagnosing pregnancy in pictures of genitalia of lowland pacas *Cuniculus paca* after a training session

Corrected monthly pregnancy rates were positively and significantly correlated with the expected monthly pregnancy rates calculated from genitalia collections (El Bizri et al., 2018; Table 1; Figure 4). The annual pregnancy rates calculated from hunting registers were on average 39.1%, presenting an inverted U-shaped pattern of changes across years, with a peak in 2012 (Table 3; Figure 5). Pregnancy rates were negatively correlated with the annual CPUE over time (Table 1; Figure 6), and years with higher pregnancy rates had a higher proportion of immature individuals (Table 1; Figure 6).

4 | DISCUSSION

We showed that local people can participate in the voluntary diagnosis of the reproductive status of game species. Although we used the lowland paca as our model species, this method can be used for any hunted tropical forest placental mammal because: (a) these share similar internal reproductive morphology; (b) world-wide, local people eviscerate specimens before eating their meat; and (c) pregnancy is a phenomenon that can be easily identified by hunters.

The high score obtained in the first round of interviews shows that most interviewees already possessed ample understanding of the reproductive biology of game species. This traditional ecological knowledge (TEK) probably starts from exposure to animals since childhood (da Cunha, 2009). At a very young age, children of both sexes are initiated into hunting practices via storytelling, and during puberty, young teens follow adults to hunts and assist

TABLE 2 Details on the number of mature paca *Cuniculus paca* females hunted in the Amanã Sustainable Development Reserve per month with their reproductive status, and the monthly pregnancy rates obtained from hunting registers before and after a correction. For more details on the calculations, see Table S2

	Number of mature females						
Month	Pregnant	Non-pregnant	Total	False negatives[a]	Monthly pregnancy rate (%)[b]	Corrected monthly pregnancy rate (%)[c]	Expected monthly pregnancy rate (%)[d]
January	6	19	25	5.3	24.00	45.33	35.82
February	10	27	37	7.1	27.03	46.23	40.11
March	16	31	47	9.2	34.04	53.71	48.71
April	10	26	36	7.8	27.78	49.32	47.28
May	6	35	41	11.7	14.63	43.09	51.58
June	12	43	55	13.6	21.82	46.51	53.01
July	15	103	118	27.1	12.71	35.68	50.14
August	10	74	84	14.3	11.90	28.91	42.98
September	8	45	53	3.9	15.09	22.54	32.95
October	8	26	34	4.1	23.53	35.60	34.38
November	7	7	14	1.5	50.00	60.53	35.82
December	1	9	10	2.7	10.00	36.84	31.52
Total/average	109	445	554	108.3	22.7	42.02	42.02

[a] Estimated number of females that were incorrectly diagnosed as non-pregnant when they were in fact pregnant (false negatives).

[b] Pregnancy rate calculated from interviews with local people before correction.

[c] Pregnancy rate calculated from interviews corrected based on the number of false negatives.

[d] Expected monthly pregnancy rates based on calculations using data from genitalia collections obtained in El Bizri et al. (2018).

