THE SOCIAL DETERMINANTS AND ECOLOGICAL CONSEQUENCES OF INDISCRIMINATE HUNTING IN TROPICAL ASIA

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Abstract

Overexploitation is one of the most prominent threats facing IUCN Red-Listed mammals and birds, particularly in the tropics. Classical bioeconomic models focused on single species have proposed techniques for managing exploited populations. Unfortunately, such models and policy instruments based on these principles have failed to prevent population collapse. I posit that this is due to the fact that hunting exploits multiple prey species simultaneously, particularly in open-access systems typical of the developing world. Moreover, the assumption that hunting is driven by economic or subsistence aims alone may be inaccurate.

Using illegal hunting of mammals and birds Southwest China as a case study, I found that hunting activity was largely sustained by resilient ungulate and passerine stocks. As hunting effort has persisted, more sensitive species have been driven locally extinct. Recreation was the main motivator of hunting, which may be widespread in the developing world but heretofore under-appreciated. Recreational hunters may be less likely to reduce effort when prey populations and catch decline, increasing the likelihood of hunting-mediated extirpations.

Monitoring trends in hunting effort largely depends on human subjects interviews, and indirect surveys are powerful tools when hunting is criminalized. However, analyzing indirect survey data has been challenging: practitioners often lack the means to analyze their findings in a scientifically sound manner. I have developed an open-source software package that permits for several novel analyses and can control for evasive responses. I then applied these techniques to determine what factors are associated with illegal hunting in Southwest China.

I explored what rules may structure hunter prey choice decisions, in order to understand how salient traits could simplify otherwise complex indiscriminate harvesting systems. In many hunting systems, the most relevant trait is body mass. I then incorporated the predicted lower bound on body mass into a theoretical model that combines indiscriminate harvesting with allometric scaling for population growth rates. This model explores the conditions under which large-bodied mammals and birds can be harvested to extinction.
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To Aniang and Zap.
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The Fermi paradox is sometimes known as the Great Silence. The universe ought to be a cacophony of voices, but instead it’s disconcertingly quiet.

Some humans theorize that intelligent species go extinct before they can expand into outer space. If they’re correct, then the hush of the night sky is the silence of a graveyard.

Hundreds of years ago, my kind was so plentiful that the Rio Abajo forest resounded with our voices. Now we’re almost gone. Soon this rainforest may be as silent as the rest of the universe.

***

Human activity has brought my kind to the brink of extinction, but I don’t blame them for it. They didn’t do it maliciously. They just weren’t paying attention.

And humans create such beautiful myths; what imaginations they have. Perhaps that’s why their aspirations are so immense. Look at Arecibo. Any species who can build such a thing must have greatness within it.

We Puerto Rican Parrots have our own myths. They’re simpler than human mythology, but I think humans would take pleasure from them.

My species probably won’t be here for much longer; it’s likely that we’ll die before our time and join the Great Silence. But before we go, we are sending a message to humanity. We just hope the telescope at Arecibo will enable them to hear it.

The message is this:

You be good. I love you.

–Ted Chiang, *The Great Silence*

What’s to do? Since few paths now exist on which my hounds can hunt hares. And from where come the tracks whence, once more, I can hear the lament of the cranes?

–Xie Lingyun, *Living in the Hills* (400 C.E.)
Chapter 1

Introduction

1.1 Overview

The problem of natural resource overexploitation has long fascinated and perplexed ecologists (Clark, 1973; May et al., 1978; Clark and Kirkwood, 1986; Bulte and van Kooten, 2001). Anticipating and preventing overexploitation has gained added urgency in the face of the massive extinction threat facing mammals and birds targeted by hunters (Rosser and Mainka, 2002; Ripple et al., 2015; Maxwell et al., 2016; Benitez-López et al., 2017). Overexploiting wildlife for bushmeat, traditional medicine, and other uses is pervasive across the tropics (Milner-Gulland and Bennett, 2003; Wright, 2005; Dirzo et al., 2014). Though tropical forests cover only 7% of the Earth’s landmass, they support up to 2/3 of its terrestrial diversity (Wilson, 1988; Myers et al., 2000; Bradshaw et al., 2008; Gardner et al., 2009).

The sheer scale of hunting pressure on wildlife is staggering. Extraction rates of large-bodied mammals across the Neotropics, Afrotropics, and Asian tropics were as high as 700-2000 kg/km², with overall basin-wide extraction as high as 6 million tons per year in the Congo (Fa et al., 2002; Robinson and Bennett, 2004; Swamy and Pinedo-Vasquez, 2014). Comparisons across space or time have shown that hunting can decimate wildlife populations,
reducing densities by as much as 75-90% (Peres, 2001; Madhusudan and Karanth, 2002; Peres and Palacios, 2007; Wilkie et al., 2011).

Hunting is the primary threat for nearly 50% of the IUCN Red-Listed mammals and 40% of the listed birds (Rosser and Mainka, 2002; Swamy and Pinedo-Vasquez, 2014; Maxwell et al., 2016). In the open-access hunting systems typical of the tropics, hunter preferences for the largest-bodied birds and mammals have resulted in these taxa being the most threatened (Purvis et al., 2000; Cardillo et al., 2005; Morrison et al., 2007; Barnosky, 2008; Fritz et al., 2009; Hoffmann et al., 2010). The loss of the largest predators, seed-dispersing frugivores, and herbivores have cascading effects that diminish ecosystem function (Wright et al., 2007; Terborgh et al., 2008; Estes et al., 2011; Galetti et al., 2013; Galetti and Dirzo, 2013).

Hypotheses regarding the root causes of extinction from exploitation have included the following broad categories. (1) Rarity drives prices to such an astronomically high level that the costs of harvesting the last remaining individuals of a dwindling species are offset (Courchamp et al., 1999; Hall et al., 2008). (2) Rarity value or spatial aggregation as populations decline and habitats are destroyed makes hunting to extinction economically feasible (Burgess et al., 2017). (3) The stability of harvest equilibria can exhibit knife-edge behavior, teetering into basins where extinction is attracting (Milner-Gulland and Mace, 1998; Jennings et al., 2001).

Yet one straightforward reason has been largely neglected in theoretical treatments of hunting (but see Milner-Gulland and Leader-Williams, 1992; Clayton et al., 1997; Keeling et al., 1999): harvest activity may be sustained by resilient stocks, permitting hunters to opportunistically exploit rare and declining prey species that they come across (Branch et al., 2013). Researchers have long noted the indiscriminate nature of hunting in the tropics, cautioning that such non-selective gear could help guarantee extinction for the most vulnerable species (Milner-Gulland and Bennett, 2003; Rowcliffe et al., 2005; Corlett, 2007; Keane et al., 2008; Ripple et al., 2016).
Identifying levers for controlling hunting pressure remains elusive (St John et al., 2013; Duffy et al., 2016; Bennett et al., 2017). The majority of published studies center poverty, subsistence, and profit as the primary motives (Damania et al., 2003; Sirén et al., 2004; Keane et al., 2011; Duffy et al., 2016)—and neglect intangibles such as social cohesion, the thrill of the chase, and cultural norms that can equally impel harvest (Barnes-Mauthe et al., 2015; Oleson et al., 2015; Boonstra and Hentati-Sundberg, 2016). An emerging body of research challenges the conception of rural, tropical hunters as *Homo economicus*. Case studies across the Neotropics and Old World tropics indicate that hunters—even fairly poor ones—may instead view the pursuit of wildlife as an inherently enjoyable activity, independent of its material benefits (Harrisson, 1961; MacMillan and Nguyen, 2014; El Bizri et al., 2015; Alfaro-Shigueto et al., 2016; Chang et al., 2017).

Integrating the social dimensions of hunting with the resulting ecological outcomes would provide novel grounds for management and further research. One major challenge facing researchers and practitioners is the indiscriminate nature of contemporary unregulated hunting in the developing world. With current technology and limited resources available for conservation, it is simply infeasible to (1) collect the detailed life history parameters necessary for species-specific population models or (2) perform standardized monitoring transects at the necessary spatial and temporal scales.

Hunter preferences can simplify complex, multi-species harvesting systems to a single, easily measured trait, such as body mass. Optimal foraging problems posit that hunters are confronted with two primary constraints—limited time and high-value prey. The principles of optimality can then identify trait thresholds for prey harvest.

Indeed, reducing the dimensionality of indiscriminate harvesting to a single trait may offer substantial benefits for monitoring and management. A trait threshold dictates a cut-off between prey species or individuals that should be ignored versus those that should be harvested. Based on this cut-off, practitioners could then assess whether or not hunter catches
were consistent with an expected distribution of prey traits. As it is much easier to measure hunter catch than it is to comprehensively survey wildlife for time series analyses, using bag data and trait thresholds could greatly enhance current hunting monitoring schemes.

Hunter motives dictate how hard prey are harvested; a greater degree of sensitivity to catch per effort may rein in otherwise excessive hunting pressure. Yet the presence of non-material gains from the sheer act of hunting alone may cause hunters to be more resistant to exiting systems as fauna decline as their perceived reward for hunting effort is not limited to catch but can also include the social values of hunting. I explore how indiscriminate hunting interacts with allometric scaling of population growth rates to predict when and where size-biased extinction can occur.

1.1.1 Field system

The extent of contemporary defaunation in Asia has been viewed as a cautionary tale of what may presage wildlife populations in the Afro- and Neotropics (Milner-Gulland and Bennett 2003; Sodhi et al. 2004; Corlett 2007). Despite rising wealth, enforcement capacity, and dwindling wildlife populations, hunting pressure in Southeast Asia has rarely come under control (Harrison et al. 2013; Wilcove et al. 2013; Steinmetz et al. 2014). In Southeast Asia, the Indo-China region—including Southwest China—has experienced some of the most intense range contractions and wildlife population collapses due to overhunting (Yang et al. 2004; Zhang et al. 2008; Kai et al. 2014; Johnson et al. 2016).

Hunting is generally illegal in Southwest China due to species and protected area restrictions under the Wildlife Protection Law of 1988 as well as prohibitions on rifles and shotguns under the 1994 and 1996 Firearm Control Laws (Li 2007; Harris 2007; Xu and Melick 2007). Between penalties for hunting on the one hand and negligible rewards due to low wildlife densities on the other, the persistence of hunting in Southwest China challenges conventional theories of hunter motives and behavior. Empirical work in Xishuangbanna Dai
Autonomous Prefecture (henceforth “Xishuangbanna”), Yunnan Province, Southwest China was used to explore the motivations of hunters and elucidate how hunter behavior dictates the outcomes of harvest.

Below, I present the major themes of my dissertation research.

1.1.2 The social dimensions of hunting

There have been two major frameworks used to predict participation in hunting. The first arose from economic rational choice theory, views hunting as one of many livelihoods, and focuses on the allocation of time to hunting versus other wage-garnering pursuits (Bulte and Horan, 2003; Damania et al., 2003, 2005; Milner-Gulland, 2011; Sirén and Parvinen, 2015). The second originated from the Theory of Planned Behavior in social psychology, focusing on the role of personal attitudes and values as well as community norms (Ajzen, 1991; St John et al., 2011; Duffy et al., 2016).

Research invoking both of these theories has assumed that hunting is primarily oriented toward subsistence or pecuniary reward. Yet evidence from sites in Asia and Latin America suggests that intangible social and cultural values may be significant for hunters (Harrisson, 1961; MacMillan and Nguyen, 2014; Alfaro-Shigueto et al., 2016). I explored hunter behavior through semi-structured surveys and evaluated predictors of hunting activity at a landscape scale using quantitative interviews in Southwest China. In Chapter 2, I found that hunting in Xishuangbanna was primarily driven by recreational urges. The pleasure of pursuit was enough to compensate for relatively trivial material rewards—a median per-trip catch of 0.47 kg and a 22% failure rate where nothing was caught—as well as increasingly punitive enforcement against illegal hunting.

To evaluate the predictors of hunting at a landscape scale, I used an indirect questioning technique to reduce response bias. Given the sensitivity of questions regarding conservation crimes such as illegal hunting, direct questioning has been shown to be highly biased.
John et al., 2014; Nuno and St John, 2015). The randomized response technique (RRT) has been the most popular, and arguably most statistically powerful, indirect questioning method for stigmatized behaviors. RRT data require specialized statistical estimators that have, to date, been foreign to the environmental sciences literatures (Keane et al., 2015).

I developed an open-source package to facilitate RRT data analysis, as these are necessary tools for conservation practitioners and researchers to understand the motives behind sensitive behaviors (Chapter 3). I provide code and simplified explanation of the mathematical motivation behind several robust and promising RRT estimators: the sum score model and item response theory. An RRT sum score is the number of sensitive traits possessed by a respondent; in Xishuangbanna, that would correspond to the sum of the number of species hunted. Previously, conservationists were limited to performing inference on individual RRT prompts, and could not pool information across multiple questions. Both of these models permit for multivariate inference: the sum score for the number of sensitive traits, and item response theory for factors that exert the same influence across all the sensitive traits.

In Chapter 4, I evaluated whether or not recreational activities and beliefs in the entertainment value of hunting could distinguish hunters from non-hunters at a broader, landscape scale. I used the forced response RRT design as well as the estimators introduced to the conservation science literature in Chapter 3. I considered the relative contribution of personal beliefs, cultural values, and socio-economic factors in predicting which individuals actively hunted songbirds in Southwest China. I found that recreational covariates—the number of outdoors leisure activities pursued, attitudinal inclinations toward viewing hunting as a form of entertainment—were highly predictive of hunting songbirds and gamebirds.
1.1.3 Integrating hunter behavior with the ecological consequences of indiscriminate harvest

The seemingly endless array of wildlife sold at markets gestures to the wide range of species harvested (Milner-Gulland and Bennett, 2003; Harris et al., 2016). Collecting detailed ecological information on each harvested species would strain the limited financial resources and personnel of managers at the forefront of the tropical hunting crisis (Harris et al., 2015). However, hunter prey preferences in conjunction with the availability of prey across different levels of desirability dictate which species are harvested (Charnov and Orians, 1973; Stephens and Krebs, 1986; Winterhalder, 1986; Diekert et al., 2016). Apart from outliers such as ivory and rhinoceros horn, hunter preferences for prey generally align with a specific trait that exhibits a consistent pattern across many species. Body mass is highly predictive of extinction risk, and in the tropics, is particularly implicated in risk to overexploitation (Cardillo et al., 2005; Fritz et al., 2009; Hoffmann et al., 2010; Barlow, 2011; Ripple et al., 2015).

In Chapter 5, I use the optimal stopping time and foraging theory models to determine reservation values—the minimum trait threshold acceptable for hunters given considerations such as the profitability of different prey species and constraints on hunter time in the field. I found that the optimal stopping time model required fewer parameters and was more consistent with catch data in Southwest China. Finally, I demonstrated how the reservation value could be combined with bag data to evaluate whether or not the catch was consistent with an expected community composition.

Terrestrial mammals larger than 1 kg and birds larger than 500 g are the most threatened by the pantropical bushmeat crisis (Purvis et al., 2000; Cardillo et al., 2005; Keane et al., 2005; Barlow, 2011). Hypotheses for size-selective defaunation include innate physiological constraints, range demands, Allee effects, behavioral traits, and hunter selection processes (Hoffmann et al., 2010; Benítez-López et al., 2017). I provide a mechanistic explanation of
body mass limits for persistence under open-access harvesting in Chapter 6 based on two key processes: allometric scaling and indiscriminate harvesting. I derive conditions in a two-species (mini- and megafauna) model for megafaunal persistence, which I subsequently extend using numerical simulation to a community of harvested prey that are solely differentiated by body mass. Given realistic parameter values, it is extremely rare that species larger than $50 - 100kg$ can persist.
Chapter 2

The pleasure of pursuit: recreational hunters in rural Southwest China exhibit low exit rates in response to declining catch

Charlotte H. Chang, Michele L. Barnes, Margaret Frye, Mingxia Zhang, Rui-Chang Quan, Leah M.G. Reisman, Simon A. Levin, and David S. Wilcove

2.1 Introduction

Overexploitation is a major driver of endangerment for the majority of IUCN Red-Listed vertebrates (Rosser and Mainka, 2002; Maxwell et al., 2016). Effective hunting management requires compliance, which rests on hunter motivations and behavior (Lee et al., 2009; St...
Understanding hunter motivations to better regulate hunting is crucial, given that hunting pressure exceeds sustainable thresholds for many species across the global tropics (Peres, 2001; Fa et al., 2002; Milner-Gulland and Bennett, 2003; Wilkie et al., 2011; Dirzo et al., 2014; Harrison et al., 2016).

Profit and subsistence have been posited as the primary motives for hunters in tropical, developing countries (Damania et al., 2005; Sirén et al., 2006; Bennett et al., 2007; Van Vliet and Nasi, 2008; Brashares et al., 2011; Golden et al., 2013a). Yet the non-material entertainment value of hunting—the thrill of the chase and social benefits provided by hunting—may also be a prominent motivator for rural villagers in tropical countries (Bennett, 2002; Loveridge et al., 2006; Rao et al., 2010; Velho and Laurance, 2013; MacMillan and Nguyen, 2014; Alfaro-Shigueto et al., 2016). We distinguish this form of recreational hunting from previous descriptions of sport or trophy hunting. Sport or trophy hunting is typically well-regulated, garners income for local communities, and involves high net-worth individuals, often from the developed world or from urban centers in both developed and developing countries (Eltringham, 1994; Getz et al., 1999; Harris and Pletscher, 2002; Lindsey et al., 2007; Yasuda, 2012); the recreational hunting described herein pertains to systems with weak to nonexistent governance and/or enforcement on hunting (El Bizri et al., 2015).

Research on recreational hunting in tropical contexts is long overdue; more than half a century ago, Harrisson (1961) already identified recreational hunting as a major threat to endangered mammals in Borneo. Yet to date, the ecological impacts of recreational hunting in the tropics are little known. Recreational hunter responses to economic sanctions, diminishing game stocks, and penalties may fail to align with expectations set out by subsistence or economic principles (Cooke and Cowx, 2006; Barnes-Mauthe et al., 2015). For instance, recreational angling has depleted certain fish stocks more than highly regulated commercial fisheries (Coleman et al., 2004; Cooke and Cowx, 2004). It is thus possible that recreational...
motives may promote high levels of hunting effort that exceed both economic and biological sustainability thresholds.

This study presents a novel characterization of a community of hunters who are primarily oriented toward recreation in a rural developing country. Collecting data on illegal hunting poses formidable challenges due to respondent concerns about legal repercussions. To overcome these challenges, we used innovative survey techniques to characterize hunter behavior without requiring respondents to admit to legal offenses. We describe how hunters in rural Yunnan Province, China respond to regulations, changes in game populations, and their hunting practices.

2.1.1 Study Site

Xishuangbanna Dai Autonomous Prefecture (henceforth, Xishuangbanna) is a biodiversity hotspot within Southwest China that is well suited for examining recreational hunting. Intense hunting effort has and continues to pose tremendous pressure on the avifauna and mammals of Xishuangbanna and surrounding regions (MacKinnon and MacKinnon, 1986; Myers et al., 2000; Yang et al., 2004; Corlett, 2007; Zhang et al., 2008; Hoffmann et al., 2010; Sodhi et al., 2010; Wilcove et al., 2013). Overhunting and forest fragmentation have driven large-bodied, economically valuable mammals and birds to extirpation; small, low-value species now dominate in abundance (Haimoff et al., 1987; Shilai et al., 1995; Harris and Shilai, 1997; Luo and Dong, 1998; Fan et al., 2014; Kai et al., 2014). Long before cash-crop smallholding transformed Xishuangbanna economically, researchers noted that hunting was oriented toward recreation, not subsistence, despite widespread and severe poverty (Tisdell and Xiang, 1996a; Xu and Wilkes, 2002). More recently, Kai et al. (2014) concluded that hunting in Xishuangbanna is a leisure activity providing at most a trivial source of income or nutrition.
In rural Xishuangbanna, smallholder agriculture is the primary livelihood, employing approximately 95% of the rural population (Hammond et al., 2015). Rubber (*Hevea brasiliensis*) and tea (*Camellia sinensis*) smallholding has lifted villagers in Xishuangbanna out of poverty and into the global middle class over the past decade (Huijun et al., 2002; Xu et al., 2005a, 2014; Yi et al., 2014). From the 1980s onwards, land parcels were allocated to and managed by individual households (Xu, 2006; Grumbine and Xu, 2011). The main ethnic groups in this region are the Dai and Han along with smaller ethnic minority groups such as the Yao, Hani, Bulang, Jinuo, and Lahu (Xu, 2006; Hammond et al., 2015).

Hunting and selling wildlife, as well as entering protected areas, are restricted under the Wildlife Protection Law of 1988 (Articles 8, 9, and 10, Chapter II) (Sharma, 2005; Li, 2007; Xu and Melick, 2007; Yu et al., 2013). Under the 1994 Hunting Firearm, Ammunition, and Equipment Administration Regulation and the 1996 Firearm Control Law, gun ownership is *de facto* illegal (Harris, 2007; Zhou et al., 2010). Yet hunters in Xishuangbanna primarily use firearms and hunt in protected areas (Santiapillai et al., 1994; Luo and Dong, 1998; Kai et al., 2014). Mammals and birds are largely limited to native forest, and most remaining forests are in protected areas where hunting is prohibited, thus, by default, hunting activity in Xishuangbanna is typically illegal (Chang et al., 2013; Dayananda et al., 2016).

Beginning in the 1980s, the Yunnan Province Forestry Bureau moved all villages outside of protected area boundaries (Lai and Wang, 1998; Xu et al., 2005b; Allendorf and Yang, 2013). Our study occurred in four villages located less than five kilometers from the boundaries of two Xishuangbanna National Nature Reserve protected areas (Figure 2.1). The two protected areas are strict no-take areas where hunting, logging, and other extractive activities are prohibited, and together contain 1200km² of lowland and montane rainforest (Santiapillai et al., 1994; Zhang and Cao, 1995; Wang and Carpenter, 1998; Kram et al., 2012; IUCN and UNEP-WCMC, 2015). These villages, as well as surrounding villages in the county, all have running water, electricity, cell phone coverage, and paved roads provid-
ing access to the nearest urban center (Appendix 1, Table A1). The number of households per village ranged from 23 to 83 (Appendix 1, Table A1). Nearly every household in the studied region has a refrigerator and there are currently no records of protein insecurity or malnutrition in Xishuangbanna (Hammond et al., 2015).

