

1 **Poverty ~~and low taste preference~~not taste drives the consumption of protected**  
2 **species in Madagascar**

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## Abstract

Bushmeat consumption in Madagascar is increasingly acknowledged as one of the major threats to its wild vertebrates. Nevertheless, few studies have examined the drivers of the consumption of protected versus legally huntable wild species, or examined its variance across Madagascar's protected and unprotected areas. This research provides a novel study of the consumption of protected, unprotected, and fish/eel species between forest types (deciduous and rainforest), as well as across a gradient of protected habitat (National Park, Reserve, Unprotected). Members of 1750 households were interviewed across four regions, including two national parks, two reserves, and two unprotected forests. Household demographic, socioeconomic, cultural, and geographic variables were explored as possible predictors of bushmeat consumption. We found that poorer households reported consuming greater quantities of protected species whereas wealthier households reported consuming greater quantities of fish and eel. Households located inside Andasibe-Mantadia National Park, Madagascar's most visited protected area, reported consuming the greatest quantities of protected species. Interviewees' most favoured meat was from ~~domestic~~ animals livestock, and fish. The consumption pattern of wild species reflected interviewees' stated preference for species that are either unlisted (e.g. tilapia fish) under Malagasy species protection laws, classified as pest (e.g. bushpig) and/or game species (e.g. tenrec). Most protected species (such as lemurs and carnivores) were interviewees' least favoured wild meats. Given the lack of cultural affinity, and low preference for the consumption of most protected species, our results suggest that improving accessibility to domestic meat is a promising strategy for reducing the consumption of protected species.

**Keywords:** Bushmeat, food insecurity, poaching, hunting, illegal trade, protected areas.

## Introduction

Bushmeat consumption is one of the greatest threats to global biodiversity (Bennett and Robinson 2000; Milner-Gulland and Bennett 2003; Fa et al. 2006; Ripple et al. 2016). Consequently, understanding its patterns and drivers is important in developing effective conservation strategies for reducing its impact on wildlife populations, and ensuring human livelihoods that depend upon it for subsistence are not jeopardized.

Madagascar, one of the world's biodiversity hotspots, is widely acknowledged as a conservation priority (Goodman and Benstead 2005; Brooks et al. 2006; Funk and Fa 2010). Its rapidly growing human population is mostly rural and poor (IFAD 2016), with many dependent upon their surrounding landscape for subsistence. In rural households surrounding a protected area in northwestern Madagascar, wild species are reportedly an important source of nutrition (Golden et al. 2011), as is the case for much of continental Africa (Brashares et al. 2011). In Madagascar, the consumption of protected animals is widespread (García and Goodman 2003; Randrianandrianina et al. 2010; Razafimanahaka et al. 2012; Golden et al. 2013b), and is principally driven by poverty (Golden et al. 2011; Jenkins et al. 2011; Golden et al. 2014a; Borgerson et al. 2016; Reuter et al. 2016b), often at unsustainable rates (Golden 2009).

Current research on bushmeat consumption in Madagascar has almost exclusively focused on single sites or single regions. As a result, our understanding of the potential different drivers of the consumption of unprotected and protected species across Madagascar's forests is unclear. Given that Madagascar's rural population occupies an extremely diverse landscape, surrounding forests of different protected

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status, the examination of the consumption of unprotected versus protected species at a multi-region level is important for understanding spatial patterns at a national scale. This has implications not only for Madagascar's management of its protected species and protected areas but also for protected area planning globally.

Madagascar's legislation permits seasonal hunting of specified endemic species, and unrestricted hunting of pest species. This legislation is mostly in accord with the IUCN Red List and CITES (Rakotoarivelo et al. 2011), and forbids hunting of the majority of Madagascar's endangered mammals. Given the illegal hunting of protected species and the unsustainable exploitation of game species is widespread, understanding the drivers of illegal and legally hunted species is important in ensuring the efficacy of Madagascar's protected species framework.

