

Toward a quantification of risks at the nexus of conservation and health: The case of bushmeat markets in Lao PDR

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▶ **To cite this version:**

Mathieu Pruvot, Kongsy Khammavong, Phonesavanh Milavong, Chanfong Philavong, Daniel Reinharz, et al.. Toward a quantification of risks at the nexus of conservation and health: The case of bushmeat markets in Lao PDR. Science of the Total Environment, 2019, 676, pp.732 - 745. 10.1016/j.scitotenv.2019.04.266 . pasteur-03214747

HAL Id: pasteur-03214747
https://riip.hal.science/pasteur-03214747

Submitted on 2 May 2021

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Science of the Total Environment 676 (2019) 732–745

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

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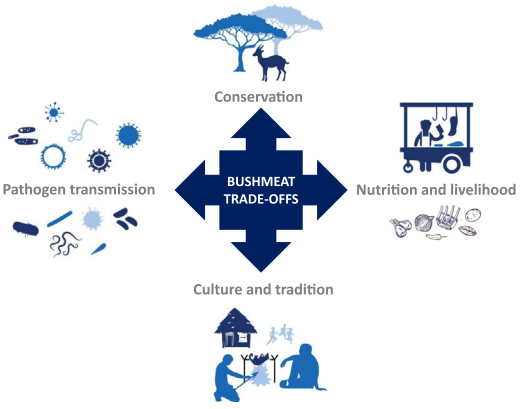
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HIGHLIGHTS

- Bushmeat trade in Lao PDR is considerable and likely exceeds sustainable levels.
- Bushmeat consumption in urban centers is not a necessity but a preference.
- High contact rates between consumers and bushmeat add to the transmission risk.
- Integrated assessment of conservation, food security and food safety risks needed

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 17 December 2018
Received in revised form 16 April 2019
Accepted 17 April 2019
Available online 22 April 2019

Editor: Damia Barcelo

ABSTRACT

Trade of bushmeat and other wildlife for human consumption presents a unique set of challenges to policy-makers who are confronted with multiple trade-offs between conservation, food security, food safety, culture and tradition. In the face of these complex issues, risk assessments supported by quantitative information would facilitate evidence-based decision making.

We propose a conceptual model for disease transmission risk analysis, inclusive of these multiple other facets. To quantify several processes included in this conceptual model we conducted questionnaire surveys with wildlife consumers and vendors in semi-urban centers in Lao People's Democratic Republic (Lao PDR, Laos) and direct observations of consumer behaviors. Direct observation of market stalls indicated an estimated average of 10 kg

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https://doi.org/10.1016/j.scitotenv.2019.04.266
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Keywords:
Bushmeat consumption
Risk analysis
Zoonotic diseases
Wildlife conservation
One Health
Food security

bushmeat biomass per stall per hour. The socio-demographic data suggested that consumption of bushmeat in urban areas was not for subsistence but rather driven by dietary preference and tradition. Consumer behavioral observations indicated that each animal receives an average of 7 contacts per hour. We provide other key parameters to estimate the risk of disease transmission from bushmeat consumption and illustrate their use in assessing the total public health and socio-economic impact of bushmeat consumption.
Pursuing integrative approaches to the study of bushmeat consumption is essential to develop effective and balanced policies that support conservation, public health, and rural development goals.

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1. Introduction

Wildlife trade and the consumption of wild meat (or "bushmeat") have increasingly been scrutinized for their role in zoonotic pathogen emergence into human populations (Chomel et al., 2007; Karesh et al., 2005; Kilonzo et al., 2013; Swift et al., 2007; Wolfe et al., 2005; Greatorex et al., 2016). There is growing evidence for the presence of zoonotic pathogens in traded and consumed bushmeat (Kilonzo et al., 2013; Kurpiers et al., 2016; Schoder et al., 2015; Smith et al., 2012), and pathogen spillovers into humans have repeatedly occurred as a result of wild meat consumption (Calattini et al., 2007; Kalish et al., 2005; Mouinga-Ondeme et al., 2012; Wolfe et al., 2004). When the anthropic factors (i.e. socio-economic, behavioral) and the pathogen characteristics allowed it (Wolfe et al., 2005; Plowright et al., 2017), some of these spillover events resulted in significant outbreaks and pandemics. Indeed, the contacts of hunters with great ape carcasses likely caused Ebola virus spillovers to humans and subsequent human outbreaks in Gabon and the Democratic Republic of Congo (Georges-Courbot et al., 1997; Leroy et al., 2004). The 2002–2003 Severe Acute Respiratory Syndrome-Coronavirus (SARS-Co) outbreak was linked to contacts with traded masked palm civets (*Paguma larvata*) likely infected from a bat reservoir (Bell et al., 2004; Li et al., 2005; Wang et al., 2006). Notoriously, the emergence of Human Immunodeficiency Viruses (HIV) was linked to repeated spillover of Simian Immunodeficiency Viruses from sooty mangabeys (*Cercocebus atys*) and chimpanzees (*Pan troglodytes*), including the pandemic virus from the HIV1-group M (Hahn et al., 2000). Moreover, the high contamination of carcasses and the lack of inspection and cold chain increase the risk that bushmeat carries and transmits diverse foodborne pathogens (Bachand et al., 2012).

The impact of wildlife hunting, trade and consumption are obviously not limited to zoonotic disease transmission. The increasing demand for wild meat, combined with intense demographic, environmental, and climatic changes, is resulting in what is now referred to as the sixth mass extinction (Ceballos et al., 2015; Dirzo et al., 2014; Milner-Gulland and Bennett, 2003). The situation is particularly critical in the humid tropics where low productivity of tropical forest can only sustain levels of offtake well below current demand (Robinson and Bennett, 2004), resulting in large scale depletion and extirpation of wildlife species (Dirzo et al., 2014; Ripple et al., 2016), and eventually in "empty forests" (Harrison, 2011; Redford, 1992). The Lao People's Democratic Republic (Lao PDR, Laos) is following this path, with sparse but clear evidence of wildlife over-harvesting, even in protected areas (Claridge and Nooren, 2001; Clendon, 2001; Johnson et al., 2012; Krahn and Johnson, 2007). For instance, the estimated wild pig (*Sus scrofa*) and muntjac (*Muntiacus muntjak*) harvest across ten villages in the Nam Et-Phou Louey National Protected Area was at least 63% and 36% of the estimated standing biomass per year, respectively (Johnson et al., 2012), well above the estimated maximum sustainable yearly offtake of 10% for wild ungulates in tropical forests (Robinson and Bennett, 2004). As a result, decrease of wildlife abundance and local extirpation of species are observed across the region (Gomez and Shepherd, 2018; Harrison et al., 2016; Tungittiplakorn and Dearden, 2002; Vongkhamheng et al., 2013). Like in many other parts of Southeast Asia and the world (Mainka and Trivedi, 2002), over-harvest is amplified by the development of trade routes linking rural areas to urban centers (Clements et al., 2014), the replacement of traditional hunting equipment for more effective methods (e.g. riffles, electrified wire traps, poisoning), and an increase in food demand due to population growth (Clendon, 2001; Johnson et al., 2012; Krahn, 2005).

Indeed, the "bushmeat crisis" is also intricately linked to food security and the livelihood of rural communities (Arnold et al., 2011; Bennett, 2002; Cawthorn and Hoffman, 2015; Nasi et al., 2011; Rao and McGowan, 2002). In communities that derive a significant portion of their protein and micronutrients from bushmeat, as is the case in rural Laos (Johnson et al., 2012; Krahn, 2005; World Food Programme, 2007), losing access to wild meat (as a result of policy or wildlife depletion) could have severe adverse health effects, and increase food insecurity and malnutrition (Cawthorn and Hoffman, 2015; Golden et al., 2011). Some rural communities were also shown to derive significant livelihood from bushmeat trade (Schulte-Herbrüggen et al., 2013), although the structure of trade networks and the socio-demographic background of their actors are likely to influence the level of reliance on this activity for livelihood. Furthermore, for communities in which wildlife hunting and consumption has deep cultural, social and traditional roots, decreased access to wildlife may affect well-being (Johnson et al., 2003).