Figure 2.1: A map of Xishuangbanna Dai Autonomous Prefecture (inset; henceforth, Xishuangbanna). In the top figure, Yunnan Province is shown with a red border, and Xishuangbanna is filled in dark blue. In the inset map of Xishuangbanna, urban centers and protected areas are depicted.

2.2 Methods

We surveyed active hunters using mixed methods: bag records (BR), a quantitative survey (QS), and semi-structured interviews (SS). Our surveys were designed based on the lead author’s ethnographic observations, informal interviews, and sustained interactions with local
communities over the past three years. Given the extreme sensitivity of discussing illegal hunting, both surveys used snowball sampling wherein trusted hunter informants provided contacts to interview. Of the 50 men approached for this study \( n_{BR} = 10, n_{QS} = 30, n_{SS} = 5 \), five refused to participate.

The lead author wrote all of the questionnaire instruments in Mandarin Chinese and translated the results back to English. Two local women (both mixed Dai-Han ethnicity) were trained as enumerators and conducted all interviews in the Xishuangbanna dialect. The enumerators formerly worked for the Yunnan Tobacco Corporation and managed stock for shopkeepers in villages and rural townships; as such, they were familiar with residents in all the study villages, which increased respondent trust and helped avert non-response bias.

All participants were asked for verbal consent before beginning the questionnaires. We informed participants about the survey, its purpose, and potential risks. Participant names were not recorded. Unless otherwise noted, quantities are reported in terms of their means and standard errors. Permission for this study was granted by Princeton University’s Institutional Review Board (#7274) and Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences (#2015.52).

2.2.1 Bag records (BR)

Ten hunters agreed to fill out data sheets for hunting trips taken between July 2015 to June 2016, spanning a full wet and dry season cycle. They listed hunting trip duration, the number of hunters in the party, and marked the number of individuals caught for a range of small-to large-bodied mammals and birds (Appendix I, Table A2). A total of 57 trips taken by 10 focal hunters were recorded.
2.2.2 Quantitative survey (QS)

Respondents provided socioeconomic information including their age, ethnicity, marital status, sources of income, crops grown, and average monthly income (RMB) in the wet and dry seasons. Household size and the number of working adults were recorded. The quantitative survey was piloted with nine hunters in a village outside the sampling frame to ensure comprehensibility. Questions pertaining to hunting activity were phrased in the conditional tense (e.g., *If you could successfully capture two large pheasants (and nothing else) each hunting trip, would you continue hunting?*) to minimize non-response. Thirty hunters were surveyed.

Ultimately, the QS sample was 70% Yao, 23.3% Dai, and 6.7% Han, with the ages spanning 20-70 years. Although the study region demographics are 29.8% Han, 20.7% Dai, and 6.7% Yao (Yunnan Statistical Bureau 2013), a separate large-scale study showed that the ratio of hunters among the Yao versus the Dai is 3:1, and that anywhere from 8.7% to 43.4% of the rural, adult male population had hunted at least one species of bird in the past year (C.H. Chang, *unpublished data*). As such, our sample is broadly representative of the hunting population. Below, we explain additional QS sections in greater detail.

**Hunting practices**

We characterized behavior on hunting trips by identifying typical trip lengths, weapon usage patterns, and consumption outcomes for captured game (Appendix 1, Table A3). We investigated whether hunters tended to interact with small and select groups of individuals based on shared identity (location, kinship, ethnicity, age). Hunters ranked the relative importance of four reasons for hunting: recreation, desire to eat bushmeat rather than domestic meat, economic concerns, and “Other”, an open-ended field for any additional motivations, such as subsistence consumption.
Preference for different animal groups

Respondents ranked focal taxa in descending order from most to least desirable to hunt. The pilot study participants identified a set of nine mammals and birds that are commonly hunted (Appendix 1, Table A4). Pilot respondents indicated they would get confused assigning ranks to each of the four large-bodied bird species, and indicated that ranking only two at a time would be easier. Thus, each QS respondent ranked seven of the nine example taxa (i.e. only two of the large bodied birds in the set at a time), and the rank scores ranged from 1-7 (most- to least-preferred).

Exit scenarios: How would hunters respond to changes in catch success?

To determine how hunters may respond to reductions in catch success (corresponding to declines in animal populations), we created hypothetical catch scenarios. In each scenario, hunters were asked to state if they would continue to hunt or stop hunting (a decision to exit the system permanently). By interviewing a pilot group of hunters (n = 9), we determined typical trip length and baseline catch rate (animals/trip) for three categories of prey: large mammals, large birds, and small birds (Appendix 1, Table A3). The pilot interviews indicated that the typical trip length was two days and provided baseline catch rates per hunting trip: one boar or muntjac, two large birds, or five small birds. The pilot respondents stated that the typical trip usually yielded only one type of game—mammals only, large birds only, or small birds only. The baseline trip lengths and catch rates were used to create the hypothetical catch rates.

For each prey category, the hypothetical catch rates were 50%, 20%, or 10% expected catch success relative to the baseline. Because the typical catch per trip was so low for all prey categories, these scenarios were presented as successfully obtaining the baseline catch for each prey category once per two, five, or 10 trips. This method of assessing exit willingness was preferred to fractional catch (e.g. 0.4 large birds per trip in the 80% reduction case) as it
more accurately reflects the reality of hunting in this and other degraded systems. Hunters are not assured of catching anything on a given trip, and measure success in terms of the proportion of trips that yield game (Kai et al., 2014).

### 2.2.3 Semi-structured interview (SS)

To elucidate hunter attitudes toward regulation, and to examine hunting behavior in more detail, we used semi-structured interview prompts (Appendix 2). Respondents reflected on hunting regulations and enforcement, as well as environmental conditions. Five respondents (three Yao and two Dai) were interviewed across the four villages, none of whom participated in the QS survey or the BR data collection. The interview findings are either summarized or paraphrased.

### 2.2.4 Data analysis

Recorded catches (bag records), prey preference scores, exit scenario responses, and hunter social interactions (quantitative survey) are reported in terms of the mean ± standard error of the mean. We used a linear model to regress prey preference against body mass, and local regression (LOESS) to characterize the different exit scenarios in the quantitative survey.

### 2.3 Results

#### 2.3.1 Bag records

The mean trip length was $1.9 \pm 0.02$ days ($n_{BR} = 57$, range: [1, 5]). Hunting parties averaged $2.3 \pm 0.04$ hunters ($n_{BR} = 39$). 61.5% of the recorded trips were group hunts, and 38.5% were solo trips.

Only one type of game was usually caught per trip—that is, mammals, large birds, or small birds. On only five trips out of the 57 records (8.8%) were more than one group of
prey captured together (large birds and large mammals, \( n_{BR} = 4 \); large birds and small birds, \( n_{BR} = 1 \)). The average catch per trip for each group of prey was 0.25 ± 0.01 boar and muntjac, 0.47±0.01 large-bodied birds (phasianids, imperial pigeons, great barbet), and 0.56 ± 0.03 small-bodied birds (passerines and near-passerines, primarily bulbuls in genus \textit{Pycnonotus}). This would translate to catching one boar or muntjac once every four hunting trips, and catching one bird (large or small) once every two hunting trips.

### 2.3.2 Quantitative survey results

**Demographic characteristics**

The mean household annual income was USD$ 4354 ± 113, with an average annual per-capita income (including children) of USD$ 1172.16 ± 42.48 (\( n_{QS} = 29 \)). The mean number of residents per household was 4.7±0.05 individuals. All respondents were farmers, and 80% of respondents were rubber smallholders. Apart from rubber, respondents grew 1.2 ± 0.03 crops (e.g. sugarcane, \( n_{QS} = 30 \)). Most members (c. 64%) of the household farmed the family landholding. The rest were typically children in school.

Reported per-capita annual incomes were slightly higher than the Xishuangbanna state average ($1096) (Hammond et al., 2015). 76% of interviewed households had per-capita annual incomes above China’s poverty line (RMB2500/USD$375). Families whose per-capita incomes fell below the national poverty line were equally distributed across the four surveyed villages. Before the price of oil crashed, rubber sold at four times its current value, and fewer households in the study region fell below the national poverty line (Fox, 2014). 83% of surveyed households had agricultural incomes above tropical developing country averages (Angelsen et al., 2014).
**Hunter motivations**

The possible range of ranks that could be assigned to each type of motivation was one to four. Respondents ranked leisure as the primary motivation to hunt ($1.3 \pm 0.03, n_{QS} = 21, \text{range: } [1,3]$) followed by the desire to eat bushmeat over domestic alternatives ($1.8 \pm 0.03, n_{QS} = 25, \text{range: } [1,3]$). Economic motivations came in last place ($2.3 \pm 0.07, n_{QS} = 16, \text{range: } [1,4]$). All of the respondents using the ‘Other’ category ($n_{QS} = 5$) said they hunted because it was a fun activity.

**Interactions between hunters**

Respondents shared information often (57.1%) or sometimes (17.9%) with other hunters ($n_{QS} = 28$). All respondents joined group hunts; 22.2% often, 29.6% sometimes, and 48.1% rarely hunted with others ($n_{QS} = 27$). The results for group hunting and information sharing were similar.

Respondents tended to interact with their own ethnic group; 70% solely interacted with their own ethnic group, 19% with their own and other ethnicities, and 11% with other ethnic groups only. Friends were always consulted but not necessarily family; 21% solely associated with their friends, and 79% with friends and family. This trend was not necessarily due to age similarity in friendship groups; 76.9% of respondents communicated with hunters of all age groups. However, the respondents overwhelmingly associated with members of their own village (70.3% with an additional 14.8% that included other villages); only 14.8% solely interacted with hunters from other villages.

**Game preferences and hunting practices**

The respondents significantly preferred hunting larger bodied game over smaller-bodied species (Figure 2.2, $F_{1,7} = 77.6, p < 4.9 \cdot 10^{-5}, R^2_{adj} = 0.91, n_{QS} = 30$). Grey peacock-pheasant and bar-backed partridge were more preferred than the predicted relationship be-
tween rank score and mass. Hunters preferred barbet less than would be expected from the rank-body mass relationship.

Figure 2.2: Hunters preferred larger game species. A linear model was fit between rank score and the focal taxas mass (log-transformed), and the grey band corresponds to the 95% confidence interval. The points and associated error bars show the average rank (and standard error of the mean) for the focal taxa. The game species masses are provided in Appendix 1, Table A4. The abbreviated labels represent the following: BR, boar; MJ, muntjac; SP, Silver Pheasant (*Lophura nycthemera*); GP, Grey Peacock-Pheasant (*Polyplectron bicalcaratum*); IP, Imperial Pigeon (*Ducula* spp.); BP, Bamboo Partridge (*Arborophila* spp.); BT, Barbet (*Psilopogon* spp.); BL, Bulbuls (family Pycnonotidae); and TL, Tailorbird (*Orthotomus* spp).

Generally, captured game was not sold, but instead was eaten at home or shared with friends and family (Table 2.1). Respondents typically used generalist gear, chiefly guns (67%) and snares (32%). There was no indication that hunters tended to specialize on one type of weapon over others; hunters who used snares or mist nets also reported using guns.
Table 2.1: Frequency of usage for various weapons (Weapon) and consumption pathways (Game Consumption) for hunted game. Snares and guns are widely used. Most captured game is shared with friends (Share) or consumed at home (Home), rather than being sold at market (Sell). Frequency of usage denotes respondents who never, rarely, sometimes, or often engage in a particular activity.

**Exit decisions**

The exit scenario responses exhibited three clear thresholds for exiting the system: (1) after pigs and muntjac were extirpated (an early exit); (2) after large birds were extirpated (mid-way exit), and (3) declining to exit even when the catch was limited to small birds (late exit). We explored whether or not richer households tended to exit earlier or later. Typically, respondents who exited early (strategy 1) had higher per-capita incomes than those who would exit later, but some of the lowest-income respondents would also exit early (Figure 2.3).

Indeed, many respondents reported they would continue hunting notwithstanding major reductions in the expected catch for mammals and birds (Figure 2.4). Even when the expected catch was limited to small birds, as many as 36.7% of respondents said they would continue hunting. Yet small birds had the lowest preference rankings (Figure 2.2), which should have led to high exit willingness. And even when the expected catch rate for small birds was extremely low (1 successful trip out of 10), 16.7% of respondents stated they would still not exit.
Figure 2.3: The proportion of respondents who would continue to hunt in different scenarios of catch success. The first point for each group of game corresponds to the baseline level of catch for each group on a typical hunting trip; the other points correspond to 50%, 20%, and 10% of the baseline catch success. Hunters were prompted to imagine that they could only hunt large mammals (LM), large birds (LB), or small birds (SB) within each set of scenarios. A LOESS curve (span = 1.15) was fit for the proportion of hunters who would continue hunting for each category of game (LM, LB, and SB).

Discrepancies between stated and revealed preferences can complicate the interpretation of exit scenario data. One cause for concern would be if the hypothetical exit scenarios substantially diverged from reality. The bag records revealed low catch rates for all three of the prey groups (mammals, large birds, and small birds), consistent with the exit scenarios.

In addition, the respondents felt that the nine focal taxa were less common in the past year compared to a decade ago and that larger-bodied game had declined more severely than smaller species. The proportion of respondents perceiving a decline in abundance for the focal taxa were: 92.9% for muntjac; 86.7% for silver pheasant and imperial pigeon, 77.8%
for grey peacock-pheasants, bamboo partridges, and pigs, 69.6% for barbets, and 15.4% for bulbuls and tailorbirds. There was a strong association between perceived decline and body mass (Spearman’s $\rho = 0.82$).

### 2.3.3 Semi-structured interview

**Qualitative perceptions of hunting**

All respondents ($n_{SS} = 5$) indicated that hunting in this landscape does not provide many material benefits. One illustrative example was a respondent’s assertion that “there aren’t really any [benefits from hunting]. Mostly it’s fun and occasionally you get to eat wild meat. . . . Now that [hunting] is illegal,. . . if they (hunters) see something they’ll shoot it.” Four
of the five interviewees explicitly stated that hunting was and continues to be entertaining. For instance, one of the SS respondents stated that “[People continue to hunt because it] is their hobby. Going into the forest to hunt is fun and sometimes you get to enjoy wild meat.”

The interviewees noted that hunting weapons (mainly guns) have “become more advanced” in the past 20 years. All respondents ($n_{SS} = 5$) reported that catch rates have plummeted, and attributed the decline to overhunting and habitat degradation. “Many forests have been cleared for agriculture, and there are fewer animals in the forest... Before, the forest grew very thick, so there were more wild animals. But now the forests are very damaged, so there are many fewer animals.” Hunters also noted that forest fragmentation and advances in technology have made accessing the forest easier; “there are roads and cars so you don’t have to walk everywhere.”

**Hunter opinions on enforcement**

Anti-hunting and arms-restriction enforcement has ramped up in the past decade. All of the quantitative survey and semi-structured interview respondents were aware of the national firearms ban and believed that no birds or mammals can be legally harvested, which is, in fact, more restrictive than the law actually is. Of the nine focal taxa presented in the ranking activity, only silver pheasant, imperial pigeon, and grey peacock-pheasant are actually protected by law.

Hunters deploy a variety of tactics to avoid penalties for illegally owning guns and hunting. Rangers patrol too infrequently to catch hunters at significant rates, and villagers know when patrols have arrived in a particular location. One interviewee issued the prescriptive that one should “be like a mouse with the cat; when the cat comes, the old mouse hides,” and then bluntly stated, “you can’t be punished if you don’t get caught.”

The hunter interviewees resented the fact that the forestry police rely on informants. Only one of the respondents felt positively about informants, stating that they are “pretty
grateful [to informants], maybe someday I can change my ways... Most people should feel the same, but some might not get it.” All of the other interviewees reported that they disliked informants and would retaliate. One stated, “[I think about] getting even. If you report me this time, then when you go up [into the mountain to hunt], I’ll report you. I think most people would have the same idea.” As a result, it is “riskier to report a local [for illegal hunting] over an outsider.” Devolving regulation to or co-policing hunting activity with village committees may be more palatable to villagers. One respondent stated, “We are more afraid of the forestry police. But we respect the village committee more because they work for us, so we believe in them more.”

Nonetheless, the interviewees expressed their belief in the state’s legitimacy to regulate hunting and firearms, despite their enjoyment of hunting and regular disregard of these laws. One respondent stated that, “People have to follow the country’s laws. You can only go into the forest to play [euphemism for hunting] when it’s not illegal... If there weren’t restrictions [on hunting] then local people would be very happy, [but] we have to follow the laws.” Others elaborated that, “We [villagers] wouldn’t demand [to change the law], we can only respect the law.”

2.4 Discussion

We found that recreation was ranked as the main force driving hunting in both the quantitative surveys and semi-structured interviews in our rural study area in tropical Southwest China. Most hunting catch was shared or eaten at home rather than being sold at market, reinforcing our finding that profit does not seem to be a primary motivation. We presented a novel questioning technique—exit scenarios—to measure how hypothetical reductions in game availability would affect the rate of hunting, and found that hunting activity in Xishuangbanna was surprisingly resilient to reductions in catch. Respondents repeatedly opined that the degraded landscape of monoculture agriculture with scattered forest pre-
serves harbored very few game species, which was confirmed by the low catch rates reported on the bag records. Semi-structured interviewees asserted that on a typical hunting trip, one could almost be assured of returning empty-handed. Yet most interviewees expressed an eagerness to continue hunting even if game populations declined more precipitously, which supported the quantitative survey exit scenario results.

The entertainment value of hunting may, in fact, be widespread but heretofore overlooked in rural developing world settings (Harrison et al., 2016). Although this study focused on hunters living in relatively wealthy and comfortable conditions, previous research has described poverty-stricken hunters who nonetheless prize the thrill of the chase. For poor subsistence hunters in Vietnam, the enjoyment of hunting was itself a major reward, with one hunter stating, “Even if I can get enough food for living from other livelihoods I still like to go to the forest to hunt until my health would not be strong enough for trapping... I like trapping” (MacMillan and Nguyen, 2014). Alfaro-Shigueto et al. (2016) observed poor artisanal fishermen in Peru shooting endangered Waved Albatross (Phoebastria irrorata) for sport, with no obvious material gains. Just as cultural and social values are recognized as important dimensions of wildlife exploitation (Barnes-Mauthe et al., 2015; Oleson et al., 2015), so too should the entertainment or recreational value of hunting be considered more broadly, especially if it attenuates decisions to stop hunting in response to dramatic game population crashes.

Another driver for sustained hunting behavior is a cultural or gustatory preference for wild meat even when domestic alternatives are readily available (Fa et al., 2002; Zhang et al., 2008; Lee et al., 2009; Scheffers et al., 2012; Morsello et al., 2015). Respondents in the quantitative and semi-structured interviews indicated a preference for wild meat over domestic poultry or pork. Local villagers are largely well-nourished with ample access to domestic poultry and livestock (Hammond et al., 2015). The low catch rates from the bag
records indicate that hunting would not provide a stable source of food, similar to the findings of [Kai et al. 2014].

Expecting hunters to reduce hunting effort in response to declining catch may not be realistic if hunting is a form of leisure; if the entertainment value of hunting is not strongly linked to successfully catching prey, then the pleasure of pursuit could sustain hunting activity even when game become increasingly rare and elusive. The combination of body size preference and reluctance to stop hunting promotes hunting-down-the-web defaunation; there is no reduction in hunting effort as valuable game species become rarer, thereby preventing any natural recovery of overexploited species (Pauly, 1998; Cowlishaw et al., 2005; Wilkie et al., 2011).

Respondents exhibited a strong preference for large game, and larger body size was strongly correlated with a greater perception of decline, similar to global patterns of mammalian endangerment (Cardillo et al., 2005; Davidson et al., 2009). Although the hunter respondents preferred large prey, they were nonetheless willing to continue hunting even when catch rates were vanishingly small and limited to low-value taxa, as shown by the trip records and the quantitative survey. They tended to use generalist weapons such as rifles that can target volant and non-volant vertebrates. Such generalist gear permits high levels of overall extraction (Rao et al., 2005; Van Vliet and Nasi, 2008; Abernethy et al., 2013). In Xishuangbanna, these hunting dynamics may explain the regional extirpation of large-bodied birds and mammals such as Green Peafowl (Pavo muticus) and Sambar deer (Rusa unicolor) (Luo and Dong, 1998; Han et al., 2009; Kai et al., 2014).

Persistent willingness to continue exploiting wildlife stocks despite low catch has been documented in regions mired in deep poverty as well as relatively wealthy communities with market access (Cinner et al., 2009). To our knowledge, our examination of hunter exit decisions is novel, but the artisanal fisheries exit decision literature echoes our results. Rural poor fishers in the Philippines would opt to continue fishing even if they were offered
buy-outs that exceeded their monthly expenditures by 150% (Muallil et al., 2011). At the other end of the economic spectrum, relatively well-off households in rural East Africa would continue to fish despite anticipated catch declines of 50% or more (Daw et al., 2012).

The late exiters (those that would continue hunting even when their catch was limited to low-biomass prey such as passerines) had the lowest mean and median incomes, presenting a potential caveat to our study. Yet domestic poultry and livestock and refrigeration are readily available for even the poorest villagers in the focal landscape (Hammond et al., 2015; Chang et al., 2016). Leisure was also the top ranked motivation for the poorest respondents. We believe that the income difference in exit thresholds did not manifest a livelihood poverty trap, but was rather a result of the fact that lower-income respondents lived in rural, high mountain villages where alternative leisure activities such as karaoke are limited.

Noncompliance with hunting regulations is a major cause for concern (St John et al., 2011; Nuno et al., 2013b; St John et al., 2013). The appropriate scale for regulation is subject to debate between top-down and bottom-up perspectives. Currently, Chinese laws and regulations regarding wildlife and exploitation are centrally determined and enforced at state and county levels (Grumbine and Xu, 2011). China is exceptional in the degree of public trust invested in the law and the widespread belief that the government need not consult its citizens when setting laws (Shi, 2001; Li, 2004). As such, there is typically acknowledgment of the law’s legitimacy, even on the part of inmates (Zhang et al., 1999). China extensively disseminates its laws, resulting in high rates of legal awareness (Li, 2004).