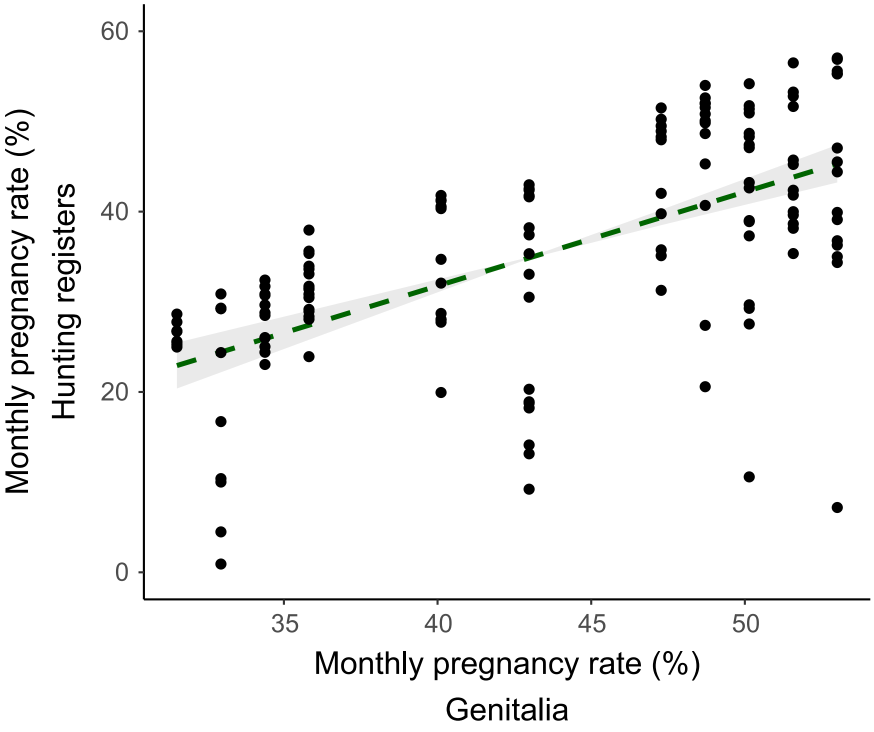


FIGURE 4 Relationship between the monthly pregnancy rates of lowland pacas *Cuniculus paca* determined by researchers through genitalia examinations and by hunting registers conducted by local people along 17 years in the Amanã Sustainable Development Reserve. Data on the pregnancy rates from genitalia were obtained from El Bizri et al. (2018)

TABLE 3 Details on the number of mature paca *Cuniculus paca* females hunted in the Amanã Sustainable Development Reserve per year with their reproductive status, the annual pregnancy rates obtained from hunting registers after a correction, the catch-per-unit-effort (CPUE; ind hunter^{-1} hr^{-1}) of nocturnal paca hunting events and the proportion of immatures (individuals < 5.5 kg) within the total number of individuals hunted. For more details on the calculations, see Table S2

	Number of mature females					
Year	Pregnant	Non-pregnant	Total	Pregnancy rate (%)	CPUE (ind hunter^{-1} hr^{-1})	Proportion of immatures (%)
2002	1	37	38	21.93	0.31	17.57
2003	1	31	32	22.43	0.27	12.05
2004	3	25	28	30.01	0.33	15.63
2005	5	22	27	37.82	0.31	12.24
2006	7	41	48	33.88	0.25	12.77
2007	8	32	40	39.30	0.21	3.37
2008	3	35	38	27.19	0.24	10.38
2009	6	18	24	44.30	0.21	8.57
2010	12	23	35	53.59	0.16	19.40
2011	7	19	26	46.22	0.27	10.00
2012	19	23	42	64.54	0.21	28.41
2013	9	30	39	42.38	0.22	12.66
2014	6	22	28	40.73	0.24	18.67
2015	5	15	20	44.30	0.18	25.81
2016	11	38	49	41.75	0.21	10.23
2017	3	9	12	44.30	0.28	22.73
2018	3	25	28	30.01	0.21	21.21
Total/average	109	445	554	39.10	0.24	15.39

in the butchering and cooking of animals (Bonwitt et al., 2017; MacDonald, 2007). This TEK on the reproductive cycles of species play a particularly important role in influencing the younger generation's capacity to detect and hunt animals, and can be used in local management strategies to avoid overhunting (Berkes, Colding, & Folke, 2000). Vieira, von Muhlen, and Shepard (2015), in a study in the Brazilian Amazon, indicated that hunters communally agreed not to take pregnant females or hunt during the reproductive season to guarantee the sustainability of game populations. In another example, hunters' impressions of the body condition of adult female barren-ground caribou *Rangifer tarandus* in Canada corresponded to the reproductive status of the animals after dissection (see Lyver & Gunn, 2004). Thus, if pregnant animals can be identified during hunting events, it may be possible to develop more effective management strategies that take into account the reproductive biology of the game species.