Therefore, it is clear that the hunting, trade, and consumption of wildlife are concurrently concerns for zoonotic disease transmission, significant sources of nutrients and/or livelihood for some communities, and major causes of biodiversity loss. On a policy level, these aspects can appear as competing priorities between wildlife conservation, sustainable use, food safety, food security, and cultural aspects. In Southeast Asia, these challenges have been further complicated over the past 15–20 years by a shift from subsistence hunting to wildlife trade in rural areas (Bell et al., 2004; Bennet and Robinson, 2000; Duckworth et al., 1999), along with an urbanization of wildlife consumption (Singh, 2008). It was previously suggested that wildlife consumption by urban dwellers represents a greater risk for disease emergence as the wildlife pathogens funneled to these urban centers have more opportunities for cross-species transmission, and get introduced into densely populated areas of mostly naïve individuals (Swift et al., 2007). Furthermore, the blurring of boundaries between subsistence hunting and wildlife trade with urban communities (Bennet and Robinson, 2000; Nasi et al., 2008) challenges wildlife conservation and rural development policy to adequately address the tradeoff between wildlife protection and sustainable use (Krahn and Johnson, 2007; Singh, 2008). Indeed, maintaining sustainable subsistence hunting for communities that truly rely on these resources depends on the ability to reduce consumption in urban centers where alternatives protein sources are readily available (Rao and McGowan, 2002; Solly, 2004).

The management of these tradeoffs between food safety, food security and conservation, further complicated by the urbanization of bushmeat consumption requires integrative multi-disciplinary approaches, which initiatives such as One Health, EcoHealth, and Planetary Health may facilitate (Osofsky and Pongsiri, 2018). Furthermore, the formulation of effective evidence-based public health, conservation, and development policies has been hindered by the lack of qualitative and quantitative data across all of these issues. A risk analysis framework can be useful to the multi-disciplinary management of such complex systems, including the joint identification of problems and threats,

collection and integration of relevant data, and the facilitation of policy formulation (OIE - World Organisation for Animal Health and International Union for Conservation of Nature and Natural Resources, 2014). In particular, quantitative risk analysis (QRA) allows an evaluation of the probability of certain outcomes of interest, under variable and uncertain conditions, as a basis for decision making (Nauta, 2000), and may be particularly suitable to explore systems with multiple tradeoffs, as long as sufficient quantitative data is available to characterize the system. QRA models have been used in diverse disciplines (Vose, 2008), but are particularly popular for food safety (Notermans and Teunis, 1996) and foreign animal disease risk assessments (Miller et al., 2017; Peeler et al., 2015). Although their application to the risk of disease transmission from bushmeat consumption and wildlife trade has been recommended (OIE - World Organisation for Animal Health and International Union for Conservation of Nature and Natural Resources, 2014), only a few instances exist to date (Franssen et al., 2017; Simons et al., 2016; Wooldridge et al., 2006). Given the flexibility of QRA methods such as Monte Carlo simulations, we further recommend their use as a tool for multi-disciplinary data integration for the evaluation of the multiple trade-offs of the bushmeat system.

In this study, we take a first step toward addressing the complexity of bushmeat consumption in urban centers in Laos. Although a full QRA is beyond the scope of this manuscript, we present a conceptual model of the QRA of the zoonotic disease transmission in the Lao bushmeat system, inclusive of the nutrition and conservation aspects. We then report on a number of surveys and direct observations aiming at filling information gaps identified during the development of this conceptual model. These surveys document essential quantitative information on demography, behaviors and practices of urban wildlife consumers and vendors, and detailed descriptions of wildlife-consumer interactions. Throughout the manuscript we provide estimates for key parameters that would be required to develop a full QRA model. We also report on the attitude and risk perception of wildlife consumers and vendors, as it is essential to the interpretation of behavioral data and the design of effective intervention strategies (e.g. education, policy). Finally, we discuss the policy relevance of both qualitative and quantitative information to the management of the tradeoffs between food safety, food security, and conservation.

2. Material and methods

2.1. Conceptual risk analysis model

We developed a conceptual model (Fig. 1) to illustrate the application of a QRA framework to the Lao bushmeat system. In a QRA context, the multiple tradeoffs mentioned earlier represent multiple threats for which risk must be assessed. Each threat can be conceptualized as the result of multiple processes (the nodes and links of Fig. 1) that emerge from the interaction of four components: wildlife, humans, human behaviors, and pathogens. While Fig. 1 is primarily focused on the risk of zoonotic disease transmission from wildlife to vendors and consumers, the processes related to other threats can be expanded as needed, allowing the integration of these perspectives within the QRA framework. Table 1 provides examples of processes and factors influencing other threats.

In this conceptual model, the wildlife/bushmeat distribution chain processes, made up of interacting human and wildlife components, drive the flow of wildlife in and out of the market through a number of intermediaries. It is also influenced by consumer behaviors (frequency and quantity of consumption) which create the demand for bushmeat. The time between each step of the distribution chain can also be useful in estimating the persistence of pathogens within an infected specimen. Within the market, behaviors and practices of vendors and consumers result in diverse interactions with bushmeat, and potential exposure to zoonotic pathogens. The quantity of traded bushmeat, the type of products sold (i.e. live, dead, dried, smoked), the time it takes to sell them, the handling of wildlife and bushmeat, their preparation (e.g. killing, dressing, cooking) according to preference and tradition, and finally their consumption determine the exposure of vendors and consumers to pathogens. For a given pathogen, a proportion of the animals entering the market are infected. Pathogen characteristics influence its persistence in the bushmeat and the dose-response for different transmission routes eventually determines the probability of infection.

For this disease transmission risk conceptual model (Fig. 1), data gaps were particularly significant regarding the bushmeat distribution chain (i.e. wildlife component), the socio-demographic background of

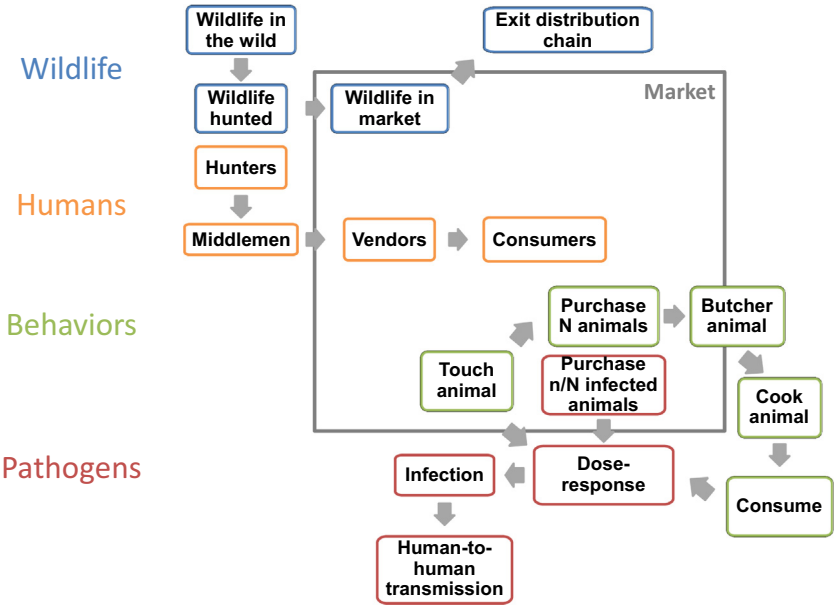


Fig. 1. Conceptual model for a multi-disciplinary quantitative risk analysis of zoonotic disease transmission from the bushmeat trade in Laos. The model shows the processes related to four components: wildlife (blue), humans (orange), behaviors (green), and pathogens (red). These components interact to produce key processes such as the distribution chain driving the flow of wildlife in and out of the market, the interactions of wildlife vendors and consumers with bushmeat driving their potential exposure to zoonotic pathogens, and the pathogen characteristics driving the prevalence, persistence and eventually the dose-response leading to infection.

Table 1
Examples of processes and factors influencing the risk of multiple hazards related to bushmeat trade and consumption, and corresponding variables documented in this study.