Respondents to our quantitative and semi-structured surveys were aware of laws governing hunting, and expressed a surprising degree of acceptance. In fact, our interviewees believed that all species are banned for hunting, which is stricter than the law. The perception that all birds and mammals are protected from harvest may be due to two factors: (1) restricted access to protected areas, as there are no large forest patches outside of protected lands (Xu et al., 2014), and (2) the firearms ban, as hunters in this region typically use guns.
Respondents did not argue that they should be permitted to hunt, nor did they invoke ancestral rights, sovereignty, or self-determination, as has been the case in other rural tropical contexts (Colchester 2000; Perreault 2003; El Bizri et al. 2015). All of the respondents stated that the state was morally correct in setting and enforcing laws to protect wildlife.

Yet acknowledging the law does not guarantee compliance, and we assert that top-down hunting and firearm restrictions has provoked defiance in Xishuangbanna. While inadequate patrolling has permitted hunting to continue in Xishuangbanna, the perception that enforcement relies on unfair tip-off and forced interrogation tactics has encouraged bottom-up cooperation against the state. It is thus challenging to conduct research on the efficacy of state intervention; enforcement has succeeded in making public conversation about hunting highly sensitive, especially with outsiders, but has not curbed excessive hunting effort.

Strong kinship ties and shared ethnic identity reinforced by the traditional Chinese system of ‘guanxi’ (interpersonal connections) may be a powerful guarantor of confidentiality and deterrent to reporting one’s neighbor for illegal hunting violations (Hwang 1987; Wang et al. 2008). Our results on the interactions between hunters and their confederates suggest that there is some degree of ethnic homophily at play (Barnes-Mauthe et al. 2013; Barnes et al. 2016). This is most likely due to the fact that hunters tend to associate with members of their own villages, or those nearby.

For a diffuse and relatively invisible behavior such as hunting, village-level enforcement in rural settings may be powerful and more effective than top-down control (Ostrom et al. 1994, 1999; Gibson et al. 2005). The semi-structured interviewees preferred that regulation of hunting be devolved to individual villages rather than county- and state-level forestry and environmental protection bureaus. Community programs can produce rapid and marked changes in the rates of illegal hunting. In Thailand, village interventions led to increased tiger (*Panthera tigris*) abundance and reduced illegal hunting (Steinmetz et al. 2014). Similarly, village committees in Cambodia were able to enforce protection for the Critically Endangered
Giant Ibis (*Thaumatibis gigantea*), fostering a local ethic of protecting habitats and nesting sites [Clements et al. 2010](https://doi.org/10.1017/S0006320710000647). Future work in Xishuangbanna should verify the appropriate scale for regulating hunting, and identify potential interventions that could curb hunting behavior or direct it in a more sustainable fashion. One method would be to incorporate enforcement instruments or hunting legislation into exit scenarios to assess how different interventions could curtail excessive hunting effort.

Managing natural resources succeeds or fails based on the motivations of human users. We found that hunting in Southwest China is largely driven by a desire for outdoor recreation. Discounting the recreational component of hunter motivations can lead to inaccurate expectations about the impact of particular interventions. When catch rates and recreational utility are decoupled, regulation must use additional levers to shift behavior toward desired trajectories.
### Appendix 1

Additional information on the study location and interview question design.

<table>
<thead>
<tr>
<th>Village</th>
<th>Households</th>
<th>Distance via road to nearest urban center (km)</th>
<th>Percent of access road to urban center that is paved</th>
</tr>
</thead>
<tbody>
<tr>
<td>NP</td>
<td>23</td>
<td>8.84</td>
<td>74%</td>
</tr>
<tr>
<td>SJ</td>
<td>50</td>
<td>35.1</td>
<td>80%</td>
</tr>
<tr>
<td>YQ</td>
<td>83</td>
<td>25.3</td>
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</tr>
<tr>
<td>XM</td>
<td>60</td>
<td>3.2</td>
<td>100%</td>
</tr>
</tbody>
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<td>60</td>
<td>3.2</td>
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**Table A1**: The characteristics of the focal villages. The names of the villages are represented using symbols to protect respondent anonymity.
<table>
<thead>
<tr>
<th>Group</th>
<th>Common name</th>
<th>Local name</th>
<th>Species name</th>
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</thead>
<tbody>
<tr>
<td><strong>Large mammals</strong></td>
<td>Wild boar</td>
<td>Ye zhu or Dong</td>
<td><em>Sus scrofa</em></td>
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<td></td>
<td>Muntjac</td>
<td>Ji zi</td>
<td><em>Muntiacus muntjak</em></td>
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<tr>
<td></td>
<td>Grey peacock-pheasant</td>
<td>Guang gui or He hua</td>
<td><em>Polyplectron bicalcaratum</em></td>
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<td></td>
<td>Partridge spp.</td>
<td>Tuan ji</td>
<td><em>Arborophila ssp.</em></td>
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<td></td>
<td>Silver pheasant</td>
<td>Bai xian</td>
<td><em>Lophura nycthemera</em></td>
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<td></td>
<td>Wild junglefowl</td>
<td>Ye ji</td>
<td><em>Gallus gallus</em></td>
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<tr>
<td></td>
<td>Chinese francolin</td>
<td>Ma ji</td>
<td><em>Francolinus pintadeanus</em></td>
</tr>
<tr>
<td></td>
<td>Mountain bamboo-partridge</td>
<td>Zhe gu</td>
<td><em>Bambusicola fytchii</em></td>
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<tr>
<td></td>
<td>Hornbill spp.</td>
<td>Da zui qiao</td>
<td>Primarily <em>Anorrhinus australis</em></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Small birds</strong></td>
<td>Smaller barbet spp.</td>
<td>Gu du lu ke or Naoe bao</td>
<td>Primarily <em>Psilopogon asiaticus</em></td>
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<td></td>
<td>Woodpeckers</td>
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<td><em>Chrysocolaptes spp.</em></td>
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<td>Laughingthrush</td>
<td>Shan fu</td>
<td><em>Garrulax spp.</em></td>
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<td><em>Pycnonotus</em></td>
</tr>
<tr>
<td></td>
<td>Unidentified small bird</td>
<td>Xiao niao</td>
<td>Primarily genera <em>Pycnonotus</em>, <em>Turdidae</em></td>
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</tbody>
</table>

Table A2: The list of species provided on the hunting trip data sheets. Common name denotes the species or genus of interest.
<table>
<thead>
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<th>Variable</th>
<th>Measure</th>
</tr>
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<tbody>
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<td><strong>Behavior on trips</strong></td>
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<tr>
<td>Long hunt trip duration</td>
<td>Days</td>
</tr>
<tr>
<td>Short hunt trip duration</td>
<td>Hours</td>
</tr>
<tr>
<td>Weapon usage</td>
<td>Frequency (0-3)</td>
</tr>
<tr>
<td>Consumption outcomes for hunted game</td>
<td>Frequency (0-3)</td>
</tr>
<tr>
<td><strong>Information sharing and group hunting</strong></td>
<td></td>
</tr>
<tr>
<td>Family members that also hunt</td>
<td>Checklist</td>
</tr>
<tr>
<td>Participation frequency</td>
<td>Frequency (0-3)</td>
</tr>
<tr>
<td>Topics for discussion</td>
<td>Checklist</td>
</tr>
<tr>
<td>Ethnicity of confidants and trip participants</td>
<td>Checklist</td>
</tr>
<tr>
<td>Age of confidants and participants</td>
<td>Younger, Same, Older</td>
</tr>
<tr>
<td>Whether confidants and participants are friends, family, or both</td>
<td>Yes/No</td>
</tr>
<tr>
<td>Whether confidants and participants reside in same village as respondent</td>
<td>Yes/No</td>
</tr>
</tbody>
</table>

**Table A3:** Questions regarding hunter behavior on trips and interactions with other hunters. The “frequency” 0-3 score corresponds to never, rarely, sometimes, and always. For checklists, the respondent indicated whether each item was or was not relevant (e.g. “Ethnicity of confidants and participants” checklist would have check boxes for each of the ethnic groups).
Appendix 2: Semistructured interview guide.

Section 1: Why hunters hunt in an era of high risk (perception)
1. What recreation options do local people have?
2. What livelihood options do local people have?
   a. What crops do farmers grow?
   b. How does this differ from the situation twenty years ago?
3. What thoughts do local people have regarding hunting?
4. Why do people continue to hunt now?
5. What are the upsides of hunting, if any?
   a. Before, what did people feel the benefits of hunting were?
6. What are the downsides of hunting?
7. What has made it easier to be a hunter in the past 20 years?
8. What has made it harder?
   a. Can you describe how the forest and animals have changed since you started hunting as a youth?
   b. Has the regulation of hunting changed since your youth?
9. Have any of these changes affected your or others decisions to hunt?
10. Many respondents have stated that young people (post-90s) hunt much less than their elders. What is causing this trend?
11. How do you feel about this trend where young people are hunting less and less?
    a. What is good about it?
    b. What is bad about it?

Section 2: Enforcement and leakage
1. Are all forests equally protected?
   a. Is it more or less risky to hunt in certain areas?
   b. What about different distances to villages?
2. How do people select which places they want to go hunt?
   a. Do they think differently about国有林(nationalized forest), farmland,集体林 (community forest), and protected areas?
   b. Are there any trade offs in terms of risk and reward?
3. What precautions can hunters take to avoid punishment?

Section 3: Enforcement and reasons for hunting
1. In the interview, lots of people have mentioned that hunting is really tightly enforced now.
   a. What are the laws?
   b. What is protected? / What is illegal to do?
   c. Historically, were there local rules in your community about getting pigs, muntjac, and other prized animals?
   d. Are there any local rules in the community about getting animals now?
2. How does the local village committee enforce these laws?
   a. How do forestry rangers in villages enforce these laws?
   b. How do the forestry police at the county, state, or provincial level enforce the law?
3. How does the forestry police get information about people hunting?
4. How do local people feel about this?
   a. How do they feel about the way the policies get this information?
   b. How do they feel about people who provide this information?
5. What risks, if any, do people face when they report people in their village for hunting? What about if they report outsiders from the village? What about outsiders who know or are related to people in the village?
6. What if the village forest/protected area ranger reports that a local person is illegally hunting? What risks and rewards might he receive?
   a. What if they report an outsider? Would they face the same level of risk? Would they gain the same level of benefits?
7. Do people generally respect local institutions (village committee) more than centralized ones (county/state/provincial level)? Are people more afraid of local institutions than centralized ones?

Section 4: Enforcement and interviews
1. What do you worry about when participating in this interview?
   a. We know each other well. How do you think the general population would respond to my last interview? To this interview?
   b. What would other people worry about when participating in this interview, particularly people who do not know us well?
2. What are the potential repercussions of responding to this interview?
   a. What about the previous interviews that I have done?
3. Do you think these repercussions are likely to happen?
4. Would people have responded differently to this interview a decade ago?
   a. What has caused people to respond differently?
Chapter 3

Randomized Response Techniques for Conservationists

Charlotte H. Chang, Maarten J.L.F. Cruyff

3.1 Abstract

Illegal activities that exploit biodiversity present grave conservation challenges. Monitoring and identifying the drivers of conservation crimes—violations of laws designed to protect natural resources from overexploitation—is a priority for conservation research and management. As direct questioning about illegal behaviors can induce non-response or evasive answers, researchers have adopted more complex indirect questioning techniques. The randomized response technique (RRT) is one of the most prominent and powerful indirect survey methods used in conservation, yet analyses of these data require sophisticated statistical models. To date, there has not been user-friendly software to perform inference on RRT data. We present an overview of three RRT models that cover single or multiple questions and provide an R package, zapstRR (ZoologicAl Package for RRT), that is accessible for experienced and
new R users. With this package, researchers can estimate the prevalence of conservation crimes, the number of illegal activities performed by individuals, perform regression, and correct prevalence estimates for evasive response bias. These models are illustrated with data from a case study on illegal bird hunting in Southwest China.

### 3.2 Introduction

Conservation crimes such as illegal logging, hunting, trapping, and fishing are among the gravest threats to global biodiversity (Hoffmann et al., 2011; Velho et al., 2012; Abernethy et al., 2013; Taylor et al., 2015; Maxwell et al., 2016). Although spatial, gear, species-specific, and/or seasonal restrictions seek to prevent overexploitation, the presence of rules alone is not enough to curtail conservation crimes (Butchart et al., 2010; Yu et al., 2010; St John et al., 2011, 2013). Managers would ideally obtain unbiased estimates of the prevalence of conservation crimes and oftentimes the sole method available is interviews. Yet respondents have a strong incentive to avoid self-incrimination, thereby rendering direct questioning ineffective (Blank and Gavin, 2009; Gavin et al., 2010; St John et al., 2010; Nuno et al., 2013b). Direct questioning may also compromise respondent safety, violating ethical principles (St John et al., 2014; St. John et al., 2016).

The randomized response technique (RRT) has become increasingly popular with practitioners and researchers seeking to pinpoint the prevalence of conservation crimes (St John et al., 2014; Nuno and St John, 2015). RRT has been used to address pressing issues such as bushmeat hunting and consumption (Solomon et al., 2007; Razafimanahaka et al., 2012; Conteh et al., 2015; Randriamamonjy et al., 2015), non-compliant recreational and commercial fishing practices (Blank and Gavin, 2009; St John et al., 2010; Arias and Sutton, 2013; Thomas et al., 2015), and retaliatory wildlife killings due to human-wildlife conflict (St John et al., 2012, 2015; Santangeli et al., 2016). RRT has even permitted researchers to evaluate the success of conservation interventions (Lewis, 2015).
When conducting randomized response questionnaires, respondents use a randomizer—such as a die roll, a card deck, or a spin top—and answer based on the combination of its outcome and their own true state (Warner, 1965; Boruch, 1971; Kuk, 1990). The randomizer outcome is known only to the respondent. The respondent’s true state may or may not be reflected in their answer, thereby ensuring confidentiality (Lensvelt-Mulders et al., 2005a; St John et al., 2012, 2014). Because the distribution of the randomizer is known by design, a statistical model can be specified that corrects for response randomization. Despite the premise that RRT should reduce biased answers, respondents may sometimes lie or fail to state “yes” when instructed by the randomizer (Clark and Desharnais, 1998; Coutts and Jann, 2011; Ostapczuk et al., 2011). This tendency to consistently answer “no” to avoid admitting guilt is known as evasive response bias.

Typically, researchers aim to assess how demographic, sociocultural, economic, or psychological covariates associate with the sensitive trait of interest. Although there are several robust RRT statistical models (Lensvelt-Mulders et al., 2005b; Böckenholt and van der Heijden, 2007; Cruyff et al., 2007; van den Hout et al., 2007; Cruyff et al., 2008a; Fox and Meijer, 2008; Gingerich et al., 2015; Blair et al., 2015; Cruyff et al., 2016), the absence of user-friendly software implementing these methods has handicapped prevalence analyses and regression modeling (Keane et al., 2015; Nuno and St John, 2015). One notable deficit is the difficulty in performing joint inference over multiple RRT items. For reasons such as the accuracy of recall, and question interpretability, it is often most sound to ask detailed questions about individual activities, rather than a blanket statement (e.g. “In the past year, have you hunted tigers?” instead of “Do you hunt illegally?”) (Newing et al., 2011; Golden et al., 2013b; St John et al., 2014; Bennett et al., 2017). Virtually every application of RRT in the environmental sciences has encompassed multiple conservation crimes (Solomon et al., 2007; St John et al., 2010, 2012; Razafimanahaka et al., 2012; Thomas et al., 2015; St John et al., 2015; Santangeli et al., 2016).
To encourage and facilitate the usage and analysis of RRT data, we introduce an open-source R (R Core Team, 2016) package (zapstRR: ZoologicAl Package for RRT) for univariate and multivariate RRT data (Table 3.1). The package contains three models that allow for prevalence estimation as well as regression analysis for individual (binary) and multiple (ordinal scores or joint inference over several prompts) RRT items. One of the models can estimate the rate of evasive response bias and produce corrected prevalence and regression statistics. These models are briefly described in Section 3.4. We illustrate the models with a case study on illegal bird hunting in Southwest China (Section 3.3, Chang et al. 2016, 2017).

<table>
<thead>
<tr>
<th>Description</th>
<th>Single</th>
<th>Multiple</th>
<th>Evasive</th>
<th>Function</th>
</tr>
</thead>
<tbody>
<tr>
<td>Univariate RRT (3.1)</td>
<td>✓</td>
<td>–</td>
<td>–</td>
<td>RRunivariate</td>
</tr>
<tr>
<td>Sum score (3.3)</td>
<td>–</td>
<td>✓</td>
<td>–</td>
<td>RRsumscore</td>
</tr>
<tr>
<td>Item response theory (3.5)</td>
<td>–</td>
<td>✓</td>
<td>✓</td>
<td>RRirt</td>
</tr>
<tr>
<td>RRT data simulation</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>RRsimulate</td>
</tr>
<tr>
<td>RRT power analysis</td>
<td>✓</td>
<td>✓</td>
<td>–</td>
<td>powerRRT</td>
</tr>
</tbody>
</table>

Table 3.1: An overview of the functions in the package. A ✓ indicates that the estimator possesses a particular attribute or is suitable for the intended analysis. “Single” denotes an individual RRT prompt; “multiple”: multivariate inference over several RRT items. “Evasive” represents evasive response bias (failing to answer ‘yes’ when prompted or when that is the truthful state). The manuscript does not discuss RRsimulate or powerRRT but the package vignette presents example code.

3.3 A conservation crime case study in Southwest China

Xishuangbanna Dai Autonomous Prefecture (henceforth, Xishuangbanna) is a biodiversity and cultural hotspot within Southwest China with more than 13 distinct ethnic groups, some of which historically practiced subsistence hunting (MacKinnon and MacKinnon, 1986; Myers et al., 2000; Xu, 2006; Sturgeon, 2010). Overexploitation has extirpated several mammal and avian species over the past 20-50 years (Yang et al., 2004; Corlett, 2007; Kai et al., 2014).
In that period, villagers were re-settled out of the protected area system, and smallholder rubber (*Hevea brasiliensis*) and tea (*Camellia sinensis*) became the primary income source for villagers (Lai and Wang 1998; Xu et al. 2005a; Grumbine and Xu 2011; Allendorf and Yang 2013; Hammond et al. 2015).

Gun ownership, hunting, and entering protected areas are illegal under two national laws: the 1988 Wildlife Protection Law (Articles 8, 9, and 10, Chapter II; Sharma 2005; Li 2007; Xu and Melick 2007; Yu et al. 2013) and the 1996 Firearm Control Law (Harris, 2007). Although the regulations on protected area access and hunting have been more aggressively enforced in the past decade, illegal hunting persists in this landscape (Kai et al. 2014; Chang et al. 2017).

Our study occurred in 20 villages located nearby two Xishuangbanna National Nature Reserve protected areas (Figure 1 in Chang et al. 2017). The villages were randomly selected from a GIS vector layer, and were constrained to lie within 5km of the nearest protected area. Within each village, 10 households were selected at random and the male head of the house was interviewed. 200 adult male (≥ 18 years of age) villagers were interviewed between February–March 2015. The lead author wrote the questionnaire on (1) socio-economic covariates, (2) attitudes toward bird hunting, and (3) bird hunting activity in the past year in Mandarin Chinese and translated it back to English. Ethical oversight was conducted by the Princeton University Institutional Review Board (#6682) and Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences (#2015.2).

As admitting to hunting birds reveals several criminal activities—gun hunting, entry into protected areas, and exploitation of protected species—we used RRT to determine whether or not the respondents had hunted three focal bird taxa (barbets *Psilopogon* spp., bulbuls (genera *Pycnonotus, Iole, Hypsipetes, Ixos*), and partridge *Arborophila* spp.) in the past year. We asked “Have you hunted x in the past year?” and the question order
was randomized (Qualtrics Offline Surveys). We sought to evaluate the following research questions using these data:

1. What was the prevalence of hunting each of the three bird species?

2. How many species did hunters capture in the past year?

3. What characteristics distinguish hunters from non-hunters?

4. Were the data significantly affected by evasive responses?

We used two RRT designs: forced (Warner, 1965; Boruch, 1971), currently the most popular RRT design used in conservation, and disguised response (Kuk, 1990), which may provide additional respondent protection through the use of playing cards instead of verbal (dis)agreement (Blair et al., 2015). Below, we describe the question designs and statistical models for RRT data.

### 3.4 Randomized response models

Each RRT question design explicitly specifies conditional misclassification probabilities, i.e. the probability that the answer is misclassified given the true state of the respondent on the sensitive trait. In the literature on randomized response, the notation used to describe statistical models varies from paper to paper. To avoid confusion and facilitate interpretation, we present a unified notation based on conditional misclassification probabilities.

Let the random variable $Y$ denote the observed response, for $y \in \{0 = \text{no}, 1 = \text{yes}\}$, and $Z$ the true sensitive trait state ($z \in \{0 = \text{absent}, 1 = \text{present}\}$).

#### 3.4.1 Conditional misclassification probabilities

**Forced response** In the forced response (FR) design (Boruch, 1971), the respondent either answers truthfully, or with a forced ‘yes’ or “no”, depending on the outcome of a randomizer.
In our study, respondents rolled a die and were instructed to answer ‘yes’ if the die showed 1, “no” for 6, and answer truthfully otherwise. The conditional misclassification probability that a hunter \((z = 1)\) answers ‘yes’ is therefore \(P(\text{truthful ‘yes’}) + P(\text{forced ‘yes’}) = \frac{2}{3} + \frac{1}{6}\). Analogously, the probabilities that a non-hunter \((z = 0)\) answers “no” is \(P(\text{truthful “no”}) + P(\text{forced “no”}) = \frac{2}{3} + \frac{1}{6}\).

As such, in our case study, the conditional misclassification probabilities for the forced response design were:

<table>
<thead>
<tr>
<th>Observed response ((y))</th>
<th>True state ((z))</th>
<th>Hunter</th>
<th>Non-hunter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yes</td>
<td>(p_{y=1</td>
<td>z=1} = \frac{5}{6})</td>
<td>(p_{y=1</td>
</tr>
<tr>
<td>No</td>
<td>(p_{y=0</td>
<td>z=1} = \frac{1}{6})</td>
<td>(p_{y=0</td>
</tr>
</tbody>
</table>

**Disguised response** We implemented the disguised response design ([Kuk](#)) with two decks of cards \((n = 15 \text{ cards/deck})\), each of which had fixed proportions of red and black cards. The “yes” deck contained 80\% red and 20\% black cards, and “no” contained 20\% red and 80\% black cards. The respondent was instructed to report the color of card drawn from the deck corresponding to their true answer, and then return the card to the deck and shuffle the deck to ensure a random ordering of cards.