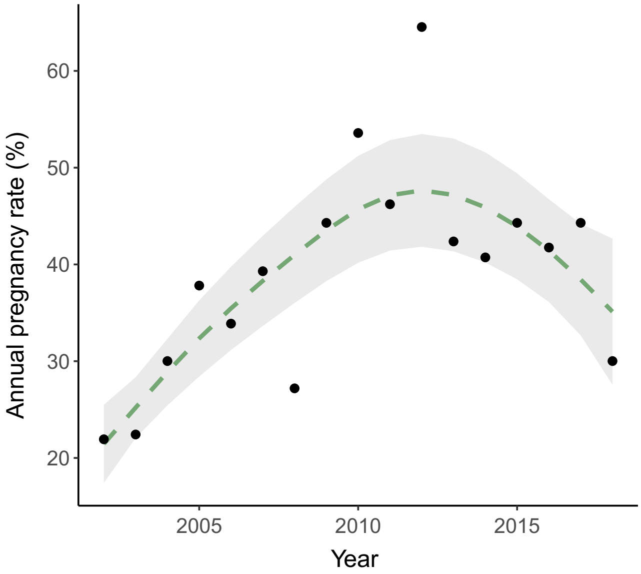


FIGURE 5 Temporal trends of annual pregnancy rates of lowland pacas *Cuniculus paca* determined by hunting registers conducted by local people along 17 years in the Amanã Sustainable Development Reserve

Several interviewees were unable to identify small conceptuses in pictures of pregnant genitalia. Though we acknowledge that a number of interviewees may have guessed their answers, we argue that they may have classified them as non-pregnant actually believing they were correct, given the difficulty in detecting early pregnancies. This is supported by the rate of correct responses for non-pregnant specimens, which was much higher than expected in a random guessing situation (90% vs. 50% respectively).

In our study, before the training, younger people were better at diagnosing pregnancy than older people. This could be explained by two factors: hunting frequency decreases with age, and therefore younger people may be more frequently in contact with hunted animals; and older people claimed that their weaker vision impaired them for properly seeing small conceptuses in the pictures, so younger people may have benefited from the method used in the study. Conversely, as exemplified in other citizen scientist studies (e.g. Ratnieks et al., 2016), we showed that after a short training session the difference between these age groups was overcome, and we significantly improved our interviewees' ability at diagnosing pregnancy, especially for early pregnancy stages.

Thus, we claim that local peoples' ability at diagnosing pregnancy after training is similar overall, and will be even higher when they are handling the specimens themselves, since they would be able to palpate the uterus in search for any sign of pregnancy, as they do while processing game. A previous training also allows for a direct calculation of pregnancy rates without the need for extensively correcting the data as we did here, considering that only a small proportion of pregnant individuals (around 10% from very early gestations) would