Hazard	Influencing processes/factors	Variables documented in this study (model component[a])
Wildlife depletion and species extinction	Level of wildlife offtake	
	Abundance of wildlife	
	Population dynamic	
	Law enforcement	Attitude of vendors toward law enforcement (B)
	Bushmeat species composition	Species preference (B)
	Demand for bushmeat products	Frequency and quantity of consumption per consumer (B)
		Frequency and quantity of bushmeat purchases (B)
Food insecurity	Nutritional needs	Frequency and quantity of consumption per consumer (B)
	Availability and acceptability of alternative sources of nutrients	Demographic characteristics of consumers (H)
		Motivations for bushmeat consumption (B)
Loss of livelihood	Profitability	Frequency and quantity of bushmeat purchases (B)
	Dependency on activity for livelihood	Demographic characteristics of vendors (H)
	Availability and acceptability of alternative sources of livelihood	Demographic characteristics of vendors (H)
Loss of cultural identity	Demographic characteristics	Demographic characteristics of vendors and consumers (H)
	Perception	Perception of conservation, legal, and disease risks (H)
	Motivations for wildlife hunting/trade/consumption	Motivations for wildlife consumption (B)
Pathogen transmission	Pathogen characteristics (host species, prevalence, persistence, infectivity, virulence)	Bushmeat species preference (B)
	Decay of pathogen along distribution chain and food preparation	Distribution chain steps and time between steps (W)
		Preparation and cooking preference (B)
	Types and intensity of contacts between humans and wildlife	Contact rate (B)
		Frequency of consumption (B)
		Quantity bushmeat purchased per consumer (B)
	Wildlife disease risk perception	Knowledge and Risk perception for wildlife diseases (B)

[a] Model component: W = Wildlife; H = Human; B = Behavior; P = Pathogen.

vendors and consumers (i.e. human component), and their perception, attitude and practices toward bushmeat (i.e. behavior component). Surveys were set up in wildlife markets to fill these data gaps. Mindful of the necessity for multi-disciplinary integration, we also identified a range of information that would be complementary and allow exploring some aspects of the multiple trade-offs. Table 1 summarizes the variables that were informed during these surveys and how they related to each threat, process or influencing factor, and model component.

2.2. Consumer surveys

In this manuscript, we broadly define the term "consumer" as any market visitor who shows interest in, comes in contact with, purchases, or actually consumes bushmeat. Consumer surveys were conducted in 13 markets previously identified as hotspots for wildlife trade (Greatorex et al., 2016) or more recently discovered as having high volumes of bushmeat during routine monitoring of markets (unpublished data). Between October 2016 and January 2017, each market was visited twice during periods of high attendance by consumers, based on preliminary observations (Greatorex et al., 2016). Observers were posted at strategic locations in each market that allowed observation of market consumers approaching stalls or purchasing bushmeat. Given the illegal and sensitive nature of wildlife consumption, consumers were not approached until they exited the market. Using a standard scripted introduction we briefly explained the purpose of the study. A total of 182 of 226 consumers (81%) that were approached provided written consent to be interviewed, and were asked 26 questions documenting general socio-demographic information (e.g. age, occupation, origin, salary, education level) (Supplementary document 1), motivations and practices regarding bushmeat consumption, and knowledge and risk perception of wildlife disease. Five staff trained for reliability and consistency conducted the interviews that lasted 10–20 min. For wildlife consumers who declined to participate, minimal essential information was determined (age, sex, origin, profession, purchased items) or guessed when necessary (age, sex). We compared respondents and non-respondents on this information and no difference was observed in their sex, age distribution, nationality, ethnicity (for the respondent of Lao nationality), and the distance between the market and their main living location (Supplementary document 2, Table S1). The remaining of this manuscript, therefore, focuses on the 182 respondents who accepted to participate in the full interview.

Wildlife consumer interviews documented their bushmeat species preference and yearly frequency of consumption, as well as the proportion of wildlife purchased live. Consumers were asked if they consumed raw meat and what were their cooking preference (i.e. rare, medium, or well-done). Awareness and knowledge of wildlife disease were assessed, as well as the perceived risk of disease transmission from wild meat. The association of this perceived risk with sex, education and prior knowledge of wildlife diseases was assessed using ordinal logistic regressions. Finally, the interview documented the motivations for bushmeat consumption. This included a description of the use of bushmeat, the perceived health benefits, the effect of social and familial environment (as incentive or disincentive), and the willingness to stop consuming wildlife in relation to disease risk, conservation risk, and legal risk.

2.3. Behavioral observations

During the same market visits described above for consumer surveys, we randomly selected stalls that displayed wildlife or bushmeat for sale to estimate contact rates. For each stall, individual animals, batches of animals, or animal parts were counted and identified by species or closest level of taxonomic classification (hereafter, species). From afar (10–15 m), we then observed and counted contacts established by consumers with these items, for a period of 20 min per stall. Most items were individual animals and contacts were counted for each animal, but when animals were sold as parts (e.g. wild boar, muntjac) or batches (e.g. small squirrels, rats, and bats), contacts were counted per part or per batch. For a subset of these observations, the sex of the consumer making contact with the animal was recorded. Contact counts were conducted by two observers who logged 53 h of direct observation. When restricted to fresh and live animals (i.e. excluding dry, smoked, or pickled animals), this totaled 211 animal-hours of observations (e.g. one animal-hour could represent three animals observed for 20 min each). Average contact rates were estimated by species and by the sex of the consumer. Distributions were also fitted to the number of contacts per observation period (20 min) for several species groups: rodents (excluding live bamboo rats, giant flying squirrels, and porcupines), small carnivores, reptiles, ungulates, birds, and bamboo rats.

Concurrently, if any consumer purchased wildlife during the observation time, we recorded the species and number of purchased animals. Over a total of 51 stall-hours of observation (one stall-hour is defined as one market stall observed for 1 h), we reported the total number of purchases (i.e. clients) and purchased animals per species. Based on these counts, the total amount of purchased biomass per species was estimated using previously published average weight of each species (Greatorex et al., 2016). Based on these total amounts of observed purchased meat, we estimated the yearly total volume and retail value for an average market. We considered an average market to include five stalls and about 4 h of peak activity per day (comparable to activity levels when observations were carried out) and to be open daily (unpublished data), for a yearly total of 7300 stall-hours. The retail value was calculated based on published average value for each species (Greatorex et al., 2016).

As a proxy for exposure of wildlife consumers to bushmeat, we estimated distributions of the quantity of purchased wildlife per consumer and per purchase. This was estimated for small-sized rodents such as rats and squirrels (excluding bamboo rats and giant flying squirrels) as a number of purchased animals, and for all species as an amount of meat purchased (in kg).

2.4. Vendor surveys

Questionnaire surveys were developed and administered to wildlife vendors in three large markets located in Xieng-Khouang (Northern), Bolikhamxay (Centre), and Salavanh (Southern) provinces. These three markets were selected based on volume of traded wildlife and to provide a diverse representation of markets in Laos (Greatorex et al., 2016). We conducted surveys between April and June 2016. Forty wildlife vendors were enrolled, and five declined to participate. Here we focus on the socio-demographic characteristics of wildlife vendors and practices regarding wildlife trade that were documented by this questionnaire.

As the risk of disease transmission is expected to be different for live and dead animals, vendors were asked to estimate the proportion of animals that they sell live. The timeline of the bushmeat distribution chain is essential to understand the persistence of zoonotic pathogens in live animals or carcasses. Vendors were asked to estimate the time between hunting/capture and arrival on market, and the "shelf-life" of the wildlife products (time before the product is sold), for both live and dead animals. For each estimated duration, vendors were asked to provide a minimum, maximum and most likely value. Vendors were also asked to document their handling of both live and dead animals who were not sold on the first market day.

2.5. Distribution fitting, parameter estimates, and simulation

We provided descriptive statistics for all variables of interest, and a subset of them which were considered key to building a QRA model were reported as *parameter x* throughout the manuscript. Dichotomous and categorical variables were reported with (binomial and multinomial, respectively) confidence intervals as an indication of uncertainty. Discrete and continuous variables were fitted with the various relevant distributions using the R package fitdistrplus (Delignette-Muller and Dutang, 2015) and the best fits between candidate distributions based on the Akaike Information Criteria (AIC) were reported. For these distributions, 95% confidence intervals around distribution parameters were estimated using bootstrap sampling ($n = 1001$ iterations), as indication of parameter uncertainty.

A number of variables were documented in the wildlife vendor interviews as PERT (Program Evaluation and Review Technique) distributions following elicitation of a minimum, maximum, and most likely value (Clark, 1962). There is no consensus method to aggregate opinion elicited from multiple experts and different methods vary greatly in the final output distribution (Stärk et al., 2000; Vose, 2008). For each question of this format, we simulated a combined distribution from all of the individual PERT distributions with equal weights and fitted a continuous distribution to this simulated data.