As the red cards were associated with a ‘yes’ response, the probability that a hunter answers ‘yes’ is equal to the proportion of red cards in the ‘yes’ deck, and the probability that a non-hunter answers ‘no’ is equivalent to the proportion of black cards in the ‘no’ deck. The conditional misclassification probabilities under this design are therefore

\[
p_{y=1|z=1} = p_{y=0|z=0} = \frac{4}{5}
\]

\[
p_{y=0|z=1} = p_{y=1|z=0} = \frac{1}{5}
\]
3.4.2 The univariate model

The univariate RRT design denotes the use of a single dichotomous (binary ‘yes’ or ‘no’) question. The probability of observing response $y$ given the true state $z$ is then

$$
\pi_y^* = \sum_{z=0}^{1} p_{y|z} \pi_z, \quad (3.1)
$$

where $\pi_z$ denotes the probability of the true state $z$ (or the prevalence of the sensitive trait), and $p_{y|z}$ the conditional misclassification probability of observing $y$ given true state $z$.

The binary logistic regression model

Expression (3.1) can be extended to accommodate covariates under a binary logistic regression model. The probability that individual $i$, for $i \in \{1, \ldots, n\}$, possesses the sensitive trait is defined as

$$
\pi_{z_i=1} = \frac{\exp(\alpha + x_i'\beta)}{1 + \exp(\alpha + x_i'\beta)}, \quad (3.2)
$$

where $\alpha$ is the intercept, $x_i = (x_{i1}, \ldots, x_{ik})$ the covariate vector for individual $i$, and $\beta = (\beta_1, \ldots, \beta_k)$ the regression coefficients vector.

3.4.3 The sum score model

Researchers often seek to conduct joint inference on multiple sensitive traits (St John et al., 2012). One statistic of interest may be the ordinal sum of 0–$K$ sensitive traits. In an RRT design with $K$ sensitive questions, the sum score model (Cruyff et al., 2008b) can be used to estimate the prevalence of the total number of sensitive traits $z^+$, for $z^+ \in \{0, \ldots, K\}$. The sum score model is given by

$$
\pi_{y^+}^* = \sum_{z^+ = 0}^{k} p_{y^+|z^+} \pi_{z^+}, \quad (3.3)
$$
where $y^+ \in \{0, \ldots, K\}$ is the sum of “yes” responses, and $p_{y^+ | z^+}$ the probability of observing $y^+$ “yes” responses given $z^+$ sensitive traits.

The ordinal regression model

The ordinal regression sum score model extends Expression (3.3) to include covariates in predicting the true cumulative sum score probabilities:

$$
\pi_{z_i \leq s} = \frac{\exp(\alpha_s - x_i'\beta)}{1 + \exp(\alpha_s - x_i'\beta)},
$$

(3.4)

for $s = 0, \ldots, K - 1$, where $\pi_{z_i \leq s}$ is the cumulative probability of having $s$ sensitive traits or less, and $\alpha_s$ the corresponding intercept for each sum score level ($s$).

The larger the intercepts, the more the cumulative probabilities approach 1. The $\beta$ coefficients indicate the change in the cumulative probabilities as the corresponding predictors, $X$, increase with one unit. Hence, a positive (negative) coefficient decreases (increases) the probability of possessing no sensitive traits, and increases (decreases) the probabilities of having one or more sensitive traits.

3.4.4 The IRT model

The item response theory (IRT) model is a multivariate model for the analysis of $K$ randomized response items. The model is characterized by a person parameter, $\theta_i$, representing the individual’s propensity for possessing sensitive traits (Rasch 1961; Coombs 1964), and item parameters, $\gamma_k$, denoting the degree of sensitivity of the $k$-th trait—akin to the trait’s rarity (van der Linden and Hambleton 1997; Fox 2005; Revelle 2014b). The IRT model for randomized response is given by

$$
\pi_{y_{i,1}, \ldots, y_{i,K}} = \sum_{k=1}^{K} \left( \prod_{j=0}^{j=1} p_{y_j | z_j} \prod_{k=1}^{K} \pi_{z_{ik}} \right),
$$

(3.5)
where $\pi^*_{y_1,\ldots,y_K}$ represents the probability of observing the response profile $y_1, \ldots, y_K$ (e.g. \{0 \ldots 0, 0 \ldots 1, \ldots 1 \ldots 1\}) for individual $i$. The term $\prod_{k=1}^K \pi_{z_{ik}}$ denotes the product of the probabilities of the true states of individual $i$ across all the items. The probability of possessing sensitive trait $k$ is

$$
\pi_{z_{ik}=1} = \frac{\exp(\theta_i - \gamma_k)}{1 + \exp(\theta_i - \gamma_k)}.
$$

(3.6)

For prevalence estimation, $\theta_i$ is set to 0 for all $i \in \{1, \ldots, n\}$. For regression analysis, we specify $\theta_i = x_i' \beta$. The IRT model assumes local independence: the items must be independent given the value of $\theta_i$. As a consequence, the model has degrees of freedom to spare. With two items, for example, there are four possible response profiles, $y_{i,1}, y_{i,2} \in \{00, 01, 10, 11\}$, that are used to estimate three parameters: $\gamma_1, \gamma_2$ and $\theta_i$. The model therefore has one degree of freedom.

We can use this degree of freedom to estimate an additional parameter, $\phi$, which represents the rate of evasive response bias. This approach has been successfully applied to quantify non-compliance with RRT designs, and yields prevalence estimates that are corrected for evasive responses (Böckenholt and van der Heijden 2007; Cruyff et al. 2008; Cruyff et al. 2016).

### Modeling evasive response behavior

The IRT model assumes local independence: the items must be independent given the value of $\theta_i$. As a consequence, the model has degrees of freedom to spare. With two items, for example, there are four possible response profiles, $y_{i,1}, y_{i,2} \in \{00, 01, 10, 11\}$, that are used to estimate three parameters: $\gamma_1, \gamma_2$ and $\theta_i$. The model therefore has one degree of freedom.

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### 3.4.5 Parameter estimation

The parameters of the univariate, sum score, and IRT models can be estimated by maximization of the corresponding log likelihood functions. This procedure yields Maximum Likelihood Estimators (MLEs), which have two desirable properties: estimates are bound to the interval $(0, 1)$, and standard errors are optimally efficient.

However, with randomized response data, boundary solutions occur when an observed response frequency is below its minimum expected value (most often when
\[ \sum_{i=0}^{N} y_i < Np_{y=1|z=0}. \] In the univariate forced response design, for example, this arises when the observed proportion of ‘yes’ responses is below the minimum expected value of 1/6 (the probability of a forced ‘yes’). In that case the prevalence estimate will be 0, but the standard error will no longer be interpretable; it will be either extremely large or impossible to compute. Boundary solutions can result from a combination of low sensitive trait prevalence and evasive response bias.

In case of a boundary solution, there are two ways to obtain the standard errors. The first is to use a Method of Moments Estimator (MME), and another is to perform a nonparametric bootstrap. The MME can yield negative prevalence estimates, but its standard errors are still trustworthy (Cerquera et al., 2012). Under boundary conditions, we recommend the MME approach for the univariate model without predictors, and the bootstrap for the remaining models.

To test the significance of predictors in models with boundary solutions, we recommend the likelihood-ratio (LR) test. To perform this test, the model with and without the predictor(s) of interest should be fitted. The test statistic equals twice the difference of the log likelihood values of the models and has an approximate chi-squared distribution with the degrees of freedom equal to the number of predictors minus the number of predictors in the null model. When boundary solutions occur, the LR test performs much better than the standard t-test statistic.

### 3.5 Evaluating a conservation crime using randomized response data

We explore the four research questions that we presented in Section 3.3.

**Research Question 1:** What was the prevalence of hunting each of the three bird species?
The prevalence estimates for barbet, bulbul, and partridge hunting are MMEs obtained with the univariate model (3.1) (Table 3.2). Based on the prevalence estimate for bulbul hunting and its 95% confidence interval, we can conclude that hunting for bulbul is present (significantly greater than 0). Our univariate data for barbet and partridge hunting demonstrate boundary conditions where the possibility of hunting is not statistically confirmed (barbet), but can also not be dismissed (partridge).

Because the lower confidence bound of barbet hunting was 0 (originally negative and reset to 0), we cannot conclude that its prevalence is significantly greater than 0. On the other hand, the prevalence estimate for hunting partridge was negative (i.e. $\hat{\pi}_{z=1,FR} = -0.4; \hat{\pi}_{z=1,DR} = -1.6$). However, its non-negative upper bound (around 7.5%) means that the possibility that partridges are hunted cannot be excluded.

There was no evidence of significant differences in the prevalence estimates produced by the forced and disguised responses. Moreover, the proportion of respondents who felt that the design preserved their anonymity and was “easy to answer” was similar (FR=69.9% and DR=72.9%). In subsequent sections where zapstRR functions are applied to the case study data, only the forced response data were used; to date, the forced response design has been the primary RR technique employed in the conservation science literature [Solomon et al., 2007; St John et al., 2010; Razafimanahaka et al., 2012; Arias and Sutton, 2013; Conteh et al., 2015].

<table>
<thead>
<tr>
<th>Bird</th>
<th>$\hat{\pi}_{z=1}$ (%)</th>
<th>SE (%)</th>
<th>95% CI (%)</th>
<th>$\hat{\pi}_{z=1}$ (%)</th>
<th>SE (%)</th>
<th>95% CI (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Barbet</td>
<td>1.2</td>
<td>4.1</td>
<td>(0, 9.3)</td>
<td>2.8</td>
<td>5.0</td>
<td>(0, 12.6)</td>
</tr>
<tr>
<td>Bulbul</td>
<td>19.4</td>
<td>5.0</td>
<td>(9.7, 29.2)</td>
<td>28.4</td>
<td>5.9</td>
<td>(16.9, 40.0)</td>
</tr>
<tr>
<td>Partridge</td>
<td>-0.4</td>
<td>4.0</td>
<td>(0, 7.5)</td>
<td>-1.6</td>
<td>4.8</td>
<td>(0, 7.7)</td>
</tr>
</tbody>
</table>

Table 3.2: Prevalence estimates ($\hat{\pi}_{z=1}$) for illegal bird hunting in Southwest China produced by RRunivariate from Expression (3.1).

**Research Question 2:** How many species did hunters capture in the past year?
We estimated the prevalence of hunting 0, 1, 2, or 3 bird species (barbet, bulbul, and/or partridge) in Southwest China with the sum score model \(3.3\). Table \ref{tab:prevalence} shows the prevalence MLEs for the four sum scores. According to these estimates, about 82.4\% of the population did not hunt any of the bird species, and less than 1\% hunted more than one. The MLE for hunting 2 birds was on the boundary of the parameter space, so the reported SEs are likely not trustworthy. In this case, the bootstrap 95\% confidence intervals would be preferred to those obtained with the MLE procedure.

<table>
<thead>
<tr>
<th>Sum score</th>
<th>(\hat{\pi}) (%)</th>
<th>SE</th>
<th>t-value</th>
<th>p-value</th>
<th>95% CI (\text{MLE})</th>
<th>95% CI (\text{boot})</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>82</td>
<td>8.2</td>
<td>10.0</td>
<td>(10^{-16})</td>
<td>(66.2, 98.5)</td>
<td>(68, 95.8)</td>
</tr>
<tr>
<td>1</td>
<td>17</td>
<td>11.5</td>
<td>1.5</td>
<td>0.15</td>
<td>(0, 39.4)</td>
<td>(0, 31.5)</td>
</tr>
<tr>
<td>2</td>
<td>0</td>
<td>6.3</td>
<td>0.01</td>
<td>0.99</td>
<td>(0, 21.4)</td>
<td>(0, 13.1)</td>
</tr>
<tr>
<td>3</td>
<td>0.8</td>
<td>2.2</td>
<td>0.4</td>
<td>0.72</td>
<td>(0.5)</td>
<td>(0.3)</td>
</tr>
</tbody>
</table>

Table 3.3: Prevalence estimates \((\hat{\pi})\) for the number of bird species hunted (“sum score”) using \(\text{RRsumscore}\).

**Research Question 3:** What characteristics distinguish hunters from non-hunters?

To illustrate the application of the three RRT regression models (univariate logistic, ordinal, and item response), we used the covariate age (standardized to \(z\)-scores) to predict which individuals did and did not hunt the focal birds (Table \ref{tab:logistic}).

For bulbul, age did not have a significant effect in predicting hunting activity under binary logistic regression. However, for barbet and partridge, the logistic regression model produced extremely large parameter estimates, and failed to generate meaningful SE’s. Due to a combination of low prevalence—particularly for partridge—and relatively small sample size \((n = 189)\), there was insufficient power to properly identify the logistic regression parameter. However, the likelihood ratio \(\chi^2\) statistics trended toward significance in both cases, suggesting some effect associated with age. The positive \(\hat{\beta}_{\text{age}}\) estimates for barbet and partridge indicate that older people were more likely to hunt those birds than the young.
Table 3.4: Parameter estimates for age evaluated using logistic (3.2), ordinal sum score (3.4), or IRT regression (3.6). The \( p \)-values were assessed for (1) the \( t \)-statistic and (2) the likelihood ratio test (against a covariate-free null). The function calls were \texttt{RRunivariate}, \texttt{RRsumscore}, and \texttt{RRirt}, respectively.

\[
\begin{array}{cccccccc}
\text{Model} & \text{Bird} & \hat{\beta}_{\text{Age}} & \text{SE} & \text{t-value} & \text{p-value} & \chi^2_{(1)} & \text{p-value} \\
\hline
\text{Logistic} & \text{Barbet} & 133.4 & - & - & - & 3.1 & 0.08 \\
& \text{Bulbul} & -0.08 & 0.33 & -0.02 & 0.82 & 0.06 & 0.8 \\
& \text{Partridge} & 161.1 & - & - & - & 3.4 & 0.07 \\
\text{Ordinal} & \text{All 3} & -1.66 & 1.0 & -1.6 & 0.1 & 7.5 & 0.01 \\
\text{IRT} & \text{All 3} & 0.17 & 0.11 & 1.5 & 0.1 & 1.7 & 0.2 \\
\end{array}
\]

In the ordinal regression model, the intercept \( \alpha_2 \) (for a cumulative sum score of two or fewer species) was large (\( \hat{\alpha}_2 = 15.1, SE = 645.3 \)), indicating that the probability of hunting two or fewer bird species approached 1. Thus, the probability of hunting three bird species was near 0. However, \( \alpha_2 \) had an extremely inflated standard error, which was more likely to occur as \( s = K - 1 \) is near the boundary of the parameter space. \( \hat{\beta}_{\text{age}} \) was negative, suggesting that younger men had a propensity to hunt more species than the elderly. As these estimates were on the boundary, the LR test was preferred, and was significant for age.

The IRT model did not generate a significant result for age. As such, the IRT regression indicated there was insufficient evidence for a common, clear effect of age on the probability of hunting the three focal bird species. The item intercepts (not shown) indicated that partridge had the highest sensitivity (largest value of \( \gamma \)) and bulbul the lowest.

**Research Question 4:** Were the data significantly affected by evasive responses (\( \phi \))? 

The IRT evasive response model indicated that about 16.9\% of the respondents consistently answered ‘no’ to all three questions, irrespective of the randomizer and their own true state (Table 3.5). The model estimated slightly higher prevalences of illegal bird hunting after correcting for evasive response bias than the univariate estimates (Table 3.2).

However, although the estimate of \( \phi \) was substantial, it was not significant. One could argue that with a relatively small sample size of 189, the power to obtain a significant
estimate may be insufficient. In such cases, one could model average estimates arising from a null model (without evasive response bias) and a model with $\phi$.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>$\hat{\pi}$ (%)</th>
<th>SE</th>
<th>t-value</th>
<th>p-value</th>
<th>95% CI</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>$P$(Barbet)</td>
<td>6.5</td>
<td>6.3</td>
<td>1.03</td>
<td>0.3</td>
<td>(0, 18.9)</td>
<td>(0, 20.2)</td>
</tr>
<tr>
<td>$P$(Bulbul)</td>
<td>28.5</td>
<td>9</td>
<td>3.2</td>
<td>0.002</td>
<td>(10.9, 46)</td>
<td>(13.1, 46.4)</td>
</tr>
<tr>
<td>$P$(Partridge)</td>
<td>4.6</td>
<td>6.1</td>
<td>0.8</td>
<td>0.5</td>
<td>(0, 16.5)</td>
<td>(0, 17.5)</td>
</tr>
<tr>
<td>$\phi$</td>
<td>16.9</td>
<td>11</td>
<td>1.5</td>
<td>0.1</td>
<td>(0, 38.5)</td>
<td>(0, 38.4)</td>
</tr>
</tbody>
</table>

Table 3.5: Prevalence estimates of the IRT model corrected for evasive response bias ($\phi$) with \texttt{RRIrt}. The prevalence estimates for illegal hunting for the three bird species ($P$(bird)) were corrected in light of the evasive response estimate ($\phi$).

3.6 Discussion

The three randomized response technique (RRT) models—univariate, sum score, and item response theory (IRT)—can work in tandem to uncover latent patterns in the data. From the univariate logistic regression model, it appeared that age would depress the probability of bulbul hunting, and potentially increase the propensity to hunt barbet and partridge, though the first estimate was insignificant and the last two suffered from inadequate statistical power. The sum score model indicated that older individuals likely hunted fewer bird species than the young. Under the IRT model, older individuals were more likely to hunt the focal bird species, though the predictor was ultimately not significant.

Interpreting the multivariate models relies on the question context. In Xishuangbanna, Chang et al. (2017) observed that hunters would indiscriminately and opportunistically target many species of birds and mammals. As such, the ordinal sum scores represent successful kills rather than intent or ideation—as hunters would potentially seek to kill any of the four focal bird species.

Previously, researchers have used univariate regression (Solomon et al., 2007; Jones et al., 2008; Razafimanahaka et al., 2012) or have deployed post-hoc multivariate analyses where
RRT-induced noise could not be controlled \cite{stjohn2012}. The sum score and IRT models thus permit for novel analyses that have been heretofore inaccessible for conservation practitioners and researchers. One benefit of these models is that best practices from the perspective of research design—detailed and specific question prompts—translate to greater statistical power.

For instance, one powerful insight is the proportion of the population that commits multiple conservation crimes. If a very small proportion of individuals are responsible for the vast majority of illegal activities in a landscape, an intervention could be much more targeted than if the activities were more diffusely spread. Our package facilitates such analyses with the models \eqref{eq:3.3} \eqref{eq:3.5}. In addition, item response theory can estimate and correct for evasive response bias.

Our case study demonstrated that the simplest methods for analyzing RRT data (Expressions \eqref{eq:3.1} \eqref{eq:3.2}) can be sufficient, but struggle when there is substantial non-compliance, relatively rare behaviors, or smaller sample sizes. Given that management may seek perfect compliance with regulations, it is alarming that the commonly used estimators tend to fail in situations where the prevalence is low. Moreover, edge cases could be driven not by low prevalence but rather by evasive response bias \cite{bockenholt2007,cruyff2007,gingerich2015,cruyff2016}. Our data had a non-trivial but statistically insignificant level of evasive responses. Controlling for one-sided lying would improve inference for future applications of RRT.

Edge cases are particularly likely for rare activities—be it because of truly low prevalence of the activity or, more worrisome, dwindling populations for exploitation. In the package, users can estimate the statistical power of different sample sizes for specified prevalence levels \texttt{powerRRT}. Further information can be found in the package vignette.

Despite the difficulties inherent in RRT implementation and analysis, it remains one of the most powerful and statistically efficient questioning techniques for stigmatized behaviors.
Importantly, by anonymizing individual responses, RRT also affords a degree of protection to the studied population, which is critical to conducting ethical research. We contribute to the utility of this survey approach by comparing existing and new techniques, and by making all of these estimators easily accessible in the R package zapstRR.
Chapter 4

Hunters just want to have fun: recreational covariates and hunting in Southwest China

Charlotte H. Chang, Sophie J. Williams, Maarten J.L.F. Cruyff, Simon A. Levin, David S. Wilcove, Mingxia Zhang, Ruichang Quan

4.1 Introduction

Although biodiversity conservation has achieved significant progress in sectors such as protected area establishment and human-wildlife conflict resolution (Yu et al., 2002), excessive and unregulated hunting pressure is still a major threat to vertebrates, particularly in the developing world (Ahumada et al., 2011; Abernethy et al., 2013; Ripple et al., 2015; Maxwell

\[1\]To be submitted. Findings from this chapter have been presented at the 2015 Association for Tropical Biology and Conservation (ATBC), Asia Pacific Chapter Meeting in Phnom Penh, Cambodia; 2016 Conservation Asia Meeting (ATBC and Society for Conservation Biology (SCB), Asia Section) in Singapore; 2017 ATBC Meeting in Mérida, Mexico.

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et al., 2016; Ripple et al., 2016). The litany of negative impacts to ecosystem function post-defaunation include reduced biotic seed dispersal (Terborgh et al., 2008; Harrison, 2011; Poulsen et al., 2013; Peres et al., 2016) and trophic cascades (Estes et al., 2011; Ripple et al., 2016). In many regions, understanding the motivations of poachers lags behind documenting the ecological consequences of defaunation.

China is a case in point. While the government has expanded protected areas and established human-wildlife conflict compensation (Bawa et al., 2010; Wu et al., 2011; Chen et al., 2013), illegal poaching has persisted (Corlett, 2007; Zhang et al., 2008; Corlett, 2014). Poaching is a particularly prominent problem in Southwest China where the economic and socio-cultural factors influencing hunting activity are poorly understood (Shilai et al., 1995; Corlett, 2007; Han et al., 2009; Kamp et al., 2015; Turvey et al., 2015).

As increased attention has been devoted to enforcing wildlife protection measures, asking questions about illegal poaching has become increasingly challenging (St John et al., 2014; Nuno and St John, 2015; Chang et al., 2017). Indirect questioning techniques can reduce non-response and social desirability bias, offering improved estimation of illegal activities (Lensvelt-Mulders et al., 2005a; St John et al., 2010). To date, two classes of indirect questioning have been employed in the conservation science literature: the randomized response technique (RRT) (Blank and Gavin, 2009; Gavin et al., 2010; Razafimanahaka et al., 2012; St John et al., 2012, 2015; Santangeli et al., 2016) and the unmatched count technique (Nuno et al., 2013b).