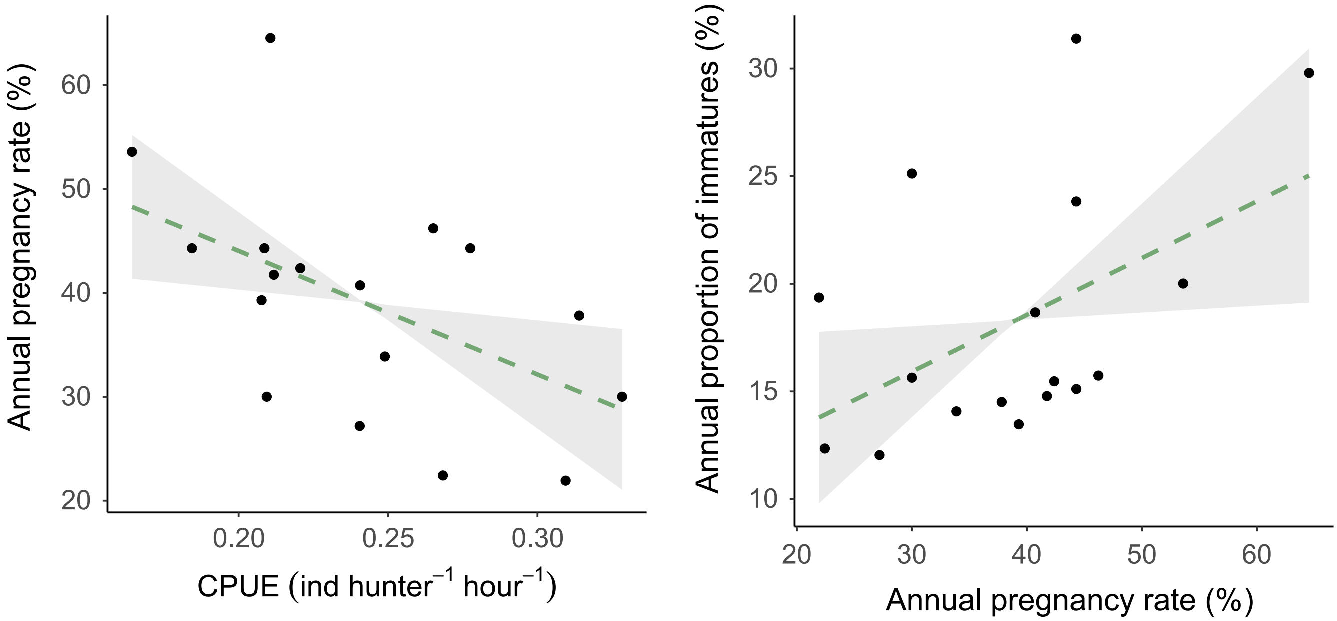


FIGURE 6 Relationship between the catch-per-unit-effort (CPUE) and annual proportion of immature individuals in hunted populations with the annual pregnancy rates of lowland pacas *Cuniculus paca* determined by hunting registers conducted by local people along 17 years (2002–2018) in the Amanã Sustainable Development Reserve

be incorrectly diagnosed, which is similar to the proportion of under-detected pregnancies by transabdominal ultrasonography (Mayor, López-Gatius, & López-Béjar, 2005). Our claim is supported by the strong match between local and laboratory diagnoses of pregnancy, which shows that citizen scientists in rural communities are able to collect accurate information of the natural cycle of the species in the wild.

Our citizen-science monitoring of annual reproductive rates has also proved to be reliable for assessing density-dependent responses of populations to hunting, which is difficult to obtain in the field. To our knowledge, this technique has not been applied for tropical game species before our study. In addition, the highest pregnancy rate value obtained in our study (64.5%) is similar to that obtained by Mayor et al. (2017) through genitalia collections in the Peruvian Amazon (62.8%), used to refine the intrinsic rate of population increase (r_{max}) in the paca. Mayor et al. (2017) estimated a minimal cost of US $2.75 per biological sample obtained through community-based collections. Therefore, in the present study, the citizen-science diagnosis of pregnancy generated savings of US $1,743.50 for the paca alone. Accordingly, we advocate that the method presented here can be useful for faster, easier, low-cost and accurate assessments of sustainability. Using this method to properly assess hunting impacts would aid more effective strategies to protect wildlife from overexploitation, and decision-makers and local leaders can be provided with accurate tools to implement tangible policies aimed at minimizing food insecurity.

Globally, around 45% of the protected areas are fully or co-managed by local people (Garnett et al., 2018; UNEP-WCMC & IUCN, 2016), and thus, subjected to direct human use of fauna. We believe that the present method shows great potential to be applied in several contexts around the world, and even improved when integrated into new technologies currently used in participatory monitoring systems, such as smartphones and specific monitoring software (see van Vliet et al., 2017).

Very few studies on life-history parameters of tropical species have relied on data obtained in the wild, and even fewer have obtained such data with the collaboration of local people, even though these are the main actors responsible to manage game populations. Here, we provide a tool to overcome the challenge of obtaining reproductive data on game species in the wild, offering a practicable method that improves sample size for wildlife research. We confirmed that the diagnosis of pregnancy in game specimens undertaken by local people integrated in a citizen-science program is useful to assess hunting effects and provides accurate data for evaluating hunting sustainability for tropical mammals. Finally, this study offers the opportunity for locally produced data to be integrated into educational programs and policies, providing significant information that can be used against food insecurity and wildlife overexploitation world-wide.

ACKNOWLEDGEMENTS

We sincerely thank the people from the Yavarí-Mirín River, Amanã Sustainable Development Reserve and Juruá River, without whom this work would not be possible. We also thank T.Q. Morcatty, L. Luiselli and an anonymous reviewer for useful comments on the manuscript, and C.L.B. Franco for building the map. This work was supported by the Gordon and Betty Moore Foundation, the National Council for Scientific and Technological Development (CNPq), the IVITA, the Museo de la Universidad Nacional de la Amazonía Peruana, the Earthwatch Institute and the Fundación Autónoma Solidaria.