To illustrate the use of these parameters in the context of a QRA, we modeled the yearly protein intake from wildlife meat consumption. We simulated a yearly number of consumption events for 1000 wildlife consumers based on the distribution of consumption frequency obtained from the consumer survey (*parameter 2*), and drew a weight of meat for each purchase based on the distribution of weight of meat per purchase obtained from the direct observations (*parameter 6*) (appropriate in absence of significant correlation between frequency and weight of purchase). The yearly total weight of wildlife meat was summed for each simulated consumer. This yearly total weight was compared to the yearly average of per capita total domestic meat consumption for Lao PDR (FAOSTAT, 2018). We also estimated the proportion of yearly protein requirements based on an assumed 30% protein content of cooked bushmeat (US Department of Agriculture, 2018), a recommended dietary allowance (RDA) of 0.8 g protein/kg body weight/day (Trumbo et al., 2002), and an assumed body weight of 60 kg.

3. Results

3.1. Who are wildlife vendors and consumers?

All 35 wildlife vendors that were interviewed were females with ages ranging from 25 to 65 (median = 40). Two vendors reported hunting the animal themselves, while the rest reported purchasing animals directly from a hunter (49%), from another vendor (11%) or from a middleman (34%), indicating that the majority of wildlife sold in the markets had already transited through at least one additional person. We found two types of wildlife vendors in the market, vendors holding a stall at a permanent location in the market (40%) and occasional vendors displaying products on temporarily installed mats (60%). The group of occasional vendors included eight ethnic minority groups compared to three ethnic groups represented among permanent vendors. The occasional vendors used shorter distribution channels (Wilcoxon rank sum test, $p = 0.058$) and came from further away (Wilcoxon rank sum test, $p = 0.003$). However, 34 (97%) wildlife vendors came from less than 10 km away from the market location. Overall, 23 (66%) wildlife vendors reported that this was their main professional activity. Farming was the main professional activity for 9 (26%) vendors. Prior to becoming involved in wildlife trade, wildlife vendors reported they were primarily farmers (74%) or traders in other goods (17%).

Demographic characteristics were documented from 182 wildlife consumer who were interviewed (Table 2). Mean and median duration of education for wildlife consumers were nine years and range spanned primary, secondary, and higher education. In this sample of wildlife consumers, males had longer duration of education than females ($\beta = 1.9$, $p = 0.01$) (Supplementary document 2, Fig. S1, B). The three most represented occupations were traders, farmers, and government officials, representing a total of 54% of wildlife consumers (Supplementary document 2, Fig. S1, B). All monthly income categories were represented in the interviewed wildlife consumers, with the mode in the USD 100–350 category (41% of respondents), followed by the USD 350–700 (25%). Low (USD 50–100) and very low (<USD 50) income categories represented 10.9% and 11.5%, respectively, while the income of the rest of the consumers (11.4%) ranged in the four categories between USD 700 and > USD 4600 (Supplementary document 2, Fig. S1, C).

3.2. What and how much is sold and consumed?

All vendors reported selling both live and dead animals. They were asked to estimate an average proportion of live animals among sold animals, which ranged between 0.1 and 0.5 with median of 0.2, and a beta distribution was fitted to these estimates (Table 3, *parameter 1*).

Table 2
Demographic characteristics of wildlife consumers interviewed in urban centers in Laos.

	Sex (Female)	Nationality (Lao)	Ethnicity (Lao Loum among Lao nationality)	Age (Year)	Distance from market to main residence (km)	Education (years)
Sample size (n=)	182	182	149	182	182	182
Mean/proportion	40%	81%	89%	43.6	86	9.3
Median	–	–	–	42	19	9
Minimum	–	–	–	19	0.05	0
Maximum	–	–	–	91	800	19
Standard deviation	–	–	–	14.5	146	5.0
95% confidence interval	33–48%	75–87%	82–93%	41.5–45.7	64–108	8.5–10.1

From the responding wildlife consumers, the reported yearly frequency of consumption ranged from 0 to 365 (median = 5, mean = 25, and SD = 49) days a year, and was best approximated by a negative binomial distribution (Table 3, *parameter 2*). Sixty-one percent (61% [95% CI: 54–68]) indicated that they only purchased dead animals while the rest purchased both live and dead animals (Table 3, *parameter 3*). Species reported to be the most purchased by wildlife consumers were squirrels, wild birds, wild boar, and muntjac by 59%, 34%, 25%, and 23% of respondents, respectively (Fig. 2A; refer to Supplementary document 3 for species designation). We also compared these reported preferences to the direct consumer observations during which we recorded the number of purchases per species, the number of purchased animals per species, and the total weight of biomass per species (Fig. 2B, C, and D, respectively). In all four measures of species preference, unspecified squirrels were among the top five most consumed species of bushmeat. Unspecified wild birds, wild boar, muntjac, and small flying squirrels also frequently (in three of the four measures of preference) appeared among the top five preferred species.

The different rankings of species resulted from the inter-play between consumer preference, availability of the species on the market, and the average body mass of each species. Large-bodied animals represented the bulk of the total biomass sold with monitor lizard, muntjac, and wild boar reaching 160, 94, and 67 kg sales, purchased by 27, 37, and 36 consumers, respectively over 51.5 stall-hours of observation (Fig. 2D). The ranking according to the total number of individuals sold, indicated that wild birds, squirrels, and bats species incurred the greatest volume of offtake and trade. Total observed purchase amounts, by mass of meat and equivalent individuals are compiled by species in Table 4, along with the estimate for the yearly total volume and retail value for an average market. The total biomass sold during our observation (51.5 stall-hours) was 502 kg, or an average of 10 kg per stall-hour.

Table 3
Parameters estimates for key components of a quantitative risk analysis integrating public health, conservation, and nutrition considerations for the Lao bushmeat trade.

Parameter	Description	Data source	Distribution type	Distribution parameters [95% confidence interval][a]
Parameter 1	Proportion of traded animals sold alive	Vendor survey	Beta	alpha = 2.66 [1.85–4.57] beta = 7.88 [5.33–14.30]
Parameter 2	Yearly frequency of consumption	Consumer survey	Negative binomial	size = 0.47 [0.39–0.59] mu = 25.6 [20.6–31.4]
Parameter 3	Proportion consumers only purchasing dead animals (vs. a combination of dead and live animals)	Consumer survey	Binomial	*p* = 60.8 [54.0–68.1]
Parameter 4	Number of consumers per stall in 20 min period	Direct observations	Negative binomial	mu = 2.04 [1.67–2.43] size = 1.33 [0.91–2.17]
Parameter 5	Number of animals per purchase for small-sized rodents	Direct observations	Poisson	lambda = 2.28 [1.97–2.59]
Parameter 6	Amount of meat per purchase for all species (in kg)	Direct observations	Log Normal	mean = 0.75 [0.63–0.90] sd = 4.69 [4.14–5.30]
Parameter 7	Capture-to-market time for live animals (in days)	Vendor survey	Gamma	shape = 5.00 [4.78–5.23] rate = 3.06 [2.91–3.21]
Parameter 8	Time-on-market for live animals (in days)	Vendor survey	Weibull	shape = 1.77 [1.76–1.79] scale = 1.68 [1.68–1.70]
Parameter 9	Proportion of vendors keeping live animals at home if unsold the first day	Vendor survey	Binomial	*p* = 91% [75.8–97.8]
Parameter 10	Fate of live animals if unsold on first day: fed and returned to market (p1), killed and consumed (p2), or processed and sold at reduced price (p3)	Vendor survey	Multinomial	p1 = 54.3% [40–72.6] p2 = 22.9% [8.6–41.1] p3 = 22.9% [8.6–41.1]
Parameter 11	Hunting-to-market time for dead animals (in days)	Vendor survey	Gamma	shape = 15.1 [14.4–15.8] rate = 13.8 [13.3–14.5]
Parameter 12	Time-on-market for dead animals (in days)	Vendor survey	Gamma	shape = 3.03 [2.92–3.18] rate = 4.39 [4.19–4.60]
Parameter 13	Fate of unsold dead animals: eaten by vendor (p1), smoked (p2), sold discounted (p3)	Vendor survey	Multinomial	p1 = 54.3% [40.0–72.5] p2 = 31.4% [17.1–49.7] p3 = 14.3% [0.0–32.5]
Parameter 14	Proportion of consumers reporting eating bushmeat raw	Consumer survey	Binomial	*p* = 13.1% [8.7–19.3]
Parameter 15	Meat cooking preferences: raw (p1), medium (p2), well done (p3).	Consumer survey	Multinomial	p1 = 4.1% [1.2–8.2] p2 = 3.6% [0.6–7.6] p3 = 92.3% [89.3–96.4]
Parameter 16 to 22	Count of contacts per animal of different species groups in 20 min periods	Direct observations	Negative binomial	See Supplementary document 2, Table S2
Parameter 23	Proportion of wildlife vendor interrupting wildlife sales after being controlled by enforcement authorities	Vendor survey	Binomial	*p* = 57.1% [39.5–73.2]
Parameter 24	Duration of trade activity interruption after control by enforcement authorities (in days)	Vendor survey	Weibull	shape = 0.73 [0.50–0.97] scale = 9.36 [3.40–15.3]

[a] Exact 95% confidence were estimated for binomial and multinomial distributions; bootstrap 95% confidence intervals were used for all other distributions.