Under RRT, respondents deploy a randomizing device and answer based on its outcome, which can conceal or reflect their true state. For the unmatched count technique, interviewees are randomly given a control list of several non-sensitive items or an experimental list which also contains the sensitive item. We used RRT to evaluate illegal bird hunting in Southwest China, a national and international biodiversity hotspot (Tang et al., 2006), where overexploitation has decimated avian and mammalian populations, such as the Green
peafowl (*Pavo muticus*), hornbills, gaur (*Bos frontalis*), and Malayan sun bear (*Helarctos malayanus*) (Han et al., 2009; Kai et al., 2014; Chang et al., 2017).

Chang et al. (2017) addressed a major knowledge gap by exploring the motivations and behaviors of hunters in Southwest China. For the surveyed population of trusted hunter informants, recreation emerged as a major reason for hunting. However, at a broader scale, it was unclear what factors distinguished hunters from non-hunters. In this chapter, we estimated the prevalence of illegal hunting targeting four focal bird species: two gamebirds and two passerines. We identified factors—socioeconomic and attitudinal—that predisposed individuals to hunt. We evaluated the severity of evasive response bias in our RRT data. These analyses leveraged cutting-edge models for RRT data that are novel to the conservation science literature (Böckenholt and van der Heijden, 2007; Cruyff et al., 2008a; Fox and Meijer, 2008; Cruyff et al., 2016). Below, we describe the study system and the questionnaire design.

### 4.2 Methods

#### 4.2.1 Study location and legal context

Our study was performed in Xishuangbanna Dai Autonomous Prefecture (henceforth “Xishuangbanna”). Within XSBN, the national nature reserve (Xishuangbanna National Nature Reserve) contains several large protected lowland and montane tropical rainforest tracts (Clarke, 1999; Mo et al., 2011; Xu et al., 2014; Yi et al., 2014). The indigenous people of Xishuangbanna have traditionally practiced hunting (Xu, 1985, 2006), and the impacts of hunting have interacted synergistically with population growth and deforestation, leading to the local extirpation of mammal and bird species (Kai et al., 2014; Chang et al., 2017). Currently, the primary rural livelihoods are rubber (*Hevea brasiliensis*) smallholding in the lowlands or Pu’er tea plantations (*Camellia sinensis assamica*) in the highlands (Xu, 2006; Yi et al., 2014; Hammond et al., 2015).
As currently implemented, under the 1988 Wildlife Protection Law (WPL) and the 1994 Hunting Rifle and Ammunition Control Act, it is prohibited to own guns or engage in hunting in XSBN (Li 2007). Moreover, most forest-dependent vertebrates occur solely in protected areas (PA), and human access to PAs is generally prohibited under the 1994 Regulations on Nature Reserves Act (Article 18) (Harris 2007; Kram et al. 2012).

### 4.2.2 Survey design

The lead author wrote the survey in Mandarin Chinese with assistance from two co-authors (R. Quan and M. Zhang) on grammatical and vernacular edits. The survey was piloted with 20 hunter informants outside of the final sample. 200 adult male villagers (ages 18-65) were surveyed across 20 villages surrounding two protected areas in Xishuangbanna. Each village was located within 5km of a protected area, and site selection was conducted \textit{a priori} from published geospatial data (Xu et al. 2014). The dominant ethnic group in each village and altitude were used to stratify the sample.

The survey enumerators were two local fourth-year undergraduate students who were fluent in the local dialect. The enumerators and lead author approached the village committee for permission before conducting the survey. The enumerators walked the main paths in the village and selected every 3rd, 4th, or 5th household to interview. Generally the male head of household was interviewed. If a respondent refused to participate (2% of households), the enumerators went to the house next door.

The survey was performed using the Qualtrics Offline application for tablets. Permission was granted for the study by the Princeton University Institutional Review Board (\# 6682) and Xishuangbanna Tropical Botanical Garden (Introduction Letter \# 2015.2).
Socioeconomic and psychographic background information

Participants answered a variety of demographic and psychographic questions. Respondents reported their age, ethnicity, material wealth, household per-capita income, rubber plantation area, and crop area for all other commodities (e.g. bananas, pineapples, sugarcane, corn). One of the clearest indicators of wealth in Xishuangbanna is the ownership of a car (Hammond et al., 2015); as such, wealth was given a score of 0 if the respondent did not possess a pig, cow, fridge, or car; 1 for possession of a pig, cow, or fridge; 2 for two or more of the previously mentioned items; and 3 for car ownership.

The interview also touched on leisure pursuits: the number of outdoor activities (scored from 0-3: fishing, mushroom gathering, and/or wild vegetable harvesting), and entertainment activities (scored from 0-4: karaoke, basketball, tuoluo, and gambling). There was also a question about past hunting which received an ordinal score from 0-6, based on whether or not respondents had hunted several focal species a decade or more ago.

We asked questions about attitudes regarding hunting across four categories: social norms, personal attitudes, perceived behavioral control, and risk assessment (Ajzen, 1991). There were five questions in each category, and each question was scored on a 5-point Likert scale.

Illegal bird hunting in Southwest China

We selected four focal bird species—Lophura nycthemera Silver pheasant, Arborophila brunneopeectus Bar-backed partridge, Psilopogon virens Great barbet, and Pycnonotus jocosus Red-whiskered bulbul—based on hunter informant recommendations about birds that were commonly hunted or highly desired by hunters. For each species, the enumerator asked, “Since the 2014 Dai Water Splashing festival, have you hunted this bird?” Each question was implemented using forced response (RRT) and direct questioning for a total of eight
questions about bird hunting (four species and two methods of questioning). As such, there were two “blocks” of four questions.

For our forced response design, respondents rolled a die, ensuring that no one else could see its outcome. If it landed on 1, they were instructed to say “yes”, “no” for 6, and answer honestly if it showed 2 through 5. Two training questions pertaining to non-sensitive and prevalent behaviors (“Do you play cards?” and “Do you drink?”) were used to ensure that respondents understood how to comply with the question design.

The forced response questions were always presented before the direct question block. Within each block, the four bird species were randomly presented.

4.2.3 Statistical analysis

Due to the complexity and length of the survey (75 questions), 80% of respondents neglected or declined to answer at least one question, rendering some form of imputation necessary for regression analyses. We chose to impute these missing values using the hot-deck procedure wherein each missing value is replaced by an observed value from a matching respondent (Andridge and Little, 2011). Respondents were matched based on their age group (18 – 25, 25 – 35, 35 – 45, ≥ 55) and ethnicity. No variable had more than 10% missingness and most had only 1-2 missing values, well within the boundaries that are suitable for hot-deck imputation (Little and Rubin, 2014).

We then clustered the 20 attitudinal statements to generate a tractable set of predictors. For the four original attitudinal dimensions, we calculated Cronbach’s alpha for all possible combinations of questions in each psychographic dimension (3-5 questions), and alpha was uniformly low (< 0.6), indicating that the designed dimensions of behavior were not clearly divided across the questions. As such, we used hierarchical clustering (iclust in package psych), as it is an especially robust method for psychological questions (Revelle, 2012, 2014a).
Clustering produced three distinct attitudinal dimensions: fun, risk, and skill. Within the dimension of fun, statements encompassed personal and group level perceptions that hunting is an enjoyable activity and that wild birds are tastier than domestic fowl. Fun also included two elements of skill: self-confidence in accurate marksmanship and knowledge on the behavioral habits of birds. The risk dimension represented respondents’ estimated likelihood of being caught and punished by their village forestry ranger or by the state forestry police. Skill encompassed beliefs regarding one’s ability to obtain weapons (bullets and snares) and perceived talent at setting snares. Six statements did not map to any of the clusters and were excluded.

All continuous variables (age, crop area, income, fun, risk, and skill) were centered and scaled. The ordinal variables (entertainment, wealth, outdoors activity, and past hunting) were scaled to [0, 1] by dividing each level by the maximum value (Gelman and Hill 2007).

We evaluated (1) the prevalence of bird hunting in Xishuangbanna, and (2) what factors separated hunters from non-hunters. For aim (2), we generated several candidate models to predict who does or does not hunt (Table 4.2). Broadly, the hypotheses could be grouped as (1) solely economic, (2) economic and recreational activities, (3) economic and attitudinal, and (4) solely recreational activities and attitudes. All models within $\Delta AIC_c \leq 4$ of the most-supported model were averaged (Burnham and Anderson 2002).

We used several estimators for RRT data that are available in the package zapstRR (Chang and Cruyff 2017), specifically: univariate prevalence estimation, a sum score model which describes the prevalence and predictive factors behind hunting 0-4 of the focal species (Cruyff et al. 2008b), and item response theory wherein the predictors of hunting were jointly estimated across all four birds (Fox and Meijer 2008; Cruyff et al. 2016). For more details on these estimators, please refer to Chapter 3 and the original citations. Finally, we assessed whether or not there was statistical evidence of evasive response bias (failing to answer ‘yes’
honestly or when forced) using the item response theory model. Evasive response bias was tested against a null of compliance with a likelihood-ratio test.

4.3 Results

4.3.1 Survey demographics and overall attitudes

The surveyed population was 41.5% Dai, 24% Hani, 20% Yao, and the remaining 14.5% were Han Chinese, Jinuo, Bulang, Yi, or Lahu. Respondents ranged in age from 18 to 70 years, with a median of 34 and a mean of 37.6. Households ranged from 1 to 12 individuals, with a median of 5 and a mean of 5.2. The median annual per-capita income in 2015$USD was 1224 (range: [130, 21216]).

Every surveyed household owned a rubber plantation (*Hevea brasiliensis*), currently the primary livelihood for rural communities in XSBN [Xu, 2006] [Xu et al., 2014] [Yi et al., 2014] [Hammond et al., 2015] [Chang et al., 2017]. The median rubber holding was 4.4 ha (mean: 6.3, range: [0.9, 40]). Apart from rubber, respondents had anywhere from 0 to 27 hectares of other farmland (median: 0.9, mean: 1.4 hectares).

29.5% of the respondents agreed that the men of their village enjoy hunting birds. More than half of the interviewees preferred the taste of wild birds to domestic fowl (56.5%). Villagers typically perceived their village committees to be more lax at enforcement than the Forestry Police, the administrative bureau tasked with enforcing the laws protecting the Xishuangbanna National Nature Reserve; while 17 and 4.5% of the respondents did not think that their village committees would punish villagers for using snares or guns, those rates were only 5.5 and 2.5%, respectively, for the Forestry Police. Intriguingly, despite the fact that very few bird species are formally protected from hunting (Classes 1 and 2 of the Chinese Wildlife Protection Law), 53% of the respondents believed that hunting any bird was illegal.
4.3.2 Rates of hunting for individual birds and across multiple species

A substantial proportion of adult men—nearly 30% at the upper end—were still actively hunting bulbuls between 2015–2016 (Table 4.1). Although the prevalence of hunting for the other bird species was quite low (< 1.5% in all cases), the positive upper bounds suggested that as many as 7.5-9.3% of the adult men may have hunted these species.

Using the sum score model, we could identify the proportion of adult men who had hunted a sum of zero to all four of the focal species. We found that 7.2% of the respondents had hunted two species and 4.7% of the respondents hunted three species, but that none of the respondents had hunted all four birds in the past year.

<table>
<thead>
<tr>
<th>Bird</th>
<th>$\hat{\pi}$ (%)</th>
<th>SE</th>
<th>z</th>
<th>$p$</th>
<th>95% confidence interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>Barbet</td>
<td>1.2</td>
<td>4.1</td>
<td>0.28</td>
<td>0.8</td>
<td>(0, 9.3)</td>
</tr>
<tr>
<td>Bulbul</td>
<td>19.4</td>
<td>5</td>
<td>3.9</td>
<td>$1 \cdot 10^{-5}$</td>
<td>(9.7, 29.2)</td>
</tr>
<tr>
<td>Partridge</td>
<td>0</td>
<td>4</td>
<td>-0.1</td>
<td>0.9</td>
<td>(0, 7.5)</td>
</tr>
<tr>
<td>Pheasant</td>
<td>1.2</td>
<td>4.1</td>
<td>0.29</td>
<td>0.8</td>
<td>(0, 9.3)</td>
</tr>
</tbody>
</table>

Table 4.1: Estimates of hunting prevalence for each bird species in percentages.

Compliance with the RRT questionnaire: We evaluated whether there was significant evasive response bias—refusing to answer “yes” honestly or when forced by the die showing 1. We compared a covariate-free IRT model with and without evasive response bias. We found that around 12% of the responses may have exhibited one-sided lying.

However, the likelihood ratio test of the non-compliant versus the null model was not significant ($\chi^2 = 2.9, p = 0.09$). As such, we did not include a noncompliance parameter in the subsequent regression models. It is worth noting that a majority (69.6%) of the respondents felt that the forced response question design was “easy to answer” and “protected their privacy”.

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4.3.3 Predictors of hunting activity

We performed multi-model inference on a set of hypotheses regarding which socio-cultural dimensions may have influenced who did and did not hunt the four focal birds (Table 4.2). We used item response theory to jointly regress over all four bird species simultaneously.

One model (10) was clearly the most parsimonious and only contained recreational and attitudinal covariates (Table 4.2). The predictors in the most-supported model were “fun”, scores for belief statements to the effect that hunting was enjoyable at a personal and community-level, “entertainment”, the sum of the respondent’s alternative leisure activities (e.g. karaoke, basketball, tuo luo, games of chance), and “outdoors”, the sum of outdoors recreation activities (vegetable picking, mushroom gathering, and angling).

A greater perception that hunting was fun and a larger number of outdoor activities tended to increase the probability of being a hunter, for all of the focal birds (Figure 4.1). The impact of alternative entertainment on hunting activity was unclear—it could either increase or decrease the probability of hunting the focal birds.

4.3.4 Predictors of the number of species hunted

We performed ordinal regression using the sum score regression estimator (Cruyff et al., 2008b; Chang and Cruyff, 2017) with the same set of hypotheses as the previous section. Unlike the IRT model, the most supported ordinal regression models included socio-economic covariates such as age, landholdings, and wealth (Table 4.3).

After full model-averaging (Burnham and Anderson, 2002), the variables with the largest directional effect were age, wealth, outdoors activities, and past hunting activity (Table 4.4). Older and wealthier people tended to hunt fewer species. On the other hand, individuals who spent more time outdoors and who had previously hunted a greater variety of species were more likely to hunt more of the focal birds. It also appeared that more alternative entertainment activities would tend to reduce the number of bird species hunted. Never-
Figure 4.1: Estimated regression coefficients ($\hat{\beta}$) for the most parsimonious model with their confidence intervals shown. The thick bars show the point estimate with its standard errors only; the thin lines show the 95% confidence interval. When the full interval for $\hat{\beta} > 0$, that indicates that an increase in a predictor’s value is associated with a greater probability of hunting.

Nevertheless, as the confidence intervals for each of the coefficients crossed 0, the impact of these predictors on the cumulative sum scores of hunted birds were unclear.
<table>
<thead>
<tr>
<th>Model</th>
<th>Variables</th>
<th>$AIC_c$</th>
<th>$\Delta AIC_c$</th>
<th>$w_{AIC_c}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>Outdoors + Entertainment + Fun</td>
<td>757.4</td>
<td>0</td>
<td>0.8</td>
</tr>
<tr>
<td>5</td>
<td>Outdoors + Fun + Risk + Skill</td>
<td>761.9</td>
<td>4.6</td>
<td>0.08</td>
</tr>
<tr>
<td>6</td>
<td>Entertainment + Outdoors + Fun + Risk + Past Hunting</td>
<td>762.3</td>
<td>4.9</td>
<td>0.07</td>
</tr>
<tr>
<td>8</td>
<td>Wealth + Rubber + Outdoors + Fun</td>
<td>764.2</td>
<td>6.8</td>
<td>0.03</td>
</tr>
<tr>
<td>11</td>
<td>Age + Outdoors + Entertainment + Fun</td>
<td>765.9</td>
<td>8.5</td>
<td>0.01</td>
</tr>
<tr>
<td>2</td>
<td>Age + Wealth + Entertainment + Outdoors + Past Hunting</td>
<td>766.3</td>
<td>8.9</td>
<td>0.01</td>
</tr>
<tr>
<td>4</td>
<td>Rubber + Cropland + Wealth + Entertainment + Past Hunting</td>
<td>768.4</td>
<td>11.1</td>
<td>0.003</td>
</tr>
<tr>
<td>7</td>
<td>Age + Rubber + Past Hunting + Outdoors + Fun</td>
<td>768.5</td>
<td>11.1</td>
<td>0.003</td>
</tr>
<tr>
<td>3</td>
<td>Age + Rubber + Cropland + Wealth + Entertainment</td>
<td>772.5</td>
<td>15.1</td>
<td>0.0004</td>
</tr>
<tr>
<td>9</td>
<td>Age + Rubber + Cropland + Outdoors + Fun</td>
<td>773.1</td>
<td>15.7</td>
<td>0.0003</td>
</tr>
<tr>
<td>1</td>
<td>Age + Rubber + Cropland + Wealth</td>
<td>776.9</td>
<td>19.5</td>
<td>0.00005</td>
</tr>
</tbody>
</table>

Table 4.2: Comparison of multiple hypotheses on factors that drive hunting, ranging from socio-economic (age, wealth, rubber and crop landholdings) to attitudinal traits (outdoors activities, entertainment, perception of fun, risk, and skill, past hunting activity). All continuous variables were normalized while categorical variables were re-scaled to fall within the interval $[0, 1]$.  

<table>
<thead>
<tr>
<th>Model</th>
<th>Variables</th>
<th>$AIC_c$</th>
<th>$\Delta AIC_c$</th>
<th>$w_{AIC_c}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>11</td>
<td>Age + Outdoors + Entertainment + Fun</td>
<td>443.5</td>
<td>0</td>
<td>0.5</td>
</tr>
<tr>
<td>2</td>
<td>Age + Wealth + Entertainment + Outdoors + Past Hunting</td>
<td>445.4</td>
<td>1.8</td>
<td>0.2</td>
</tr>
<tr>
<td>10</td>
<td>Outdoors + Entertainment + Fun</td>
<td>447.1</td>
<td>3.6</td>
<td>0.1</td>
</tr>
<tr>
<td>5</td>
<td>Outdoors + Fun + Risk + Skill</td>
<td>447.4</td>
<td>3.9</td>
<td>0.1</td>
</tr>
<tr>
<td>9</td>
<td>Age + Rubber + Cropland + Outdoors + Fun</td>
<td>447.5</td>
<td>3.98</td>
<td>0.1</td>
</tr>
<tr>
<td>7</td>
<td>Age + Rubber + Past Hunting + Outdoors + Fun</td>
<td>449.0</td>
<td>5.5</td>
<td>0.03</td>
</tr>
<tr>
<td>1</td>
<td>Age + Rubber + Cropland + Wealth</td>
<td>451.9</td>
<td>8.4</td>
<td>0.01</td>
</tr>
<tr>
<td>3</td>
<td>Age + Rubber + Cropland + Wealth + Entertainment</td>
<td>453.7</td>
<td>10.1</td>
<td>0.003</td>
</tr>
<tr>
<td>4</td>
<td>Rubber + Cropland + Wealth + Entertainment + Past Hunting</td>
<td>454.2</td>
<td>10.7</td>
<td>0.002</td>
</tr>
<tr>
<td>6</td>
<td>Entertainment + Outdoors + Fun + Risk + Past Hunting</td>
<td>454.4</td>
<td>10.8</td>
<td>0.002</td>
</tr>
<tr>
<td>8</td>
<td>Wealth + Rubber + Outdoors + Fun</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

Table 4.3: Comparing models that explore what factors tend to increase the number of species hunted. Model 8 did not converge.
### Table 4.4: Model-averaged coefficients for the ordinal sum score model.

<table>
<thead>
<tr>
<th>Variable</th>
<th>$\hat{\beta}$</th>
<th>SE</th>
<th>95% confidence interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age</td>
<td>-1.29</td>
<td>0.89</td>
<td>(-3.03, 0.45)</td>
</tr>
<tr>
<td>Wealth</td>
<td>-0.75</td>
<td>2.19</td>
<td>(-5.04, 3.53)</td>
</tr>
<tr>
<td>Entertainment</td>
<td>-0.32</td>
<td>1.35</td>
<td>(-2.98, 2.33)</td>
</tr>
<tr>
<td>Rubber</td>
<td>-0.26</td>
<td>0.51</td>
<td>(-1.26, 0.74)</td>
</tr>
<tr>
<td>Cropland</td>
<td>-0.01</td>
<td>0.70</td>
<td>(-1.38, 1.35)</td>
</tr>
<tr>
<td>Risk</td>
<td>0.01</td>
<td>0.10</td>
<td>(-0.19, 0.21)</td>
</tr>
<tr>
<td>Fun</td>
<td>0.02</td>
<td>0.14</td>
<td>(-0.26, 0.29)</td>
</tr>
<tr>
<td>Skill</td>
<td>0.05</td>
<td>0.27</td>
<td>(-0.48, 0.58)</td>
</tr>
<tr>
<td>Outdoors</td>
<td>0.78</td>
<td>1.68</td>
<td>(-2.52, 4.08)</td>
</tr>
<tr>
<td>Past Hunting Activity</td>
<td>1.11</td>
<td>1.78</td>
<td>(-2.38, 4.61)</td>
</tr>
</tbody>
</table>

**4.4 Discussion**

We found that recreational covariates were the most supported predictors for identifying hunters. Viewing hunting as fun and participating in more outdoor activities tended to increase the probability of hunting the four focal birds while greater alternative entertainment options tended to reduce the probability of being a hunter. Up to one in three adult men had hunted bulbul in the past year, while the prevalence of barbet, partridge, and pheasant hunting ranged between 0 and 9.3%.

For the sum score of the number of focal species hunted in the past year, the most parsimonious model included demographic and economic covariates (age, wealth, cropland area) in addition to recreational predictors (belief that hunting was fun, entertainment, and outdoor activities). Younger and less wealthy individuals tended to hunt more species. As with the predictors of hunting activity for the individual species, more alternative entertainment pursuits would potentially reduce the number of species hunted, while more time spent outdoors and hunting experience would increase the number of species hunted. However, none
of the confidence intervals for these variables exhibited a clear directional effect on the sum score of species hunted.