AUTHORS' CONTRIBUTIONS

This work is part of H.R.E.B. doctoral studies, supervised by J.E.F. and P.M.; H.R.E.B. and P.M. conceived the project and designed the methodology; H.R.E.B., L.P.L., J.V.C.-S., C.F.A.V.N., J.V. and P.M. collected the data; H.R.E.B., J.E.F. and P.M. analysed the data; H.R.E.B., J.E.F., L.P.L. and P.M. led the writing of the manuscript. All the authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are available via the PANGAEA Data Publisher at https://doi.pangaea.de/10.1594/PANGAEA.906209 (El Bizri, Fa, Lemos, et al., 2019).

ORCID

Hani R. El Bizri https://orcid.org/0000-0003-1524-6292
John E. Fa https://orcid.org/0000-0002-3611-8487
João V. Campos-Silva https://orcid.org/0000-0003-4998-7216
Pedro Mayor https://orcid.org/0000-0001-5297-792X

REFERENCES

Albuquerque, U. P., da Cunha, L. V. F. C., De Lucena, R. F. P., & Alves, R. R. N. (Eds.) (2014). *Methods and techniques in ethnobiology and ethnoecology* (p. 1537). New York, NY: Springer.

Berkes, F., Colding, J., & Folke, C. (2000). Rediscovery of traditional ecological knowledge as adaptive management. *Ecological Applications*, *10*(5), 1251–1262. https://doi.org/10.1890/1051-0761(2000)010[1251:ROTEKA]2.0.CO;2

Bonney, R., Shirk, J. L., Phillips, T. B., Wiggins, A., Ballard, H. L., Miller-Rushing, A. J., & Parrish, J. K. (2014). Next steps for citizen science. *Science*, *343*(6178), 1436–1437. https://doi.org/10.1126/science.1251554

Bonwitt, J., Kandeh, M., Dawson, M., Ansumana, R., Sahr, F., Kelly, A. H., & Brown, H. (2017). Participation of women and children in hunting activities in Sierra Leone and implications for control of zoonotic infections. *PLoS Neglected Tropical Diseases*, *11*(7), e0005699. https://doi.org/10.1371/journal.pntd.0005699

Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods & Research*, *33*(2), 261–304. https://doi.org/10.1177/0049124104268644

Coad, L., Fa, J. E., Abernethy, K., van Vliet, N., Santamaria, C., Wilkie, D., … Nasi, R. (2019). *Towards a sustainable, participatory and inclusive wild meat sector*. Bogor, Indonesia: CIFOR.

da Cunha, M. C. (2009). *'Culture' and culture: Traditional knowledge and intellectual rights*. Chicago, IL: Prickly Paradigm Press.

Danielsen, F., Jensen, P. M., Burgess, N. D., Altamirano, R., Alviola, P. A., Andrianandrasana, H., … Young, R. (2014). A multicountry assessment of tropical resource monitoring by local communities. *BioScience*, *64*(3), 236–251. https://doi.org/10.1093/biosci/biu001

Dickinson, J. L., Zuckerberg, B., & Bonter, D. N. (2010). Citizen science as an ecological research tool: Challenges and benefits. *Annual Review of Ecology, Evolution, and Systematics*, *41*, 149–172. https://doi.org/10.1146/annurev-ecolsys-102209-144636

El Bizri, H. R., Fa, J. E., Bowler, M., Valsecchi, J., Bodmer, R., & Mayor, P. (2018). Breeding seasonality in the lowland paca (*Cuniculus paca*) in Amazonia: Interactions with rainfall, fruiting, and sustainable hunting.

Journal of Mammalogy, *99*(5), 1101–1111. https://doi.org/10.1093/jmammal/gyy102

El Bizri, H. R., Fa, J. E., Lemos, L. P., Vasconcelos Neto, C. F. A., Campos-Silva, J. V., Vasecchi, J., … Mayor, P. (2019). Data from: Involving local communities for effective citizen science: Determining game species' reproductive status to assess hunting effects in tropical forests. *PANGAEA*. https://doi.pangaea.de/10.1594/PANGAEA.906209