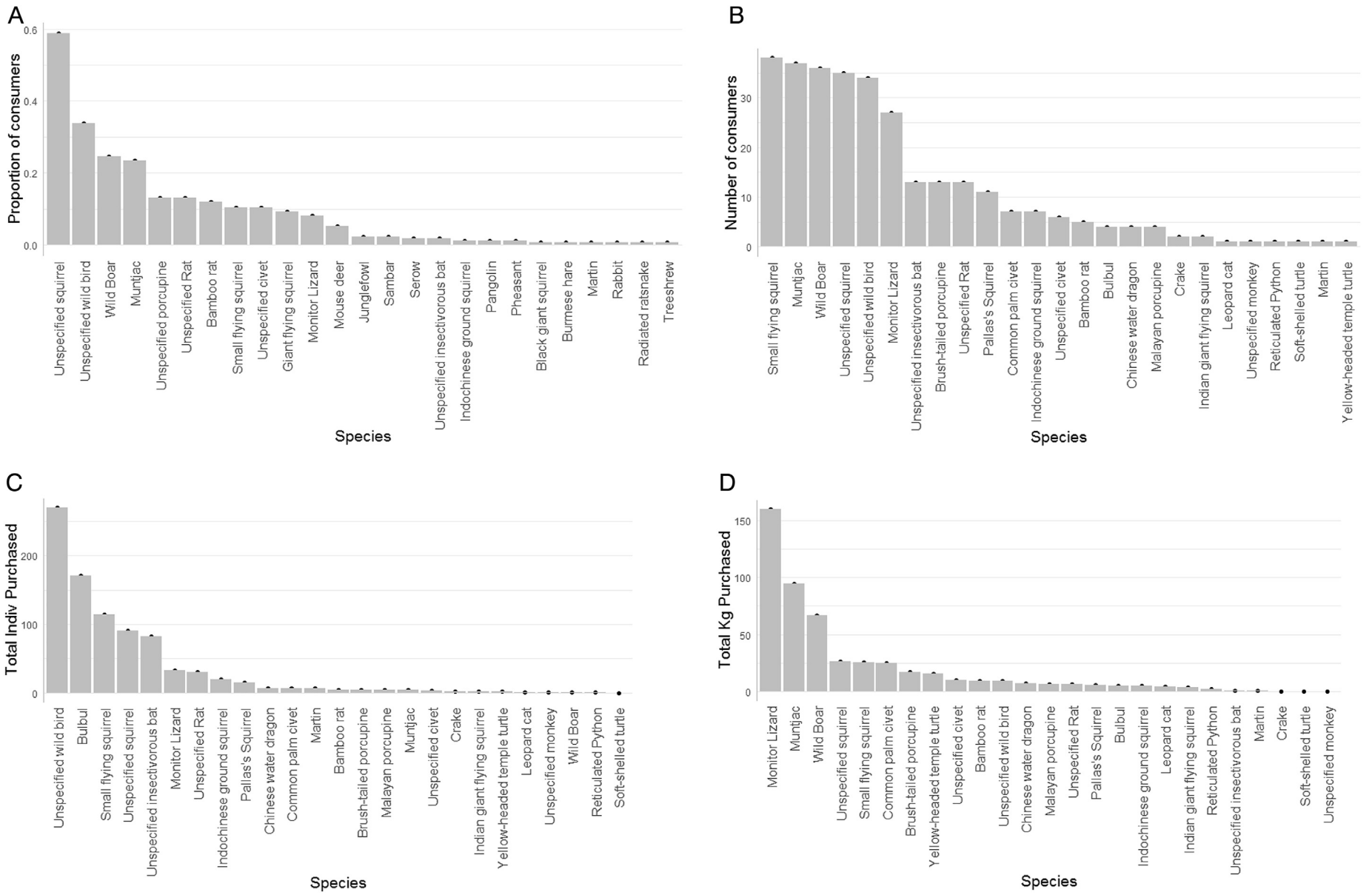


Fig. 2. Patterns of bushmeat purchase in Laos by A) reported preference of wildlife consumers for a species (proportion of respondents citing each species as preferred), B) direct market observation of the number of consumers per species, C) direct market observation of the total number of individuals purchased, and D) direct market observation of total weight of biomass purchased. Clarification on species designation provided in supplementary document 3.

The number of consumers per stall in a 20 min period ranged from 0 to 14, with a mean and standard deviation of 2.0 and 2.4, respectively. This was best approximated by a negative binomial distribution (Table 3, *parameter 4*).

Our proxies for the exposure of wildlife consumers to pathogen-carrying wildlife species consisted of the number of animals purchased or the weight of meat purchased by each consumer at each purchase. For small-sized rodents, the number of individuals purchased each time ranged between 1 and 24 with a median of 2, which was approximated with a Poisson distribution (Table 3, *parameter 5*). When considering all species, the median amount of meat for each purchase was 1 kg (Table 3, *parameter 6*).

Based on the estimated distributions of the frequency of bushmeat consumption (*parameter 2*), and amount of meat obtained per purchase (*parameter 6*),our simulation indicated that the median yearly weight of purchased bushmeat per consumer was 32 kg, representing 1.5 times the average per capita yearly meat consumption. When compared to protein RDA, the yearly percentage of dietary protein covered by bushmeat ranged from 0% to 1390% with a median of 56%. This simulation indicated that for 64% of consumers, the bushmeat purchased each year would cover less than the yearly protein needs for one person.

3.3. How do wildlife vendor and consumers interact with wildlife?

3.3.1. Distribution chain

For live animals, the combined PERT distribution of reported time from capture to market ranged between 0.5 and 6.4 days, with a median of 1.4 days (Table 3, *parameter 7*). The combined PERT distribution for the time live animals stay on markets ranged from a few hours to just over 6 days, and a median of 1.4 days (Table 3, *parameter 8*). If a live animal was not sold on the first day, vendors most often kept the animal at home rather than in the market (Table 3, *parameter 9*). If unsold, live animals were most often returned to the market the next day, killed and consumed by the vendor, or otherwise processed and sold at reduced price (Table 3, *parameter 10*). For dead animals, these durations were all shorter, with the hunted-to-market period ranging from 0.5 to 1.9 days, with a median of 1.1 days, (Table 3, *parameter 11*), and the time-on-market ranging from a few hours to 3.2 days with a median at 0.6 days (Table 3, *parameter 12*). Bushmeat is most often displayed on a table, without any mean to maintain cold chain. Unsold dead animals were either eaten by the vendor, smoked for longer conservation, or sold at lower price (Table 3, *parameter 13*).

Thirteen percent of wildlife consumers reported having ever consumed raw wild meat (Table 3, *parameter 14*). This was most often associated with *Larb*, a traditional Lao dish prepared with raw muntjac or mouse deer meat, or the consumption of raw Bamboo rat blood. A separate question documented meat cooking preferences of respondents (i.e. not cooked, medium, or well done; Table 3, *parameter 15*).

3.3.2. Contact rates

Over a total of 211 animal-hours of observation, 1484 contacts were observed, representing an average of 7 contacts/animal-hour. Disaggregation of contact rates by species (Fig. 3A) and by both species and the sex of the consumer making contact (Fig. 3B) indicates considerable differences between species and between male and female consumers.

Fitted distributions of the number of contacts per observation period (20 min) for rodents (excluding live bamboo rats, giant flying squirrels, and porcupines), small carnivores, reptiles, ungulates, birds, and bamboo rats are included in Table S2 of Supplementary documents 2 (*parameters 16–22*). For instance, contacts with rodents ranged from 0 to 24 per animal per 20 min period (mean = 2.72, sd = 3.36; Table S2, *parameter 16*).