Although the prevalence of hunting barbet, partridge, and pheasant was much lower than that of bulbul, that does not imply reduced hunting pressure for those three species. Canopy-dwelling barbets are regarded as very tricky to successfully capture and phasianids are extremely rare. Overexploitation has decimated the populations of large-bodied birds, particularly phasianids and frugivores (Luo and Dong 1998; Corlett 2007; Kai et al. 2014). These three species are all more desired by hunters than bulbuls (Chang et al. 2017); should a hunter see one within shooting range, they would likely target it, unless they were banking their shot for an even more desirable species.

Despite the numeracy and literacy of the surveyed population, we still encountered challenges with the randomized response technique. We observed a sizable, though statistically insignificant, rate of self-protective lying at around 12%, despite the protection that RRT should confer. Nevertheless, nearly 70% of the respondents trusted that the forced response design would ensure anonymity and felt that it was easy to answer, in part because of its similarity to popular gambling games.

Many of the analyses in this chapter were only possible with advanced RRT estimators. Under a conventional single-item RRT logistic regression model, we would not have been able to perform inference for barbet, partridge, or pheasant hunting due to low prevalence and an inadequate sample size. However, by pooling information over multiple items, the sum score and item response RRT estimators were able to recover meaningful information and answer important questions that have been out of reach for conservationists.

Fewer than one in ten men had hunted more than one of the focal birds in the past year. Reaching this population of hunters may have an outsize impact on the success of biodiversity conservation as these individuals are likely more skilled and intensely dedicated to hunting.
The attitudinal statements revealed that the vast majority of villagers felt that hunters would be punished for snaring or gun usage, and were aware of laws protecting wildlife from harvest. In fact, many respondents believed that all birds were protected from harvest, when in fact, of the focal bird species, only silver pheasant is listed. On the one hand, this is a cause for optimism: village officials and forestry police have successfully disseminated the laws. However, risk perception was absent from the most supported regression models for (1) distinguishing hunters from non-hunters, and (2) determining the number of species hunted. This indicates that laws protecting wildlife have had negligible effects in changing hunter behavior.

Rural villagers in Xishuangbanna have expressed antipathy toward local and regional forestry bureaus, feeling excluded from decision-making (Xu et al., 2005a; Xu and Melick, 2007; Chang et al., 2017). Currently, the limited enforcement of wildlife protection laws in Xishuangbanna has largely relied on extremely infrequent patrols (largely during the dry season) and anonymous tip-offs (Chang et al., 2017). These enforcement tactics have encouraged defiance of the forestry police—villagers are highly unlikely to be caught hunting—and have engendered distrust toward local agencies tasked with managing protected areas and wildlife conservation. Involving local communities in devising strategies to meet their aspirations while conserving wildlife has been a cornerstone of effective and ethical management (Milner-Gulland and Bennett, 2003; St John et al., 2011; Duffy et al., 2016).

Our surveyed population may present a fascinating window into the transition from subsistence or profit-oriented hunting toward rural, recreational hunting (Harris and Shilai, 1997; Yang et al., 2004; Kai et al., 2014; Chang et al., 2017). Virtually every study of hunters in the tropics has posited that generating income or putting food on the table are the primary drivers for hunters (Fa et al., 2003; Rowcliffe et al., 2005; Razafimanahaka et al., 2012; Nuno et al., 2013a; Duffy et al., 2016). Yet our study demonstrates that the most salient factors differentiating hunters from non-hunters were decidedly recreational in
scope: availability of alternative forms of recreation, perceptions that hunting is fun, and outdoors leisure activities. Case studies in the Afrotropics, Neotropics, and in Southeast Asia have repeatedly demonstrated that non-material motives can be highly salient for harvesters (Harrisson 1961; Cinner et al. 2009; MacMillan and Nguyen 2014; El Bizri et al. 2015; Alfaro-Shigueto et al. 2016).

The sum score regression results add nuance to the model that differentiated hunters from non-hunters. It was possible that more alternative entertainment options, larger landholdings, and greater wealth could depress the number of species targeted. This suggests that while hunting may be more relevant to less wealthy communities, across the board, the economic success of smallholder rubber has released individuals from subsistence poverty concerns, allowing them to pursue low-value game (Xu 2006; Hammond et al. 2015).

The dominance of recreational covariates—attitudes that hunting is fun and access to leisure activities—in predicting who hunts poses challenges and opportunities for conservation outreach. Identifying individuals in Xishuangbanna with a propensity toward hunting will be complex as attitudes and activities are not obvious traits, and are not reflected in commonly collected census data. At the same time, it is possible that alternative, regulated forms of nature recreation could serve as a substitute activity that absorbs poaching effort.

4.4.1 Conclusion

Despite legislation and enforcement restricting poaching, we found that as many as one in three adult men hunted birds in the past year. Recreational activities and attitudes were the most salient predictors of hunting activity in Southwest China rather than demographic and economic traits. For the number of species hunted, recreational covariates were still in the most supported models, but socio-economic predictors were also included. These findings reinforce other studies demonstrating that harvester motives are often extra-economic and not confined to pecuniary or subsistence reward. Our results highlight that in many
developing-world locales, the determinants of conservation crimes may be challenging to identify, and may largely be intangibles such as cultural norms and personal world-views. Nevertheless, a cause for optimism is the fact that such attitudes and activities could be leveraged to identify locally-tailed conservation interventions. Our study demonstrates the utility of novel approaches to analyze RRT data.
Chapter 5

Should I shoot or should I go? Simple rules for prey selection in indiscriminate harvesting systems

Charlotte H. Chang, Sarah E. Drohan

5.1 Introduction

The unsustainable harvest of wildlife for bushmeat, traditional medicine, and other uses gravely threatens tropical biodiversity (Dirzo et al., 2014; Maxwell et al., 2016; Benítez-López et al., 2017). One great challenge facing managers is that tropical hunting systems tend to be relatively indiscriminate, targeting a wide range of species (Milner-Gulland and Bennett, 2003; Corlett, 2007; Ripple et al., 2016). Understanding what rules hunters may use to decide which prey species to pursue would simplify monitoring and management (Larkin et al., 1984). One method to standardize comparisons across a wide range of prey is to focus on a single trait of interest, such as body mass, ornamentation, or antler size.
To date, optimal foraging theory (Krebs et al., 1974; Charnov, 1976b; Holt, 1977; Stephens and Krebs, 1986) has predicted which prey items should be included in a profit- or calorie-maximizing hunter’s diet set (Winterhalder, 1981, 1986; Alvard, 1995; Levi et al., 2011). However, this approach is relatively data-demanding, requiring estimates of profitability, handling time (the total amount of time required from searching to processing a prey item), and encounter rate for each species. Optimal stopping time models, developed by labor economists seeking to identify a job searcher’s threshold wage for accepting an offer, may also identify the set of optimal species for harvest. The lower bound for choosing to target prey items is given by a “reservation value” (ε) for a trait of interest for hunters (Diekert et al., 2016). In contrast with optimal foraging theory, stopping time problems only require the (1) trait distribution, (2) opportunity cost for hunters, and (3) value as a function of the trait (Lippman and McCall, 1976).

These two approaches to elucidate the hunter’s decision to target prey are fundamentally similar, arising from the same tenets of limited time and scarce high-value prey. Both assume that there is at least one trait that dictates prey value. Across continents, body size is both an important determinant of prey value and a significant predictor of which species are threatened by overexploitation (Purvis et al., 2000; Cardillo et al., 2005; Morrison et al., 2007; Barnosky, 2008; Fritz et al., 2009; Hoffmann et al., 2010).

Monitoring communities of harvested wildlife poses intense personnel and cost demands—and are overwhelmingly limited to single species. Existing methods require extensive fieldwork to determine life history parameters for population viability analysis, or space-for-time comparisons of populations across gradients of harvest intensity (Harris et al., 2016). Data from hunting bags—either recorded by hunters or researchers—are some of the cheapest and easiest data for conservation practitioners to collect in highly threatened ecosystems.

To date, the main tool for structured inference on the state of populations from catch data is catch-per-unit-effort (CPUE) indices (Rist, 2007; Weinbaum et al., 2013), which are
limited to single-species populations. Many studies have sought to go beyond individual species, inferring that when a preferred animal is missing from catch data, its abundance must have declined precipitously (Rowcliffe et al., 2003; Cowlishaw et al., 2005; Rist et al., 2008). Yet this assumption may be more or less accurate depending on the vagaries of hunter decision-making and environmental processes such as detectability.

We present a method to enhance the monitoring value of hunter bag (or catch) data using the expected diet set, which we term “bag back-casting”. With even limited information on the expected state of community trait distribution, practitioners could use the bag back-casting method described in this chapter to deduce changes in the community trait spectrum.

We compared the predictions of optimal foraging and stopping time models in a case study of indiscriminate hunting in Southwest China (Kai et al., 2014; Chang et al., 2017). Specifically, we evaluated the expected minimum thresholds of body mass for optimally targeted prey. We used the stopping time theory to explore whether or not hunting in Southwest China, given the current prey base, is economically rational or reflects valuations of hunting that extend beyond pecuniary reward. Finally, we describe the bag back-casting method and motivate its use with a simulated dataset.

Below, we summarize the relevant mathematical motivation for the two foraging theories.

5.1.1 Optimal stopping time problems

The original problem presented by Lippman and McCall (1976) concerned an unemployed worker seeking the best possible job offer (Equations 1-3, pages 159-160). The key assumption behind their problem formulation is that the searcher is myopic; the job seeker only compares the current offer against the potential value of one more observation.

In the context of hunting, let the random variable $X$ denote a trait value of interest to hunters (e.g. monetary rewards for body mass, amenity value for antler size), and $\varepsilon$ the reservation value—or the trait threshold that must be met or exceeded before a hunter will
shoot (e.g. a stag must exceed the $\varepsilon$ antler size to be shot). If $S$ represents the decision to shoot and $\neg S$ abstaining from shooting, then the utility ($U$) of shooting at this threshold must equal the utility of abstaining; $U(S|\varepsilon) = U(\neg S|\varepsilon)$. Hunters pay a constant cost per day, $c$. Note that a hunter only goes into the field if $E[X] > c$.

The original problem is set up as a one-off decision in an infinite time horizon. As such, shooting ends the problem and whichever animal is selected is gained as a benefit. For a given animal whose trait value is $a$, the decision to harvest this animal corresponds to $U(S|x = a) = a$. For all $x = a$,

$$U(\neg S|a) = \int_{0}^{\infty} U(x)dF(x) - c$$

where $dF(x)$ is the probability density function at trait level $x$. When trait values are finite, then it is not optimal to stay in the field forever—instead, it is optimal to shoot when $x \geq \varepsilon$.

Given that $U(S|\varepsilon) = \varepsilon$ and $U(\neg S|\varepsilon) = \int_{0}^{\infty} U(x)dF(x) - c$, then $\varepsilon = \int_{0}^{\infty} U(x)dF(x) - c$. As such, we can determine what the reservation value $\varepsilon$ should be when the trait distribution and per period costs are known. Decomposing the second term,

$$\int_{0}^{\infty} U(x)dF(x) = \int_{0}^{\varepsilon} U(\neg S|x)dF(x) + \int_{\varepsilon}^{\infty} U(S|x)dF(x)$$

$$\int_{0}^{\infty} U(x)dF(x) = \int_{0}^{\varepsilon} \varepsilon dF(x) + \int_{\varepsilon}^{\infty} xdF(x)$$

$$\varepsilon = \int_{0}^{\varepsilon} \varepsilon dF(x) + \int_{\varepsilon}^{\infty} xdF(x) - c$$
We can simplify this formulation for $\varepsilon$ by noting that $\int_0^\infty dF(x) = 1$, and derive a simpler expression for $\varepsilon$ with respect to the per-period cost, $c$. By re-arranging the terms,

$$
c = \varepsilon \int_0^\infty dF(x) + \int_\varepsilon^\infty x dF(x) - \varepsilon \int_0^\infty dF(x)
$$

$$
c = \varepsilon \int_0^\infty dF(x) + \int_\varepsilon^\infty x dF(x) - \varepsilon \left[ \int_0^\varepsilon dF(x) + \int_\varepsilon^\infty dF(x) \right]
$$

$$
\therefore c = \int_\varepsilon^\infty (x - \varepsilon) dF(x) \quad (5.1a)
$$

Using expression (5.1a), we can find the trait value that minimizes this function, thereby returning the reservation value when the trait distribution and per-period costs are known. In practice, hunters often take multiple shots. Assuming that the cost per bullet is low relative to the opportunity cost of time spent hunting, then the reservation value would be divided over the individual shot opportunities. Ultimately, the cumulative total off-take should approach or exceed the reservation value. If the cost per bullet is high, then each shot taken on a hunting trip decreases the value of each prey item, and it would be optimal to hit one’s reservation value in a single shot, thereby approximating the original problem set-up.

**Discounting:** The optimal stopping problem can be extended to consider the impact of discounting on reservation values. Let $\delta$ represent a scalar that is greater than 0. We can then represent the discount rate as a function, $\beta = \frac{1}{1+\delta}$, taking on values $< 1$. The discount rate directly impacts the per-period costs, which we will demonstrate below.

When discounting is present, we redefine $\varepsilon$ as $\beta \left( \mathbb{E}[\max\{\varepsilon, x\}] - c \right)$. We use the fact that the hunter’s reward is $x = a$, and $a \geq \varepsilon$ to observe that

$$
\varepsilon = \beta (\varepsilon + \int_\varepsilon^\infty (x - \varepsilon) dF(x)) - \beta c.
$$
Let the convenience function \( V(\varepsilon) \) denote
\[
\varepsilon + \int_{\varepsilon}^{\infty} (x - \varepsilon)dF(x).
\]

Subsequently,
\[
\beta c = \beta V(\varepsilon) - \varepsilon \\
c = V(\varepsilon) - \frac{\varepsilon}{\beta} \\
c = V(\varepsilon) - \varepsilon(1 + \delta) \\
\Rightarrow c = \varepsilon - \varepsilon + \int_{\varepsilon}^{\infty} (x - \varepsilon)dF(x) - \delta \varepsilon.
\]

If we let \( H(x) \) represent \( \int_{x}^{\infty}(y - x)dF(x) \), then \( c = H(\varepsilon) - \delta \varepsilon \) (Equation 13 in Lippman and McCall 1976).

Below, we use the infinite period single shot problem (5.1a) to derive expected reservation values in Southwest China.

### 5.1.2 Optimal foraging theory

Let the term prey\(_n\) denote an individual of species\(_n\) (multi-species harvesting) or an individual with trait value\(_n\) (intraspecific selection). We also assume that prey can be ranked in descending order based on the ratio of the reward for prey\(_n\) versus its handling time \( (h_n) \), given by \( \frac{r_n}{h_n} \) (Charnov and Orians 1973; Charnov 1976a; Stephens and Krebs 1986; Alvard 1995; Levi et al. 2011). Handling times are estimated empirically from hunter follows and are the sum of all the time it takes to successfully process a prey item, from search to shot to preparing the carcass. The encounter rate for prey\(_n\) is denoted \( \lambda_n \).
Similar to the stopping time framework, an optimal forager behaves myopically—their problem is whether or not to include prey \( n \) given that prey \( 1 \ldots n-1 \) are already in its diet (Equation 2.11 in Stephens and Krebs [1986]). Upon encountering prey \( n \), the hunter should harvest it if the benefits of taking that prey item exceed the expected benefit of waiting for a more preferred prey species:

\[
\frac{R_n}{\lambda_n} \geq \sum_{i=1}^{n-1} \frac{R_i \lambda_i}{1 + \sum_{i=1}^{n-1} T_i} \quad (5.2)
\]

\[
T_i = \lambda_i h_i
\]

5.1.3 Case study on hunting in Southwest China

Hunting in Southwest China is highly indiscriminate, targeting passerines, near-passersines, gamebirds and more resilient mammal species (e.g. wild boar \textit{Sus scrofa} and muntjac \textit{Muntiacus muntjak}) [Liang et al., 2013; Kai et al., 2014; Chang et al., 2017]. In fact, excessive hunting pressure has driven large carnivores and herbivores—such as gaur \textit{Bos frontalis} and clouded leopard \textit{Neofelis nebulosa}—to local or even regional extirpation. Rural villagers traditionally practiced swidden agriculture and hunter-gathering for subsistence. In the past 20 years, there has been widespread transition to smallholder agriculture with hunting activity concentrated on protected areas as the surrounding agricultural matrix is largely inhospitable to native birds and mammals [Yang et al., 2004; Chang et al., 2013].

A set of semi-structured interviews with hunters provided economic and demographic data [Chang et al., 2017]. Body mass dictates hunter preferences for harvesting prey as well as their recreational or economic value. In addition, hunting bag data from 57 trips from 10 hunters were recorded from April to July 2016, including trips where nothing was successfully captured. The bag data were anonymously collected with no identifying information provided.
Wildlife trait distribution: Between 2015-2016, we surveyed 250 avian point count stations across 35 transects in two protected areas in Southwest China (Xishuangbanna National Nature Reserve). Birds were surveyed by sight and sound by the lead author; all birds detected within a 100 meter radius were recorded in a 12-minute long point count. Along each transect, skilled hunter observers recorded the location and dropped a GPS point for each record of boar and muntjac tracks, feeding signs, and/or hoof marks.

Each mammal observation was separated by at least 500 meters, and each bird point count station by 250 meters for quasi-independence. Although mammals other than muntjac and wild boar were observed (namely sambar deer *Rusa unicolor*, civet *Paradoxurus hermaphroditus* or *Paguma larvata*, and the smaller Reeve’s muntjac *Muntiacus reevesi*), these species were too rare and their identification too challenging ($n \leq 3$ for each of these species) to merit inclusion in analysis. We ultimately had 3477 observations of wildlife.

Using PanTHERIA ([Jones et al., 2009](#)) and EltonTraits 1.0 ([Wilman et al., 2014](#)), we identified the average adult mass for each species, ranging from 4.84 g (*Abroscopus albogularis*) to 2.79 kg (*Great Hornbill, Buceros bicornis*) among the birds, with masses of 17.61 kg for muntjac and 84.5 kg for wild boar.

Additional data—optimal stopping time: We converted body masses to market prices (USD/kg) using sales reported for songbirds ([Liang et al., 2013](#)) and bushmeat market data in Southwest China for muntjac, boar, and gamebirds. We also sought to capture intangible values such as cultural preferences for wild meat and the leisure value of hunting by determining a tuning parameter, $\gamma$, the ratio of per-kilogram values for different taxa versus their domestic alternatives (e.g. gamebirds versus poultry, boar versus pork). $\gamma$ was multiplied by the market sale price for each category of prey ([National Bureau of Statistics of the People’s Republic of China, 2017](#)) to construct value distributions for wildlife and ranged from [1, 10]. The empirical densities of the value distributions for wildlife were found for each level of $\gamma$. 

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We also estimated the per-period opportunity cost for hunting. Chang et al. (2017) found that each hunting trip averaged two days, and the opportunity cost for hunting was given by foregone agricultural wages. The range of foregone wages associated with a two-day hunting trip were $c \in [2, 68]$ USD. With these estimates of $c$ and the wildlife mass probability density distribution, we determined the reservation values for hunters by minimizing Equation 5.1a.

Additional data—optimal foraging theory: Due to the sensitivity of illegal hunting in this landscape, hunter follows were infeasible. We were unable to acquire handling time estimates and used parameter values from shotgun hunters in the tropics (Koster et al., 2010; Levi et al., 2011). We binned our wildlife observations into several prey categories: boar, muntjac, gamebirds, large frugivores, large passerines, and small passerines. The encounter rate for each taxon was the total number of observations divided by the total time of point counts (for birds) or the total time spent walking transects (mammals).

5.2 Predictions of optimal decision-making theories

5.2.1 Optimal shooting (reservation value)

Reservation values ranged from 11 g to 83.3 kg (Figure 5.1). However, based on current market values for bushmeat ($\gamma \simeq 1$), it was rarely optimal for a hunter to enter the field as the mean of the trait distribution was lower than the per-period cost (Figure 5.1a).

With disproportionately high valuations of bushmeat relative to domestic meat ($\gamma \to 10$), the mean of the trait distribution exceeded the per-period costs and the hunter should go out. Note that the opportunity cost of each trip was held within the range of 1 to 70 USD; only the trait value distribution was manipulated with $\gamma$.

Greater values of $\gamma$ had the effect of increasing the reservation value, ceteris parabus (Figure 5.1b). In general, with increasing opportunity costs associated with hunting, we
predict that hunters should be more indiscriminate, contingent on the hunter choosing to hunt in the first place.

5.2.2 Optimal foraging theory (diet choice model)

In contrast with the stopping time predictions, a simple diet choice model indicated that only boar and muntjac should be included in the optimal diet, equivalent to a single reservation value of 17kg (the mean body mass of adult muntjac). To illustrate an application of optimal foraging theory to hunter diet, we simulated 1000 draws from a set of preferred—boar and muntjac—and non-preferred—gamebird and passerine—taxa.

In general, an optimal hunter should primarily target boar and muntjac but even in systems where there is close adherence to the principles of optimal foraging and hunter prey selection, there can nonetheless be some proportion of prey in the bag that are taken outside of the optimal prey set. Assuming different rates of compliance (from 95% to 70%) with optimal foraging principles demonstrates how a hypothetical hunter may harvest prey (Figure 5.2); with lower rates of compliance, there could be larger proportions of gamebirds and/or passerines targeted.

5.2.3 Comparison of stopping and optimal foraging models

Bag data from the same population of surveyed hunters demonstrated that hunters captured both mammals (boar, muntjac, bamboo rats) and birds (ranging in size from 50 g to 1 kg). There were 0-3 prey items reported per bag, and in 60% of the trips, only one animal was harvested; on 23% of the trips, the hunters returned empty-handed.

To compare the bag data with the prey choice and reservation value predictions, we recorded the smallest sized item captured in each bag record (for bags where only one item was caught, this would then be that item). The smallest prey captured ranged from 25.9 g (Grey-eyed bulbul, *Iole propinqua*) to 84 kg (boar) with a first quartile value of 283.2 g,
median 300.7 g, third quartile 5.3 kg, and maximum value of 84 kg. Because the hunting bag data were collected anonymously, we could not identify the opportunity cost associated with each recorded trip.

Simple diet choice rules from optimal foraging theory did not align with the bag data; the diet choice threshold, 17 kg, was greater than 75% of the trip minima. On the other hand, the trip minima fell within the range of reservation values estimated by the stopping time model; moreover, assuming that the $\gamma$ scalar was a reasonable approximation of the system, we could infer what the per-trip opportunity cost may have been for individual hunters.