El Bizri, H. R., Fa, J. E., Valsecchi, J., Bodmer, R., & Mayor, P. (2019). Age at sexual maturity, first parturition and reproductive senescence in wild lowland pacas (*Cuniculus paca*): Implications for harvest sustainability. *Animal Reproduction Science*, *205*, 105–114. https://doi.org/10.1016/j.anireprosci.2019.04.009

El Bizri, H. R., Monteiro, F. O. B., de Andrade, R. D. S., Valsecchi, J., de Araújo Guimarães, D. A., & Mayor, P. (2017). Embryonic and fetal morphology in the lowland paca (*Cuniculus paca*): A precocial hystricomorph rodent. *Theriogenology*, *104*, 7–17. https://doi.org/10.1016/j.theriogenology.2017.08.004

El Bizri, H. R., Morcatty, T. Q., Lima, J. J., & Valsecchi, J. (2015). The thrill of the chase: Uncovering illegal sport hunting in Brazil through YouTube™ posts. *Ecology and Society*, *20*(3). https://doi.org/10.5751/es-07882-200330

El Bizri, H. R., Morcatty, T. Q., Valsecchi, J., Mayor, P., Ribeiro, J. E., Vasconcelos Neto, C. F., … Fa, J. E. (2020). Urban wild meat consumption and trade in central Amazonia. *Conservation Biology*, *34*(2), 438–448. https://doi.org/10.1111/cobi.13420

Fragoso, J. M., Levi, T., Oliveira, L. F., Luzar, J. B., Overman, H., Read, J. M., & Silvius, K. M. (2016). Line transect surveys underdetect terrestrial mammals: Implications for the sustainability of subsistence hunting. *PLoS ONE*, *11*(4), e0152659. https://doi.org/10.1371/journal.pone.0152659

Garnett, S. T., Burgess, N. D., Fa, J. E., Fernández-Llamazares, Á., Molnár, Z., Robinson, C. J., … Collier, N. F. (2018). A spatial overview of the global importance of Indigenous lands for conservation. *Nature Sustainability*, *1*(7), 369. https://doi.org/10.1038/s41893-018-0100-6

Guimarães, D. A. D. A., Bastos, L. V., Ferreira, A. C. S., Luz-Ramos, R. S., Ohashi, O. M., & Ribeiro, H. L. (2008). Reprodutive characteristics of the female paca (*Agouti paca*) raised in captivity. *Acta Amazonica*, *38*(3), 531–538.

Lima, M., & Jaksic, F. M. (1998). Delayed density-dependent and rainfall effects on reproductive parameters of an irruptive rodent in. *Acta Theriologica*, *43*(3), 225–234.

Lyver, P. O. B., & Gunn, A. (2004). Calibration of hunters' impressions with female caribou body condition indices to predict probability of pregnancy. *Arctic*, *57*(3), 233–241. https://doi.org/10.14430/arctic500

MacDonald, K. (2007). Cross-cultural comparison of learning in human hunting. *Human Nature*, *18*(4), 386–402. https://doi.org/10.1007/s12110-007-9019-8

Marrocoli, S., Nielsen, M. R., Morgan, D., van Loon, T., Kulik, L., & Kühl, H. (2019). Using wildlife indicators to facilitate wildlife monitoring in hunter-self monitoring schemes. *Ecological Indicators*, *105*, 254–263. https://doi.org/10.1016/j.ecolind.2019.05.050

Mayor, P., El Bizri, H., Bodmer, R. E., & Bowler, M. (2017). Assessment of mammal reproduction for hunting sustainability through community-based sampling of species in the wild. *Conservation Biology*, *31*(4), 912–923. https://doi.org/10.1111/cobi.12870

Mayor, P., Guimarães, D. A., & López, C. (2013). Functional morphology of the genital organs in the wild paca (*Cuniculus paca*) female. *Animal Reproduction Science*, *140*(3–4), 206–215. https://doi.org/10.1016/j.anireprosci.2013.06.010

Mayor, P., López-Gatius, F., & López-Béjar, M. (2005). Integrating ultrasonography within the reproductive management of the collared peccary (*Tayassutajacu*). *Theriogenology*, *63*(7), 1832–1843. https://doi.org/10.1016/j.theriogenology.2004.08.007

Mendes-Oliveira, A. C., de Maria, S. L., de Lima, R. C. S., Fernandes, A. S., de Almeida, P. C., Montag, L. F., & de Carvalho Jr., O. (2012). Testing simple criteria for age estimation of six hunted mammal species in the Brazilian Amazon. *Mastozoología Neotropical*, *19*(1), 105–116.