3.4. How do consumers perceive the risk of disease from wildlife consumption

When asked about the overall health risk of wildlife consumption and handling, wildlife consumers indicated a high risk (28.1%), low risk (22.5%), and no risk (16.9%), while the majority (32.6%) did not know. In an ordinal logistic regression, males had lower risk perception, and there was no significant effect of education level on the perceived risk. When focusing specifically on their knowledge of any disease transmitted from wildlife to humans, 36.3% of respondents indicated that they were aware of such risk, the level of education significantly increased this proportion (OR = 1.08 [95% CI: 1.01–1.15], $p = 0.02$). When asked about what disease they were particularly referring to,

Table 4
Total mass and quantity of wildlife sold during direct observations (51.5 stall hours), and estimated yearly trade by species for a typical market in Laos (clarification on species designation provided in supplementary document 3).

Species[a]	Total mass (kg)	Total quantity (equivalent individuals)	Yearly estimate for an average market (kg)	Yearly estimate for an average market (individuals)	Total yearly retail value for an average market (in USD)
Bamboo rat	9.0	4.5	1276	638	8998
Brush-tailed porcupine	16.6	4.5	2353	636	21,064
Bulbul	5.0	171.0	714	24,239	40,902
Chinese water dragon	7.0	7.0	992	992	n.a.
Common palm civet	24.5	7.0	3473	992	18,412
Indian giant flying squirrel	3.6	2.0	510	283	7663
Indochinese ground squirrel	4.5	20.0	638	2835	8760
Leopard cat	4.0	1.0	567	142	1150
Malayan porcupine	6.0	4.0	850	567	7726
Martin	0.3	6.0	35	850	254
Monitor lizard	160.0	32.0	22,680	4536	166,290
Muntjac	94.7	4.0	13,423	559	6681
Pallas's squirrel	5.8	15.0	819	2126	6920
Reticulated python	2.0	0.5	283	71	1321
Small flying squirrel	25.1	114.0	3564	16,159	54,010
Unspecified civet	10.0	3.3	1417	472	6899
Unspecified insectivorous bat	0.4	82.0	58	11,623	8875
Unspecified monkey	0.0	1.0	0	142	2726
Unspecified rat	6.0	30.0	850	4252	6571
Unspecified squirrel	26.2	90.0	3707	12,757	30,474
Unspecified wild bird	8.8	272.0	1246	38,555	128,168
Wild boar	67.0	0.6	9497	87	1371
Yellow-headed temple turtle	15.4	2.0	2183	283	13,075
TOTAL	502		71,137		548,310

[a] Clarification on species designation provided in supplementary document 3.

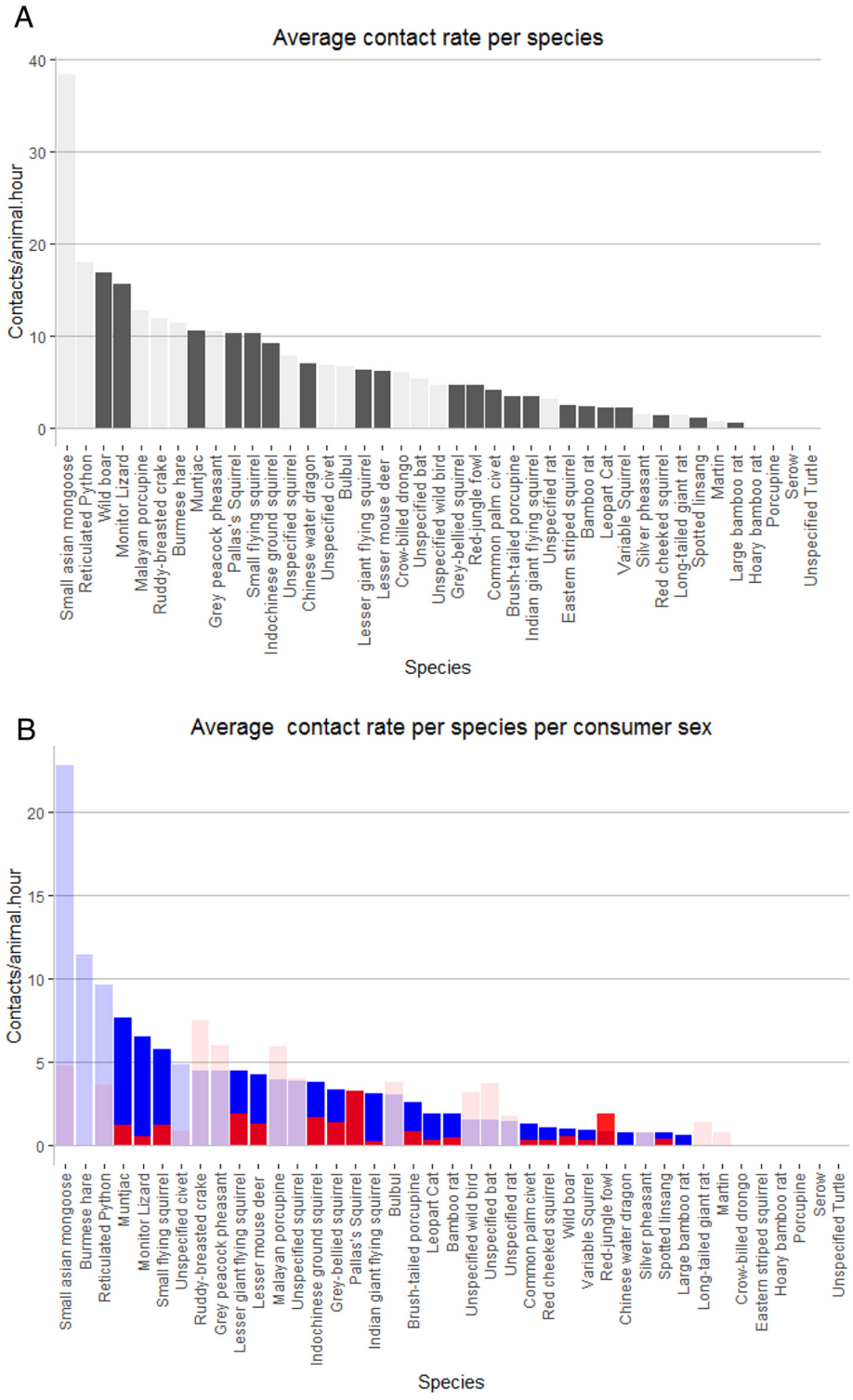


Fig. 3. Average contact rate of people with bushmeat estimated from direct observations in Lao markets A) by species, and B) by species and consumer sex. Species with less than five observation periods are indicated with grey or transparent shades. The sex-disaggregated panel indicates the number of contacts made by male subjects (blue) and by female subjects (red). Clarification on species designation provided in supplementary document 3.

"bird flu" was the most frequently cited (38%, Fig. 4A). When asked if they thought that the wildlife sold at the market they were visiting could transmit disease, the overall proportion of people responding "yes" did not vary greatly (35.2%), but interestingly, the specific diseases cited were quite different (Fig. 4B). Outside of infectious disease, other health risks frequently cited included chemicals and formalin (17%, related to rumors that some wildlife vendors inject formalin into wildlife carcasses to keep them longer), injuries from handling animals (10%), and high blood pressure (5% of respondents indicated that people having high blood pressure should not consume wildlife).

There was a positive association between prior knowledge of wildlife diseases and the perceived risk of disease from wildlife sold at the particular market that the respondent were visiting (Chi square test, $p = 0.040$). This perceived risk was also associated with the frequency of

wildlife consumption (Wilcoxon Rank sum test, $p = 0.047$). The proportion of respondents saying they would stop eating wildlife should they learn that they could get a disease from it was 84% for respondents that had prior knowledge of wildlife disease and 66% for respondents who did not (Chi square test, $p = 0.016$).

3.5. What are the motivations for selling and consuming wildlife?

The main usage of purchased wildlife was reported as food for 95% [95% CI, 91–98] of respondents, while none of the other usages were cited by more than 20% of respondents. In particular, the use as medicine was only cited by 3% of respondents. However, 46% of wildlife consumers thought certain types of bushmeat were healthier than livestock meat, such as giant flying squirrels and serrow. When asked for the motivations for preferring wildlife meat over livestock meat, 44.8% indicated that they simply preferred the taste, and 23.8% that it was traditional. Family, friends, and colleagues were often an influence encouraging consumers to purchase wildlife (in 37%, 30%, and 22% of respondents, respectively), but rarely seemed to exert a dissuasive influence (6%, 4%, and 5%, respectively). Wildlife consumers indicated they would stop consuming wildlife if they knew the animal was near extinction (74% of respondents), if they knew it could transmit a pathogen (71.5%), and if they knew police would fine them (92.5%).