### 5.3 Bag back-casting: enhancing the utility of hunter bag data

Below, we describe how bag back-casting could be performed using the reservation value. Both optimal foraging and stopping imply a “Zero-One” rule where prey above (or below) the reservation trait threshold should always be taken (or ignored) (Stephens and Krebs, 1986).

The “Zero-One” rule could then easily be represented with a vector of $R$isk to harvesting for each species. That is, each species would receive a score indicating whether or not an optimal hunter would target it. $R$ could then take the form $[0 \ldots 0, 1 \ldots 1]$ for all species in the community, or it could be approximated with a risk function. For instance, a risk function such as

$$R(x) = \frac{1}{1 + e^{-1(\alpha + \beta x)}}$$

describes the probability that a prey item would be targeted by a hunter upon encounter (Bischof et al., 2008). The parameters $\alpha$ and $\beta$ control the inflection point and steepness of the risk curve.
A researcher could infer the likelihood that the observed catch was consistent with an observed or expected trait distribution as follows. We assume that the researcher can estimate the expected trait distribution—generated from past fieldwork, from the literature, or other sources. A null bag composition could then be generated by multiplying the hunting risk function with the probability density of the expected trait distribution. The observed bag data can subsequently be compared against the null bag using a goodness of fit criterion.

We provide a hypothetical example where the cut-off reservation trait value was around 35 (arbitrary units) (Figure 5.3). We simulated an expected (null) trait distribution (lognormal with $\mu = 3.75, \sigma = 0.95$) and created a risk function with an inflection point near 35 trait units (Figure 5.3a). This risk function and the null trait distribution were used to create a null bag composition (Figure 5.3b). Subsequently, we created an observed bag by shifting the trait distribution to the left ($\mu = 2.5, \sigma = 0.95$) and applying the risk function. In this example, the observed bag was significantly different than the expected distribution using a modified Kolmogorov-Smirnov test suitable for discrete distributions ($D = 0.4112, p < 10^{-15}$, Taylor and Emerson 2011).

5.4 Discussion

Reservation values and hunter behavior in Southwest China: We found that the threshold value produced by optimal foraging theory exceeded the vast majority of catches made by Chinese hunters; however, we cannot rule out that this could be due to a mismatch between actual handling times for the prey taxa and the surrogate values that we used. In contrast, the range of reservation values produced by the stopping time model corresponded to the observed minima from hunter bags.

The stopping time problem is a fruitful method to evaluate hunter decision-making processes. It requires very few field parameters—only a trait and value distribution, and these map to the scale of typical data-gathering efforts such as site inventories, transect sampling,
or camera trapping. On the other hand, recording search and handling times for a wide
variety of species—necessary for optimal foraging diet choice—would pose an onerous data
collection burden, particularly given the increased sensitivity of conservation crimes (St John
et al., 2010, 2011). In addition, there is no way at present to integrate opportunity costs
into the optimal foraging framework.

In regions where hunting is primarily for subsistence or profit, greater opportunity costs
tend to depress the time allocated to hunting (Bulte and Horan, 2003; Damania et al., 2003,
2005). As the stopping time framework includes opportunity costs, researchers could evaluate
how changes to alternative livelihood wage rates or penalties associated with illegal hunting
would affect prey diet choice. A potentially counterintuitive result from this framework is
that elevated alternative livelihood wages would likely be associated with more indiscriminate
harvesting.

The stopping time model demonstrates that hunting in Southwest China is not eco-
nomically rational given current the current distribution of prey species (and hence, body
masses). Given the opportunity costs of typical hunting trips, the body mass distribution is
too low to justify hunting activity. However, it was reasonable to hunt if the valuation of
bushmeat included non-economic factors—cultural preferences for wild meat, the amenity
value of hunting time, and other intangibles (γ ≥ 5 – 6).

Chang et al. (2016) determined that only adult men hunt in this landscape, and that
the majority of the male population did not hunt in the past year; ostensibly, for these indi-
viduals, the benefits of hunting did not outweigh the costs of foregone income and penalties
for illegal hunting and gun ownership. On the other hand, the stopping time results suggest
that hunters likely value aspects of hunting that are not solely material.

In part, these extra-economic values may help explain why hunting in Southwest China
has continued despite intense defaunation and extremely low catch (Tisdell and Xiang, 1996b;
Harris and Shilai, 1997; Luo and Dong, 1998; Xu and Wilkes, 2002; Kai et al., 2014). The
thrill of the chase and a gustatory preference for wild meat may drive such activities (Koster et al., 2010; El Bizri et al., 2015). Even in locales where resource harvesting is primarily driven by poverty, cultural, social, and recreational values are nevertheless important and salient determinants of the value individuals place on fisheries and bushmeat (Levin et al., 1977; Cinner et al., 2009; MacMillan and Nguyen, 2014; Oleson et al., 2015; Barnes-Mauthe et al., 2015).

In contexts where non-material values drive hunting, curtailing overexploitation would be difficult to achieve through supply-side interventions alone. Related research has found that when bushmeat is an economically normal or superior good (de Merode et al., 2004; Cowlishaw et al., 2005), offering domestically-raised protein substitutes is unlikely to reduce overall consumption. Instead, demand-side policies must be pursued to reduce excessive hunting effort.

Over the past decade, despite low material rewards and high costs due to muscular enforcement that levies fines and jail time for illegal hunting, intense poaching pressure has persisted in Xishuangbanna (Tisdell and Xiang, 1996b; Kai et al., 2014; Chang et al., 2017). As wild meat is valued not just as a source of protein, but also for its cultural and social signifiers, solutions to overexploitation must extend beyond economic instruments. The non-material values attached to hunting indicate that bottom-up approaches to wildlife management could be particularly successful (Levin, 1997; Dietz et al., 2003; Levin, 2009; Grumbine and Xu, 2011). In Xishuangbanna, this could take the form of empowering village committees to set rules around hunting practices, leveraging socio-cultural beliefs to identify relevant and feasible hunting restrictions, or re-directing hunting activity to a comparable substitute such as a managed shooting ground.

Linking reservation values with monitoring for conservation: To date, it has been highly challenging to monitor indiscriminate harvesting systems. Existing indices such as catch per unit effort are designed for single species. Reservation values provide a way to
reduce complexity from multitudes of species to a single salient trait. Reservation values may even anticipate how much hunting-down-the-web may occur in the absence of management, providing a useful benchmark for mechanistic, allometric models of hunting.

Reservation values can provide useful information about harvested communities. We demonstrated how the combination of a reservation value, an expected trait distribution, and observed bag data could be used to infer whether or not there had been changes to the community of harvested prey. Evidence of a shift in the trait distribution could then be used to evaluate the success of regulations seeking to sustainably manage hunting pressure. Comparisons in bag back-casting findings across multiple sites could be used to prioritize otherwise scarce resources for monitoring and enforcement.

Although the simplicity of the reservation value elides many real-world complexities, the minimal assumptions posed by the optimal stopping technique permit for structured inference with minimal cost and time investment. Agile and adaptive management is most critically needed for the most data-poor regions of the tropics, where limited financial resources and person-hours constrain the scope of field data collection (Harris et al., 2015). The reservation value presents a promising pathway for future applied research and management of natural resources.

5.4.1 Conclusion

Both optimal stopping and foraging theory can produce reservation values for hunters that exploit a wide range of species. The reservation value simplifies the scope of monitoring and management. We found that the optimal stopping reservation value was particularly informative and required fewer field parameters than optimal foraging theory. Finally, we demonstrated how reservation values can be used to perform structured inference on the state of harvested communities relative to a reference baseline. This would enhance the monitoring value of catch data, and permit researchers to evaluate the efficacy of hunting
sustainability policies. Active hunters in Southwest China violate the key tenet of optimal stopping that hunting is only justified when the mean value of the trait distribution exceeds the individual’s opportunity cost. This finding reinforces previous research demonstrating that cultural and social intangibles were highly important to hunters in this region.
Figure 5.1: Reservation body masses and the opportunity cost of each hunting trip. In A the color of each cell (yellow to red) depicts the reservation mass; in B each line represents $\gamma$. A: When hunters do not disproportionately value bushmeat relative to domestic alternatives ($\gamma \approx 1$), it is generally not optimal to hunt; areas with dark grey correspond to parameter ranges where the optimal policy is to stay at home. B: Reservation values decline with increasing opportunity costs, contingent on the trait distribution mean exceeding the per-period cost.
Figure 5.2: Prey composition in an optimal diet. In general, only boar and muntjac are included in the diet choice model, but with differing degrees of compliance with this decision rule, there may be more or fewer gamebirds and passerines appearing in the bag. Handling times were estimated for gamebirds, (near-)passerines, muntjac, and boar from Koster et al. (2010) and Levi et al. (2011).

Figure 5.3: Using reservation values to improve the scope of inference offered by bag data. A: The probability density functions of the trait under the null (expected or historical) trait distribution versus the actual, bag-generating distribution. B: Histograms of the expected catch based on the reservation value under the null (gray), versus the actual observed values (red).
Chapter 6

Maximum viable body size of harvested species: indiscriminate hunting and allometry predict which species are too big to survive

Charlotte H. Chang, Matthew Burgess, Simon A. Levin, Stephen W. Pacala

6.1 Introduction

The plight of the world’s megafauna is an urgent threat to the integrity of tropical forest ecosystems (Galetti and Dirzo, 2013; Dirzo et al., 2014; Ripple et al., 2016; Maxwell et al., 2016). It is well-known that large body size correlates with extinction risk due to larger habitat area requirements (Lindstedt et al., 1986; Haskell et al., 2002; Ofstad et al., 2016) and slower growth rates (Hennemann, 1983; Savage et al., 2004). Moreover, large-bodied
mammals and birds experience the highest rates of overexploitation globally (Cardillo et al., 2005; Morrison et al., 2007; Fritz et al., 2009; Hoffmann et al., 2010; Barlow, 2011).

We seek to evaluate whether or not there is a hard limit on body size beyond which coexistence with humans in the face of hunting becomes impossible without management. We explored this possibility in the context of opportunistic harvesting. Across the Neotropics to the Old World tropics, researchers have consistently noted the indiscriminate nature of tropical hunting, where species ranging from tens of grams to thousands of kilograms are harvested in the same system (Wilkie and Carpenter, 1999; Fa et al., 2002; Bennett et al., 2007; Corlett, 2007; Peres and Palacios, 2007; Wilkie et al., 2011). This then suggests that indiscriminate and opportunistic harvesting would permit for effort to persist at high levels even as charismatic and valuable species decline, or are extirpated outright, as more resilient stocks provide some amount of material reward to harvesters (Milner-Gulland and Leader-Williams, 1992; Clayton et al., 1997; Rowcliffe et al., 2003; Ling and Milner-Gulland, 2006; Branch et al., 2013).

Understanding and predicting how hunting is likely to evolve under different conditions and affect wildlife populations would be a boon for conservation efforts. Limited data on game species and harvester behavior characterize many of the tropical hunting systems where the risk of overexploitation is most severe (Milner-Gulland and Bennett, 2003; Weinbaum et al., 2013; Duffy et al., 2016). However, models that solely invoked indiscriminate harvesting and allometry successfully explained the Pleistocene megafaunal extinction events. Theoretical models of Pleistocene hunter-gatherers tended to focus on (1) either the innate life history trade offs between clades, finding that larger-bodied taxa could only withstand a lower level of hunting mortality (Brook and Bowman, 2005; Charnov and Zuo, 2011; Zuo et al., 2013), and (2) subsidies by minifauna that sustained hunting effort, increased human population sizes in some cases, and acted as a complementary activity to hunting megafauna (Alroy, 2001; Bulte et al., 2006).
In this chapter, I provide a straightforward mechanistic model that combines allometric scaling and indiscriminate harvesting to explore when size-biased extinction patterns may occur. This model relies on parameters that are commonly available: allometric scaling relationships, which have been shown to be highly consistent across regions and taxa (Fenchel, 1974; Gaillard et al., 1989; Savage et al., 2004), and human population density (Center for International Earth Science Information Network, 2017). Unlike Pleistocene hunter-gatherers, there is no evidence that contemporary hunting off-take affects human population densities, which are now overwhelmingly determined by exogenous factors. We consider human population density as a fixed upper bound for hunting intensity. With the model, we explore how the prevalence of hunting changes under different conditions, and its outcomes for wildlife. This information is combined with species-specific limits for harvest effort, which are largely dictated by intrinsic rates of growth.

6.2 Integrating allometry with indiscriminate harvesting

6.2.1 Life histories and limits to persistence under harvesting

Each species has an intrinsic limit for the amount of hunting effort that it can withstand (Brook and Bowman, 2005; Zuo et al., 2013). Let the population dynamics of exploited species \( (N) \) be captured by logistic growth and mass-action harvesting:

\[
\frac{dN}{dt} = rN(1 - N/K) - qEN.
\]

The non-trivial equilibrium, \( N^* = K(1 - qE/r) \), is greater than 0 when \( E \leq r/q \).

Consider a system where multiple species are harvested. Within this set of harvested game, whichever species has the largest \( r/q \) ratio can tolerate the highest level of hunting
effort. For any given species \(i\), if its ratio is given by \(r_i/q_i\), then it follows that if any other species has \(r_j > r_i\) and \(q_j \equiv q_i\), then \(r_j/q_j \equiv \frac{r_i + \epsilon}{q_i}\), where \(\epsilon > 0\); \(E_j > E_i\). In the same vein, if \(q_j < q_i\) such that \(q_j = q_i - \epsilon, \epsilon > 0\), then \(E_j > E_i\).

Ultimately, the level of effort that is realized is dictated by both hunter prey preferences and human population density. It may fall below, meet, or exceed any given species’ biological tolerance. Below, we describe how the degree of effort exerted relates to these factors.

### 6.2.2 Indiscriminate harvesting and allometry

We assume that there is a fixed pool of maximum hunting effort, dictated by human population density \((\rho)\) and the average time allocated to hunting per person each year \((T_H)\). There is no evidence that contemporary hunting leads to increasing human population sizes \((\text{Abernethy et al., 2013})\); moreover, the average number of per-hunter hours is remarkably consistent across reported rates in the tropics \((\text{see 6.2.2 for more details})\). The upper limit for hunting effort bounded to an area is then given by \(E_{\text{max}} = \rho \times T_H\).

Our description of \(\pi\) and the dynamics of \(B\) and \(S\) has some similarities with and distinct differences from bionomic \((\text{Gordon, 1954; Damania et al., 2005})\) and apparent competition models \((\text{Holt, 1977})\). Unlike an ecological predator exploiting two otherwise non-interacting prey, we assume some background rate of hunting activity to capture the reality that entering forests and fallow lands fulfills a variety of purposes \((\text{e.g., gathering wild or medicinal vegetables})\) where hunting could be pursued opportunistically. Compared to standard open-access bionomic models, we do not assume \((1)\) an economic motive and \((2)\) that effort will inevitably reach the open-access equilibrium; effort is instead capped at \(E_{\text{max}}\). This last feature is also shared by microeconomic labor allocation problems which, however, require far more parameters and an accurate understanding of competing activities vying for an individual’s time.
The model evaluates how the proportion of active hunters \( (\pi) \) responds to and exploits a set of wildlife species. Although \( \pi \) more accurately describes the proportion of maximum hunting effort \( (E_{max}) \) exerted in a system, we denote this variable “active hunters” or “active hunting” to contrast it against \( 1 - \pi \), or the proportion of “exited hunters”.

The hunters target two categories of prey: large-bodied \( (B) \) and small-bodied \( (S) \). \( B \) represents charismatic megafauna of conservation concern that garner high rewards while \( S \) corresponds to more resilient minifauna stocks that are less valuable. Both prey species are governed by logistic growth, and are harvested under a Gordon-Schaefer process:

\[
\dot{B} = f_B(B) - B(q_B E_{max} \pi) \\
\dot{S} = f_S(S) - S(q_S E_{max} \pi) \\
f(N) = rN(1 - \frac{N}{K})
\]

(6.1)

(6.2)

In these expressions, \( f(N) \) describes the logistic growth process where \( r \) is the intrinsic rate of increase and \( K \) the carrying capacity for each prey species. The catchabilities—mortality of encountered prey—are given for each species by \( q_S \) and \( q_B \).

The dynamics of the proportion of active hunters, \( \pi \) is described by

\[
\dot{\pi} = -\pi \left( \frac{\nu}{1 + \phi_B B + \phi_S S} \right) + (1 - \pi) \beta,
\]

(6.3)

where \( \nu \) represents the exit rate, \( \beta \) the re-entry rate, and \( \phi_i \) the hunter’s valuation of each prey species.

The term \( \nu \) is akin to the inexorable decline of ecological predators in the absence of prey or the opportunity costs posed by harvesting in bionomic models. Note however that the exit rate \( \nu \) is attenuated by prey abundance. When \( \phi_i < 1 \), the abundance of prey has a sublinear effect on reducing the exit rate of hunters. \( \beta \) captures the tendency of exited
hunters to re-enter the system, be it out of curiosity, boredom, or a desire to go into the field.

**Realistic parameter values**

Published estimates of \( r_{\text{max}} \) are rare, particularly for the majority of exploited species in the tropics. For several well-studied zoo populations or flagship species for conservation, there are estimates of \( r_{\text{max}} \) values—we use two species at the ends of the body mass spectrum: muntjac (\textit{Muntiacus muntjak}) with an estimated \( r_{\text{max}} \) of 0.71, and the Indian rhinoceros (\textit{Rhinoceros unicornis}) at 0.05 (Lopes, 2014; Bengsen and Sparkes, 2016). In general, there is support for an allometric scaling relationship across many bird and mammal species where \( r_{\text{max}} = BM^{-0.25} \) (body mass in kilograms) (Fenchel, 1974; Bleweiss et al., 1978; Gaillard et al., 1989; Savage et al., 2004; Sibly and Brown, 2007; Hamilton et al., 2011; Dillingham et al., 2016).

Catchability is also rarely estimated in terrestrial hunting systems due to the sensitivity of performing activities such as hunter follows or recording illegally harvested wildlife off-take. However, there is no evidence that catchability varied significantly with body mass across seven sites covering 26 taxa where catchabilities could be estimated or were provided (Kuchikura, 1988; Milner-Gulland and Leader-Williams, 1992; Alvard, 1993; Lancia et al., 1996; Clayton et al., 1997; Rowcliffe et al., 2003; Parry et al., 2009b,a). The majority of the catchability estimates (20th to 80th quantile) only varied by one order of magnitude (\(10^{-4.9}, 10^{-3.6}\); please see Appendix A1.1 Figure 6.6 for more details). For the minifauna (< 10 kg), the median catchability was \(10^{-4.3}\). For the large-bodied species, the median was \(10^{-3.9}\).

Finally, few studies report the average level of per-hunter effort, as the sensitivity of hunting when and where it is illegal would render such questionnaires self-incriminating. Yet estimates in the Neotropics and Southeast Asia bound the average level of hunter-hours...
per year to a range between 172 (Parry et al. 2009a) and 325 (Kuchikura, 1988; Chang et al. 2017). This range is in accordance with coarser descriptions of hunting in the Afrotropics where hunters will intensively harvest for several days once every one to two months (Van Vliet and Nasi 2008).

6.2.3 Extending the model to a community of species

It is well known that hunters in open-access systems can indiscriminately target a wide range of species, often exhibiting selection solely over a trait of interest, typically body mass (Cardillo et al., 2005; Dirzo et al., 2014; Ripple et al., 2016). We extend the two-species model above (Expressions 6.1 and 6.3) to a case where a community of wildlife experiences shared predation.

Consider a set of species (\( N \)) where each exhibits logistic growth and is harvested (\( H(N) \)). We can then represent the resulting pool of wildlife as a vector, \( N = [n_0...n_M] \), where \( n_i \) is each species’ abundance, and \( 0, M \) correspond to the minimum and maximum body mass (\( BM \)) in the community of species harvested. The dynamics of prey recruitment are the same logistic growth process as in (6.1).

The maximum intrinsic rate of increase (\( r_{max} \)) for each species tends to scale inversely with body mass in grams: \( r_{max} = R(BM) = BM^{-\frac{1}{4}} \) (Fenchel, 1974; Blueweiss et al., 1978; Gaillard et al., 1989; Savage et al., 2004; Sibly and Brown, 2007; Hamilton et al., 2011; Dillingham et al., 2016). On the other hand, hunter valuation of species generally increases with body mass (\( \phi_i \propto BM \); Fa et al. 2002; Milner-Gulland and Bennett, 2003; Rao et al., 2005; Corlett, 2007; Chang et al., 2017). The dynamics of the overall set of harvested species and hunters can be presented as:

\[
\dot{N} = NR^T - H(N) \quad (6.4)
\]

\[
\dot{\pi} = -\pi \frac{\nu}{1 + \sum_{i=0}^{M} \phi_i N_i} + (1 - \pi)\beta. \quad (6.5)
\]
Note that in equation 6.4, the dynamics of each prey species are virtually identical, differentiated solely by body mass, which dictates life history parameters and hunter prey valuation, $\phi_i$. We numerically simulated (Soetaert et al., 2010) hunters targeting ten wildlife species with body masses varying from 0.5 to 1500kg—comparable to a range spanning rodents and game birds to large herbivores. The abundance of each prey species was started at 95% of its carrying capacity while the proportion of active hunters was initially very small ($\pi = 0.01$).

6.3 Results

6.3.1 A test of effort thresholds

We extracted a list of 403 species in Asia that experience hunting pressure, as determined by the IUCN (2017). We then estimated empirical $r_{\text{max}}$ values (Cole, 1954; Soetaert and Herman, 2009) using life history parameters provided by two databases (Jones et al., 2009; Wilman et al., 2014). Of the original set of species, $r_{\text{max}}$ values could be estimated for 59, including charismatic megafauna such as the Asian elephant *Elephas maximus* and Javan rhinoceros *Rhinoceros sondaicus*, as well as species that are commonly targeted by hunters such as wild boar *Sus scrofa* and muntjac *Muntiacus muntjak*.