Milner-Gulland, E. J., & Akçakaya, H. R. (2001). Sustainability indices for exploited populations. *Trends in Ecology & Evolution*, *16*(12), 686–692. https://doi.org/10.1016/S0169-5347(01)02278-9

Peres, C. A. (2000). Effects of subsistence hunting on vertebrate community structure in Amazonian forests. *Conservation Biology*, *14*(1), 240–253. https://doi.org/10.1046/j.1523-1739.2000.98485.x

Pocock, M. J., Newson, S. E., Henderson, I. G., Peyton, J., Sutherland, W. J., Noble, D. G., … Roy, D. B. (2015). Developing and enhancing biodiversity monitoring programmes: A collaborative assessment of priorities. *Journal of Applied Ecology*, *52*(3), 686–695. https://doi.org/10.1111/1365-2664.12423

Ratnieks, F. L., Schrell, F., Sheppard, R. C., Brown, E., Bristow, O. E., & Garbuzov, M. (2016). Data reliability in citizen science: Learning curve and the effects of training method, volunteer background and experience on identification accuracy of insects visiting ivy flowers. *Methods in Ecology and Evolution*, *7*(10), 1226–1235. https://doi.org/10.1111/2041-210X.12581

Rist, J., Milner-Gulland, E. J., Cowlishaw, G. U. Y., & Rowcliffe, M. (2010). Hunter reporting of catch per unit effort as a monitoring tool in a bushmeat-harvesting system. *Conservation Biology*, *24*(2), 489–499. https://doi.org/10.1111/j.1523-1739.2010.01470.x

Stasinopoulos, D. M., & Rigby, R. A. (2007). Generalized additive models for location scale and shape (GAMLSS) in R. *Journal of Statistical Software*, *23*(7), 1–46. https://doi.org/10.18637/jss.v023.i07

Steger, C., Butt, B., & Hooten, M. B. (2017). Safari Science: Assessing the reliability of citizen science data for wildlife surveys. *Journal of Applied Ecology*, *54*(6), 2053–2062. https://doi.org/10.1111/1365-2664.12921

UNEP-WCMC & IUCN. (2016). *Protected planet report 2016*. Cambridge, UK: UNEP-WCMC and IUCN.

Valsecchi, J., El Bizri, H. R., & Figueira, J. E. C. (2014). Subsistence hunting of *Cuniculus paca* in the middle of the Solimões River, Amazonas, Brazil. *Brazilian Journal of Biology*, *74*(3), 560–568. https://doi.org/10.1590/bjb.2014.0098

van Vliet, N., Sandrin, F., Vanegas, L., L'haridon, L., Fa, J. E., & Nasi, R. (2017). High-tech participatory monitoring in aid of adaptive hunting management in the Amazon. *Unasylva*, *68*(249), 53–62.

Vieira, M. A. R. M., von Muhlen, E. M., & Shepard Jr., G. H. (2015). Participatory monitoring and management of subsistence hunting in the Piagaçu-Purus reserve, Brazil. *Conservation and Society*, *13*(3), 254–264. https://doi.org/10.4103/0972-4923.170399

Weinbaum, K. Z., Brashares, J. S., Golden, C. D., & Getz, W. M. (2013). Searching for sustainability: Are assessments of wildlife harvests behind the times? *Ecology Letters*, *16*(1), 99–111. https://doi.org/10.1111/ele.12008

Zhang, X., Zhu, C., Lin, H., Yang, Q., Ou, Q., Li, Y., … Wang, H. (2007). Wild fulvous fruit bats (*Rousettus leschenaulti*) exhibit human-like menstrual cycle. *Biology of Reproduction*, *77*(2), 358–364. https://doi.org/10.1095/biolreprod.106.058958

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: El Bizri HR, Fa JE, Lemos LP, et al. Involving local communities for effective citizen science: Determining game species' reproductive status to assess hunting effects in tropical forests. *J Appl Ecol*. 2021;58:224–235. https://doi.org/10.1111/1365-2664.13633