Only twenty vendors (57.1% [39.5–73.2]; *parameter 23*) responded that they stopped selling wildlife when government law enforcement authorities came to the market to control wildlife. The amount of time they stopped ranged from 1 to 60 days with a median of 3 days, fitted with a Weibull distribution (*parameter 24*).

4. Discussion

4.1. Bushmeat consumption: who and why?

Our surveys of wildlife vendors and consumers provided important demographic information that is essential to the identification of risk groups, and the design potential public health and conservation interventions. Wildlife consumers appeared to come from a diverse socio-economic background, as indicated by the diversity of education levels, occupations, and monthly incomes. The top three professional sectors among wildlife consumers matched those of the general population (Laos Statistics Bureau, 2018), but government officials were notably found to be one of these three categories despite the illegal status of wildlife trade and consumption in Laos (Ministry of Natural Resources and Environment, 2007). This may both be an indicator and a cause for the low level of wildlife law enforcement in markets. The similarity of demographic characteristics of wildlife consumers who either responded or did not respond to the interview supports the validity of the inference made from this survey regarding wildlife consumers.

The surveys provided insights into the motivations for wildlife consumption that can be used to better target education campaigns. Almost half of wildlife consumers indicated that they thought certain bushmeat were healthier than livestock meat and this can be linked to the frequently discussed perception of bushmeat as a natural product. However, the use of wildlife products as medicine was rarely cited, which is different to patterns observed in international wildlife product trade in which medicinal use is a frequent driver of the trade (World Bank, 2005). This draws attention to the importance of distinguishing these different types of trade when designing prevention measures.

From our estimates, wildlife consumption could represent a significant portion of people's protein intake as the median yearly quantity of bushmeat purchase was comparable to average yearly per capita meat consumption (FAOSTAT, 2018). In absence of information on how the bushmeat is shared within households, it is difficult to fully estimate the proportion of protein needs covered by bushmeat. Nevertheless, in urban settings such as where these surveys were conducted, there is no reason from a nutritional and economic standpoint for consuming wildlife rather than readily available (and cheaper) domestic meat. However, the bushmeat traded in urban wildlife markets diverts precious protein resources from more remote rural communities that truly rely on this nutritional input. The absence of association between the consumption patterns and the socio-economic indicators suggest that wildlife consumption in these urban centers was indeed tied to preference and not necessity, which was confirmed by "taste preference" being the primary reported motivation for wildlife consumption. On a conservation and public health perspective, this may be problematic, as taste preference is likely to be a difficult aspect to address and change through communication or education campaigns, and change may only be achieved through law enforcement. Reducing wildlife consumption in urban centers is crucial to reducing the demand and offtake of wildlife from natural areas, and keeping wildlife offtake at sustainable levels so that communities which most depend on it can continue hunting for subsistence. It should be noted that the disruption of this illegal trade may have consequences on the livelihood of the rural community, as the income derived from the sale of bushmeat can sometimes contribute significantly to livelihood and well-being of rural households (Schulte-Herbrüggen et al., 2013). However, a previous study in Lao PDR found that the extra income earned by remote rural communities members from selling bushmeat was most often used to purchase

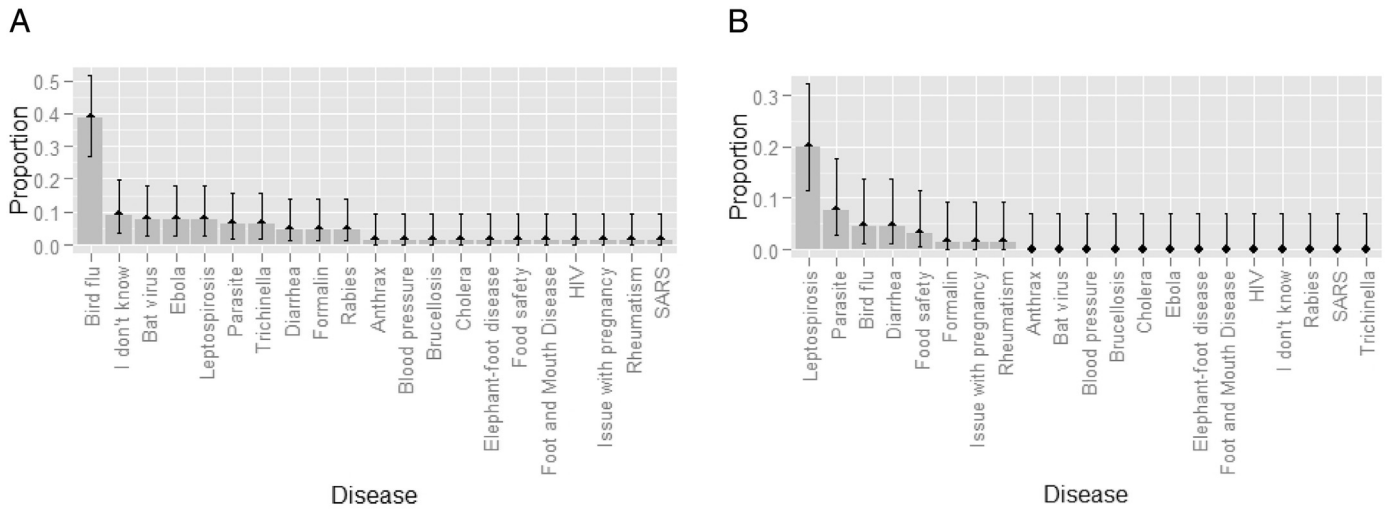


Fig. 4. Disease ranked by frequency of citation by bushmeat consumers in Laos when asked A) generally about disease transmitted from wildlife to humans, and B) specifically about disease transmitted from wildlife in the market they were visiting.

non-nutritive goods such as alcohol, sweets, and monosodium glutamate (MSG, a widely used food additive in Southeast Asia) (Johnson et al., 2012).

Refining the typology of wildlife consumers and other actors of the bushmeat trade, through an understanding of their demography, socio-cultural background, and their motivation for bushmeat trade and consumption is essential to the design of coherent, fair, and effective policy.

4.2. Characterizing the exposure to pathogens from bushmeat trade

The exposure of humans to pathogens is in part determined by the species and the quantity traded and consumed. The preference for rodents and bats is a concern as these two taxa are particularly significant for the risk of zoonotic disease emergence (Han et al., 2015; Olival et al., 2017; Wang, 2015). In Lao PDR, rodents were reported to host several zoonotic pathogens of great public health significance, such as *Leptospira* (Cosson et al., 2014), *Orientia tsutsugamushi* (Phetsouvanh et al., 2015; Lerdthusnee et al., 2003), *Rickettsia sp.* (Phongmany et al., 2006), and Hantavirus (Blasdell et al., 2011). The very high number of wild birds circulating in markets where live poultry and other mammalian hosts can be found may represent an interface for avian influenza transmission, mutation, and re-assortment of domestic and wild viruses (Moon et al., 2010; Nguyen et al., 2005). The very high volume of monitor lizard and wild boar meat sold on markets may increase the risk of food-borne parasite transmission, such as *Taenia solium*, *Angiostrongylus cantonensis*, *Trichinella spp.*, and Hepatitis E virus, all transmitted through consumption of insufficiently cooked meat and present in Laos (Barennes et al., 2008; Holt et al., 2016; Ming et al., 2017). Finally the occurrence of both bats and civets (live and dead) in the markets is of great concern, as these seem to have been key for the emergence of SARS coronavirus in 2001 (Bell et al., 2004). Further, we documented the amount of bushmeat obtained at each individual purchase, a significant factor in estimating the exposure of wildlife consumers to particular pathogens. The processing (killing and butchering) of animals was not restricted to wildlife vendors, since most live animals were processed by the consumers themselves. Although the majority of respondents (92%) reported eating the meat well done, the consumption of raw meat and blood for traditional Lao Larb dishes is of particular concern. Given the lack of cold chain and the conditions of meat preparation, foodborne pathogens are likely to be found and cause illness in consumers (Bachand et al., 2012; Jansen et al., 2019; Paulsen, 2016).