We then compared what each species’ life history would dictate for its effort limits. We chose to represent this limit as the maximum human population density, $\rho_{\text{max}}$ using the equation

$$\rho_{\text{max}} \leq \frac{r_{\text{max},i}}{q_i T_H \pi}.$$  

These values were then compared against average population density estimates across each species’ range provided by the PanTHERIA database. We assumed a reservation prevalence of hunting of 0.167 and an average of 250 hunter-hours per year (Kuchikura, 1988; Parry et al., 2009a; Chang et al., 2017).
Species whose tolerable population density thresholds were exceeded ($\frac{\rho_{\text{obs}}}{\rho_{\text{max}}} > 1$) were more endangered than those whose ratios were below 1 (Figure 6.1); for the former, their median Red List status was Vulnerable (3) while the median for the latter was Least Concern (1). This pattern was particularly pronounced for the megafauna (> 1000kg).

![Figure 6.1: Large-bodied species tend to experience human population densities in excess of their tolerable limits. We assumed that $\pi = 0.167$, and $T_H = 250$ hunter-hours/year. The colors of each point represent IUCN endangerment status ("LC" = least concern, "NT" near-threatened, "VU" vulnerable, "EN" endangered, and "CR" critically endangered).](image)

A set of 13 studies with suitable survey data were used to evaluate whether the maximum body mass at different sites under (quasi-)open-access conformed to predictions. Predicted body mass thresholds were generated for a realistic range of $\rho$ and $\pi$ values using the equation $(\rho \pi T_H q_B)^{-4}$, where $q_B$ was the average catchability for large-bodied animals ($10^{-3.9}$) and $T_H$ the average per-hunter hours/year (250). Each of the studies typically quantified the
state of hunted mammalian fauna nearby villages or in a broader landscape catchment area. Generally, the maximum body mass was at or below the predicted threshold (Figure 6.2).

![Heat map of maximum extant body mass of hunted taxa](image)


### 6.3.2 Two species model

The two species model (Expressions 6.1, 6.3) has one stable interior equilibrium which is positive for both species under certain conditions (small levels of maximum effort, relatively high rates of hunters exiting). The expressions for $B^*$, $S^*$, and $\pi^*$ at the interior equilibrium are given in Section A1.12.
However, we seek to evaluate the pressing threat that indiscriminate harvesting poses to megafauna; as such, we are particularly interested in the corner equilibria where the megafauna have been driven extinct. We will demonstrate how megafaunal extinction can emerge based on the long-run prevalence of hunting and the dynamics of the minifauna. When the megafauna are near extinction, $B \to 0$, and if

$$\pi > \frac{r_B}{q_B E_{max}},$$

then this equilibrium is stable.

Note that the abundance of minifauna dictates how hard the megafauna would be harvested as their population approaches zero in the long run:

$$\pi^*|_{B^*=0} = \frac{\beta(1 + \phi_S S)}{\beta(1 + \phi_S S) + \nu}$$

The value of $\pi^*$ depends on the equilibrium abundance of $S^*$. The positive root of $\hat{S}|_{B^*=0}$ is

$$S^* = \left[ \frac{\beta r_S W_S + \beta(-r_S) - \nu r_S - Z q_S W_S}{2 \beta r_S \phi_S} + \sqrt{(r_S(\beta W_S - 1) - \nu) - Z q_S W_S}^2 + 4 \beta r_S W_S(r_S(\beta + \nu) - Z q_S) \right]$$

In the above expression for $S^*$, $W_S$ and $Z$ are dummy variables for $K_S \phi_S$ and $\beta E_{max}$, respectively. Substituting $S^*$ back into (6.6), we obtain a closed-form expression for $\pi^*$ (Appendix A1.3, Expression 6.8). For certain values of $E_{max}, \beta$, and $\nu$, megafauna extinction is then a stable equilibrium.

To provide greater intuition on how variables under the manager’s control affect megafauna persistence, we found equilibrium levels of mega- and minifauna abundance under different parameter combinations. Megafauna only persist when the exit flux is high.
and re-entry rates of exited hunters are low (Figure 6.3a). Similarly, megafauna can persist when human population densities and average per-hunter effort levels are low (Figure 6.3b).

Figure 6.3: Megafauna rarely persist under realistic parameter values. When the grid cell is colored green, the conditions for megafauna persistence are met. The sub-figures show equilibrium outcomes under A: different hunter re-entry rates ($\beta \in [0.05, 5]$) and exit rates ($\nu \in [0.5, 500]$), and B: different levels of population density ($\rho \in [0.1, 75]$) and average per-hunter effort ($T_H \in [50, 300]$). All other parameter values are given in Table A2.2.
6.3.3 Community model: Hunting down the biomass spectrum

The combination of indiscriminate harvesting and allometric scaling for the maximum rate of population growth drove large-bodied species above 100 kg extinct in our numerical simulations (Figure 6.4). The time course evolution of the system showed that the normalized wildlife biomass \( \left( \sum_{i=0}^{M} \frac{BM_i N_i}{BM_i K_i} \right) \) declined precipitously, but hunting activity persisted (Figure 6.4a). As the simulation ran forward in time, the mass-abundance distribution exhibited increasing levels of right skew, reflecting the extirpation of the large-bodied species (Figure 6.4b).

For each species, the maximum equilibrium level of active hunting that it can sustain is given by

\[
\frac{R(BM)}{q_i E_{max}} \geq \pi^*, \quad (6.7)
\]

where \( R(BM) \) describes the relationship between body mass and the maximum intrinsic rate of increase under idealized, density-independent conditions \( (r_{max}) \). Across the full suite of harvested species, the equilibrium for the active hunters is

\[
\pi^* = \frac{\beta(1 - \sum_{i=0}^{M} \phi_{BM_i N_i})}{\nu + \beta(1 - \sum_{i=0}^{M} \phi_{BM_i N_i})}.
\]

As such, the long-run dynamics of the active hunters and the prey depends on the full set of harvested species.

We found the steady state values for \( N \) under different levels of population density (\( \rho \)) and average time spent in the field per hunter (\( T_H \)). When population density was low, generally large-bodied species \( (BM \geq 50 kg) \) would persist (Figure 6.5). However, the largest species \( (BM \geq 100 kg) \) would only avoid extirpation under the lowest levels of human population density and per-hunter effort.
(a) The normalized biomass ($W_{\text{norm}}$) declines as excessive hunting pressure extirpates the large-bodied species ($BM > 100kg$). Hunting activity rapidly rises from a starting value of 1% and reaches a stable value.

Figure 6.4: Indiscriminate harvesting and allometric scaling for population growth rates lead to the largest-bodied species becoming extirpated with only the smallest, and resilient taxa persisting. As hunters also value the small-bodied prey, $\pi$ levels out at an intermediate value. Parameter values for the simulation are provided in the Appendix A2.3.

(b) Each colored line represents the abundance of the simulated wildlife (indexed by their body mass) under harvest at a particular time step. The earlier time steps are green while later ones are yellow.
Figure 6.5: At lower population densities ($\rho$) and average effort, large-bodied species can persist. Each grid cell shows the maximum body mass of the simulated wildlife community that was still extant ($N_i > 1$) at the end of the model run. Constants provided in Table A2.3.

6.4 Discussion

Empirical data from the IUCN Red-List and site faunal surveys supported the general mechanisms presented by the model. We found that species-specific limits for maximum human population density, hence hunting effort, broadly coincided with IUCN threat status. Across the thirteen tropical sites experiencing open-access hunting regimes, the maximum body mass of hunted fauna was at or below the projected limit based on hunting prevalence and human population size at those locations.

We have shown general conditions leading to megafaunal extirpation under indiscriminate harvest, mediated by the presence of smaller and, by definition, more resilient minifauna. An extension of the base model to a community of harvested species recapitulated size-selective
extrapolation patterns. While our model should not be used to generate specific predictions of hunting sustainability, it can provide insight on system thresholds for large-bodied animal persistence. For instance, in the community model, human population densities in excess of 10 people/$km^2$ and average per capita hunting time above 100 hours drove species above 50 $kg$ extinct—these values would change with different parameterizations, but our framework provides a straightforward tool for exploring different trajectories as a function of realistic parameter spaces.

A major advantage of this model is its simplicity. Several key parameters are available from published sources (e.g. allometric scaling, catchability, and human population density). The model is agnostic to the ultimate drivers of hunting and instead assumes that there is an influx of hunters and a background exit rate. These variables could be approximated via exit-entry questionnaires, expert opinion, and other relatively low-cost techniques. Moreover, understanding the prevalence of illegal behaviors is itself an active area of research (St John et al., 2011, 2013; Duffy et al., 2016). In Chapters 3 and 4, I demonstrate robust methods to determine the prevalence of illegal activities, which is often itself a management target.

To date, models of hunting effort have required, at a minimum, estimates of the costs and benefits of harvesting (Clark, 1973; Milner-Gulland and Leader-Williams, 1992; Keeling et al., 1999; Rowcliffe et al., 2003), or have required assessment of competing activities and livelihoods (Damania et al., 2003, 2005; Lopes, 2014; Sirén and Parvinen, 2015). For many sites where charismatic megafauna are highly overexploited, these factors are unknown. Divining such complex behavioral intentions and drivers is increasingly challenging as hunting becomes a prohibited and stigmatized behavior. There are a wealth of factors that drive hunters to hunt, many of which can be hard to predict even with detailed psychometric models of behavior (Milner-Gulland, 2011; Duffy et al., 2016). On the other hand, entry and exit rates from hunting may be more easily quantified than the hidden motivations of
hunters, which may even be unknown to the hunter and would ask researchers to “open windows into men’s souls.”

Moreover, there is mounting evidence that natural resource harvesting in the tropics is motivated by a diversity of rationales (Barnes-Mauthe et al., 2015; Oleson et al., 2015; Boonstra and Hentati-Sundberg, 2016). Researchers from the Neotropics to the Afrotropics and Asian tropics have noted that many hunters seem to prize the social values of hunting—camraderie, recreation in the forest—and have found that hunting can be an inherently enjoyable activity (Harrisson, 1961; MacMillan and Nguyen, 2014; El Bizri et al., 2015; Alfaro-Shigueto et al., 2016; Harrison et al., 2016). Indeed, hunting—particularly in more defaunated landscapes—is often pursued alongside sure-bet activities such as rattan, medicinal herb, and timber gathering (Parry et al., 2009b; Siren and Parvinen, 2015; Chang et al., 2017). In short, not only is parameterizing standard bionomic models more onerous, but also an idealized Homo economicus may fail to capture important dynamics surrounding indiscriminate harvesting.

6.4.1 Conclusion

Uncovering the forces driving size-selective overexploitation beyond physiological constraints (Brook and Bowman, 2005; Charnov and Zuo, 2011; Zuo et al., 2013) has remained elusive. The model provided in this chapter does not assume profit maximization, and is therefore phenomenologically suited to capturing a wide range of motivations on the part of harvesters. Empirical data support some of the core mechanisms advanced under this framework. Predictions from the model demonstrate that at current levels of human population density, the combination of indiscriminate and unregulated harvesting and allometry spell doom for megafauna over 100 kilograms.
A1 1 Appendix I

A1 1.1 Parameter values

Across 7 studies in the tropics spanning 30 taxa, there was no evidence that large-bodied species tended to consistently experience lower catchabilities; were this true, that would counteract the general trend for allometric scaling to lead to greater vulnerability of large-bodied species to indiscriminate harvest. In fact, there was a mildly positive relationship between body mass and catchability ($\log_{10} q = -4.3 + 0.07 \log_{10} BM$).

![Figure 6.6](image)

Figure 6.6: The relationship between estimated catchability and body mass for 30 taxa.

For Figure 6.2 I found 13 studies suitable for testing the predictions of the species-specific effort threshold (equivalently the human population density) (Table A1.1). The sources are as follows: [1]: O’Kelly et al. (2012), [2]: Shanahan (2000), [3]: Harrison (2011), [4] Kai...
### Table A1.1: Site faunal inventory data sources.

<table>
<thead>
<tr>
<th>Site</th>
<th>Faunal data</th>
<th>$\rho$</th>
<th>$\rho$ source</th>
<th>$\hat{\pi}$</th>
<th>$\hat{\pi}$ source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seima</td>
<td>[1]</td>
<td>6.56</td>
<td>[10]</td>
<td>(0.19, 0.63)</td>
<td>[1]</td>
</tr>
<tr>
<td>Lambir</td>
<td>[2,3]</td>
<td>10</td>
<td>[11]</td>
<td>0.3</td>
<td>[22]</td>
</tr>
<tr>
<td>Xishuangbanna</td>
<td>[4,5]</td>
<td>27</td>
<td>[12]</td>
<td>0.39</td>
<td>[23]</td>
</tr>
<tr>
<td>Yomybato</td>
<td>[6]</td>
<td>0.133</td>
<td>[6,13]</td>
<td>0.5</td>
<td>[22]</td>
</tr>
<tr>
<td>Thungyai</td>
<td>[8]</td>
<td>9</td>
<td>[14,15]</td>
<td>0.5</td>
<td>[14]</td>
</tr>
<tr>
<td>Namdapha</td>
<td>[9]</td>
<td>4.8</td>
<td>[16]</td>
<td>0.31</td>
<td>[22]</td>
</tr>
<tr>
<td>Hukawng</td>
<td>[9]</td>
<td>2.8</td>
<td>[17]</td>
<td>0.4</td>
<td>[25]</td>
</tr>
<tr>
<td>Hkakaborazi</td>
<td>[9]</td>
<td>4</td>
<td>[17]</td>
<td>0.4</td>
<td>[25]</td>
</tr>
<tr>
<td>Taman Negara</td>
<td>[9]</td>
<td>0.49</td>
<td>[18]</td>
<td>0.4</td>
<td>[22]</td>
</tr>
<tr>
<td>Nam Et-Phou Louey</td>
<td>[9]</td>
<td>3.4</td>
<td>[19]</td>
<td>0.3</td>
<td>[26]</td>
</tr>
<tr>
<td>Bukit Barisan</td>
<td>[9]</td>
<td>5.1</td>
<td>[20]</td>
<td>0.4</td>
<td>[27]</td>
</tr>
</tbody>
</table>

$\rho$ is (humans/km²); $\hat{\pi}$ is the estimated prevalence of hunting.


### A1 1.2 Equilibria for the two species model

#### Interior equilibria

There are a total of seven equilibria, three of which are not biologically meaningful (negative values for $B^*$ and/or $S^*$). There is a trivial equilibrium where both the mega- and minifauna are extinct and two corner equilibria where the megafauna is extinct or the minifauna is
extinct. There was one interior equilibrium. As currently specified, the rate of active hunters never falls to zero.

\[
B^* = \frac{K_B}{2\beta r_B(K_B q_B r_S \phi_B + K_S q_S r_B \phi_S)} \left( q_B \sqrt{\gamma} + \beta K_B q_B r_S \phi_B (r_B - E_{\text{max}} q_B) \right. \\
+ r_B (2\beta K_S q_S r_B \phi_S - q_B (\beta K_S \phi_S (E_{\text{max}} q_S + r_S) + r_S (\beta + \nu))) \\
S^* = \frac{K_S}{2\beta r_S(K_B q_B r_S \phi_B + K_S q_S r_B \phi_S)} \left( q_S \sqrt{\gamma} + \beta K_B q_B r_S \phi_B (2r_S - E_{\text{max}} q_S) \right. \\
- q_S r_B (\beta E_{\text{max}} K_S q_S \phi_S + r_S (\beta + \beta K_B \phi_B - \beta K_S \phi_S + \nu)) \\
\pi^* = \frac{1}{2\beta E_{\text{max}}(K_B q_B r_S \phi_B + K_S q_S r_B \phi_S)} \left( r_B (\beta E_{\text{max}} K_S q_S \phi_S + r_S (\beta (0.5 K_B \phi_B + 0.5 K_S \phi_S + 0.5) + 0.5 \nu)) \right. \\
+ \beta E_{\text{max}} K_B q_B r_S \phi_B - \sqrt{\gamma} \right)
\]

In these equations, \( \gamma \) is a dummy variable:

\[
\gamma = (\beta E_{\text{max}} K_B q_B r_S \phi_B + \beta K_S r_B \phi_S (E_{\text{max}} q_S + r_S) + r_B r_S (\beta + \beta K_B \phi_B + \nu))^2 \\
- 4\beta^2 E_{\text{max}} r_B r_S ((K_B \phi_B + K_S \phi_S + 1)(K_B q_B r_S \phi_B + K_S q_S r_B \phi_S))
\]
For certain parameter values (e.g. low levels of $E_{\text{max}}$ and high exit flux rates, $\nu$), the interior equilibrium can be a stable node. I do not show the Jacobian evaluated at the symbolic, unevaluated equilibrium expressions above.

**A1 1.3 Corner equilibria: megafaunal extinction**

Note that as $B \to 0$, $\dot{B}|_{B^*=0} \approx r_B - q_B E_{\text{max}} \pi$. When the megafauna are extinct, the equilibrial proportion of active hunters is

$$\pi^* = \frac{\beta}{\beta + \frac{\nu}{1+\phi S}}.$$ 

The positive root for $S^*$ at $B^* = 0$ is

$$S^* = \left[ \frac{\beta r_s W_s - \beta r_s - \nu r_s - Z q_s W_s}{+ \sqrt{(r_s(\beta(W_s - 1) - \nu) - Z q_s W_s)^2 + 4\beta r_s W_s(r_s(\beta + \nu) - Z q_s)}} \right].$$

Substituting $S^*$ into $\pi^*$ yields the expression

$$\pi^* = \left[ \frac{Z q_s W_s - 0.5 + r_s(\beta(0.5W_s + 0.5) + 0.5\nu)}{+ \sqrt{(Z q_s W_s + r_s(\beta - \beta W_s + \nu))^2 + 4\beta r_s W_s(r_s(\beta + \nu) - Z q_s)}} \right].$$

(6.8)

Extinction of the megafauna is then guaranteed when $\pi^* > \frac{r_B}{q_B E_{\text{max}}}$. As above, $W_S$ and $Z$ are dummy variables for $K_S \phi_S$ and $\beta E_{\text{max}}$, respectively.

**A2 2 Appendix II**

Below, the parameter values used in numerical simulation or generating heatmaps for static equilibria are shown.
A2 2.1 Base model parameter values

The parameter values used for exploring mega- and minifauna equilibrium abundance in Model 6.1 are given in Table A2.2.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Description</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>$r_B$</td>
<td>0.05</td>
<td>Megafauna intrinsic rate of growth</td>
<td>time$^{-1}$</td>
</tr>
<tr>
<td>$r_S$</td>
<td>0.71</td>
<td>Minifauna intrinsic rate of growth</td>
<td>time$^{-1}$</td>
</tr>
<tr>
<td>$K_S$</td>
<td>1500</td>
<td>Carrying capacity for minifauna</td>
<td>Animals/km$^2$</td>
</tr>
<tr>
<td>$K_B$</td>
<td>100</td>
<td>Carrying capacity for megafauna</td>
<td>Animals/km$^2$</td>
</tr>
<tr>
<td>$q_B$</td>
<td>$10^{-3.9}$</td>
<td>Catchability (economic hunters)</td>
<td>% mortality/effort</td>
</tr>
<tr>
<td>$q_S$</td>
<td>$10^{-4.3}$</td>
<td>Catchability (recreational hunters)</td>
<td>% mortality/effort</td>
</tr>
<tr>
<td>$\nu$</td>
<td>0.5-500</td>
<td>Passive exit rate for hunters</td>
<td>time$^{-1}$</td>
</tr>
<tr>
<td>$\beta$</td>
<td>0.05-5</td>
<td>Re-entry rate for exited hunters</td>
<td>time$^{-1}$</td>
</tr>
<tr>
<td>$\rho$</td>
<td>5-75</td>
<td>Human population density</td>
<td>People/km$^2$</td>
</tr>
<tr>
<td>$T_H$</td>
<td>50-300</td>
<td>Per-person average hunting effort</td>
<td>Effort</td>
</tr>
<tr>
<td>$\phi_S$</td>
<td>0.0125</td>
<td>Valuation of minifauna by hunters</td>
<td>animal$^{-1}$</td>
</tr>
<tr>
<td>$\phi_B$</td>
<td>0.625</td>
<td>Valuation of megafauna by hunters</td>
<td>animal$^{-1}$</td>
</tr>
</tbody>
</table>

Table A2.2: Parameter values for steady-state levels of megafauna and minifauna under the two-species model (Figure 6.3). All values have been estimated for a representative 1 km$^2$ grid cell in the tropics; this is particularly the case for carrying capacity ($K$), human population densities ($\rho$), and catchability ($q$).

A2 2.2 Community model parameter values

Parameters used in simulating the time evolution (Figure 6.4) and steady state conditions under different values of population density and per-person average hunting effort (Figure 6.5) are presented in Table A2.3. Note that for Figure 6.5, the values of $\rho$ and $T_H$ were varied between 5-75 individuals/km$^2$ and 50-300 hunter-hours per person per year.
<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Values</th>
</tr>
</thead>
<tbody>
<tr>
<td>$r_{max,i}$</td>
<td>Maximum intrinsic rate of increase</td>
<td>$BM^{-0.25}$</td>
</tr>
<tr>
<td>$K_i$</td>
<td>Carrying capacity</td>
<td>$1043 - 0.8BM$</td>
</tr>
<tr>
<td>$\phi_i$</td>
<td>Hunter valuation of prey</td>
<td>$0.03 + 0.7 \log_{10}(BM)$</td>
</tr>
<tr>
<td>$\beta_R$</td>
<td>Passive re-entry rate for hunting</td>
<td>0.1</td>
</tr>
<tr>
<td>$q_B$</td>
<td>Large-bodied animal (&gt; 10kg) catchability</td>
<td>$10^{-3.9}$</td>
</tr>
<tr>
<td>$q_S$</td>
<td>Small-bodied animal catchability</td>
<td>$10^{-4.3}$</td>
</tr>
<tr>
<td>$\nu$</td>
<td>Exit rate for hunting</td>
<td>100</td>
</tr>
<tr>
<td>$T_H$</td>
<td>Average per-hunter effort per year</td>
<td>250</td>
</tr>
<tr>
<td>$\rho$</td>
<td>Human population density (km$^{-2}$)</td>
<td>10</td>
</tr>
</tbody>
</table>

Table A2.3: Parameter values used in simulating the community model (6.4). Relevant parameters (catchability, carrying capacity) were scaled to reasonable values for a 1km$^2$ area. Each wildlife species was represented by its body mass ($BM = (0.05, 1, 10, 50, 100, 250, 500, 1000, 1250, 1500)kg$). Note that hunter valuation included likely detection probabilities of different fauna based on their size class and their kill probability.
Bibliography