The distribution chain of wildlife products is another important component of quantifying the risk of pathogen transmission. The majority of wildlife vendors obtained the animals from a third party provider, so for each animal sold on the market, the most basic distribution chain would have at least three people coming in close contact with the animal (hunter, vendor, and consumer), and most often include additional middlemen (TRAFFIC, 2008). The information obtained on the duration of each step from bushmeat hunting to consumption suggested a rapid transit through the distribution chain, consistent with what would be expected with a poor cold-chain. This indicates that all actors along the distribution chain likely come in contact with relatively fresh animals, of higher risk for pathogen transmission.

The interactions between bushmeat and wildlife vendors and consumers are not limited to preparation and consumption. Our direct observations also documented an astounding number of contacts between bushmeat and market consumers, with an average of over seven contacts per animal per hour. To our knowledge, this is the first time that such information has been quantified. In our estimates of contact rates, we purposely separated animals for which estimates may be biased due to a low number of observations. However, it is remarkable that rarer species seem to receive particularly high numbers of contacts. Although these species are rare occurrences on markets, these disproportionately higher number of contacts may still have a significant impact on transmission, analogous to super-spreading events (Stein, 2011).

The risk that these various types of contact (consumption of live versus dead animals, bushmeat handling, and touching) represent for pathogen transmission is difficult to estimate, and likely depend on the freshness of the animal, and the type of pathogen (persistence, infectiousness, transmission route). However, our estimates of the duration of each step of the distribution chain would make it possible to quantify this risk if pathogen decay functions and infectious dose were available for particular pathogens. The information collected in this study is, therefore, essential for risk assessment and modeling of disease transmission in bushmeat markets.

4.3. Knowledge and perception of disease risk

It is not clear how truthful were the consumers and vendors in their response to the survey questions and how this may impact our observations. However, the health focus of our project seemed to put respondents at ease with the survey despite the sensitive topics, as indicated by the high response rate for both vendor and consumer surveys. About a third of wildlife consumer respondents were aware of disease transmitted from wildlife to humans. This low level of awareness of zoonotic disease, together with the observation that people with higher level of education were more likely to be aware of this risk, suggest that there may be opportunities to increase knowledge of wildlife diseases through awareness and engagement campaigns. However, it is unclear if greater knowledge of wildlife disease would have any consequence on the wildlife consumption behavior. From our surveys, there seemed to be associations between the knowledge of wildlife disease and the perceived risk of infection, as well as between this perceived risk and the frequency of wildlife consumption. However, it is not clear if this reported frequency of consumption is a good indicator of the behavioral response of interest – the willingness to decrease bushmeat consumption. When asked if they would stop eating wildlife if they learned of a particular disease risk, a higher proportion of respondents with no prior disease knowledge responded 'yes' than respondents with prior disease knowledge. This could be an indication that increasing awareness of infectious disease may be an effective approach for behavioral change, but could also indicate some level of risk tolerance. Nevertheless, these proportions are high regardless of prior knowledge and perception, which points to the value of generating wildlife disease information that has direct local relevance to the wildlife consumers, focusing on priority endemic diseases of local significance.

4.4. Volume of trade and conservation impact

Our study highlighted the considerable conservation impact alongside the strong economic incentives involved in maintaining this trade. Based on our estimates, an average market would generate close to half a million USD in trade for over 71 tons of bushmeat sold per year. Similar surveys should be repeated to assess the seasonal patterns of bushmeat trade. It is also difficult to make conclusions on the sustainability of this trade without additional information on the origin of traded animals and the total size and dynamic of the source populations. Most vendors came from less than 10 km to the market, which suggests that the impact of this type of trade may be quite local and likely to exceed the estimated sustainable offtake in wet tropical forests (Robinson and Bennett, 2004). Distance between hunting location and market has previously been used as an indicator of wildlife abundance and offtake sustainability, based on the assumption that with decreasing wildlife population, bushmeat needs to be hunted in more remote areas (Crookes et al., 2005; Milner-Gulland and Clayton, 2002). Further work is required to better characterize the source populations and local trade routes in order to assess the sustainability of this level of wildlife offtake.

Law enforcement appeared particularly ineffective at stopping traders, with only about half of vendors reporting to cease trade activity after controls from the authorities, and half of these only stopping for three days or less. This raises serious concerns about the effectiveness of current law enforcement strategies, which mostly involve wildlife confiscation in markets. Interestingly, the majority of wildlife consumers reported that they would be very likely to stop consuming wildlife if they faced a fine from enforcement authorities. This suggests that the cost of law enforcement can be internalized by wildlife vendors as part of their business operations, while this cost may not be tolerable at the individual level for a wildlife consumer. Hence, a possible effective angle for law enforcement is to reduce demand for wildlife by targeting wildlife consumers in urban centers. Here again, a good understanding of wildlife consumer demography, economic status, and motivations is essential to the design of effective policy with limited unintended consequences on more vulnerable communities.

5. Conclusion

We provided a QRA framework to quantify the risk of zoonotic disease transmission from bushmeat consumption, provided uniquely detailed information to fill important data gaps, and parameterized key elements of this model framework. Doing so, we demonstrated high rates of direct contact between bushmeat and people visiting the market, highlighting that this may be an under-estimated route of disease transmission in the bushmeat system. This approach and preliminary data are relevant to a broad range of endemic and emerging zoonotic pathogens, and will assist in improving our understanding of the zoonotic disease risk from bushmeat consumption. In particular, we encourage efforts to assess the public health (e.g. in Disability-Adjusted Life Years [DALYs]) and socio-economic impact of common endemic diseases potentially transmitted by bushmeat rather than focusing exclusively on low probability/high impact scenarios (e.g. emerging diseases such as Ebola and SARS). The flexibility of this framework allowed the inclusion of aspects related to nutrition, highlighting the significant portion of dietary needs covered by bushmeat in urban consumers. However, our socio-demographic data on these urban consumers suggested that consumption of bushmeat was motivated by dietary preference and tradition rather than nutritional needs. We were also able to derive information on the conservation impact by providing some indicators of the magnitude of the trade. Fully understanding these tradeoffs between food safety, food security, and conservation will continue to be a challenge, and will require improving the quantification of these multiple risks under integrative frameworks. Although these aspects can be somewhat contradictory from a management point of view, considering them integratively is essential to the articulation of effective and balanced policies that reduce the public health impact of zoonotic diseases, secure the nutritional status and livelihood of rural populations, and protect biodiversity across natural landscapes.

Ethics statement

Study protocols and interview material was reviewed and approved by the Wildlife Conservation Society Institutional Review Board, and the Lao National Ethics committee of the Ministry of Health under permit No. 020 NIOPH/NECHR.

Conflict of interest

Authors declare none.

Author contributions

Mathieu Pruvot: Conceptualization, Methodology, Formal Analysis, Validation, Data Curation, Writing – Original Draft, Visualization, Supervision, Project Administration; Kongsy Khammavong: Investigation, Data Curation, Writing – Review & Editing, Project Administration; Phonesavanh Milavong: Investigation, Data Curation, Project Administration; Chanfong Philavong: Conceptualization, Methodology, Investigation, Data Curation; Daniel Reinharz: Conceptualization, Methodology, Writing – Review & Editing, Supervision; Mayfong Mayxay: Conceptualization, Methodology, Writing – Review & Editing, Supervision; Sayapeth Rattanavong: Investigation, Supervision, Project Administration; Paul Horwood: Conceptualization, Project Administration, Writing – Review & Editing; Philippe Dussart: Conceptualization, Project Administration, Writing – Review & Editing; Bounlom Douangngeun: Writing – Review & Editing, Supervision, Project Administration, Watthana Theppangna: Conceptualization, Investigation, Writing – Review & Editing, Supervision, Project Administration; Amanda E. Fine: Conceptualization, Methodology, Writing – Review & Editing, Supervision, Project Administration, Funding Acquisition; Sarah Helen Olson: Conceptualization, Methodology, Writing – Review & Editing, Supervision, Funding Acquisition; Matthew Robinson: Writing – Review & Editing, Supervision, Project Administration; Paul Newton: Conceptualization, Writing – Review & Editing, Supervision, Project Administration, Funding Acquisition.

Acknowledgements

The authors wish to thank the Government of the Lao People's Democratic Republic for authorizing and facilitating this study. We wish to thank students and volunteers that have contributed to this research: We also thank Mr. Chanthala Vilayhong, Mr. Thilakoun Soukdavanh for their contribution. Thank you to Tran Phuc for her contribution producing the graphical abstract. This study was funded by the European Union under the INNOVATE program and the LACANET project (DCI-ASIE/2013/315-151).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2019.04.266.

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