Madagascar's protected areas encompass roughly 5.6% of its terrestrial area, and are critical for ensuring the conservation of its biodiversity (UNEP-WCMC 2017). Unfortunately, the *coup d'état* in 2009 has been associated with a significant increase in illegal activities (Randriamalala and Liu 2010; Allnutt et al. 2013; Schwitzer et al. 2014; Waeber et al. 2016) following the subsequent breakdown in government controls (Schwitzer et al. 2013). Recent research has also reported that Madagascar's protected areas' have only reduced deforestation marginally once accounting for other confounding factors (Eklund et al. 2016). In their effectiveness ~~in~~at protecting wildlife, Razafimanahaka et al. (2012) estimated that fewer protected species are consumed in areas of greater conservation awareness and protective legislation. However, the drivers of a household's consumption of protected and unprotected species across forests of varying protection are unknown, and would inform efforts to reduce local communities subsistence upon protected species.

Madagascar is characterised by large abiotic and biotic variation (Vences et al. 2009). This geographic variation inevitably controls what species are available for local consumption; however, in Madagascar, local consumption is also strongly influenced by a region's cultural norms (Lambek 1992; Cinner 2007; Jones et al. 2008; Golden and Comaroff 2015a; Golden and Comaroff 2015b). Madagascar has 18 ethnic groups that maintain different cultures and *fady* (taboos). However, despite the cultural importance of *fady*, its value as a conservation tool remains disputed (Horning 2003; Golden and Comaroff 2015a; Golden and Comaroff 2015b), with presumed generational erosion of *fady* resulting in widespread non-adherence (Jenkins et al. 2011). This however may not be the ultimate cause, with inter-regional migration reported to decrease rates of adherence to local *fady* at the local population level (Golden and Comaroff 2015b). This strongly supports the need for multi-region bushmeat studies to understand the wider importance of Madagascar's culture in informing consumption of wild animals.

We present findings from the first study to document the drivers of the consumption of protected and unprotected species in different forest types and notional levels of protection across Madagascar. In doing so, we are able to investigate the possible influences of ethnic, cultural, socioeconomic, forest, and the legal species and park protection framework.

## Methods

### Study Area

Four sites were chosen to encompass Madagascar's two most abundant forest types (deciduous and rainforest), and their IUCN protected status (CITE). Madagascar has adopted a categorical system of protected areas incorporating: Category 1 Strict Nature

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Reserve, forest protection forbidding human entry; Category 2 National Park, forest protection whilst supporting recreational and educational activities; and Category 3 Special Reserve, an area preserved for pure conservation (Randrianandianina et al. 2003). Our surveys were conducted across four regions including two national parks, one special reserve, one private reserve, and two unprotected forests (Table 1).

Covering approximately 1350 km<sup>2</sup> Ankarafantsika National Park (ANP) is Madagascar's largest contiguous deciduous forest (Fig. 1). Located in the northwest, Ankarafantsika is surrounded by 133 villages encompassing a population of over 37,000 (MNP 2016). Only eight villages are inside the park's boundaries, with much of their surrounding landscape transformed to [savannahgrassland](#), rice fields, or otherwise severely degraded.

The central western region of Menabe is a recognised conservation hotspot due to high regional endemism, and sustained deforestation (Zinner et al. 2013). Approximately 30 km northeast of Morondava is Andranomena Special Reserve (ASR) (20°S, 44°E). ASR contains 64.20 km<sup>2</sup> of dry deciduous forest with two villages flanking its perimeter. To its north is the privately managed forestry concession of Kirindy, now an environmental research centre. Ambadira, the most northerly and unprotected forest has experienced dramatic deforestation and habitat alteration in alignment with the expansion of the nearby Lambokely settlement (Zinner et al. 2013).

Encompassing approximately 155 km<sup>2</sup> of humid rainforest, Andasibe-Mantadia National Park (AMNP) is Madagascar's most visited protected area. Its largest village, Andasibe commune (a Malagasy administrative level) ~~is the focus~~[receives the most benefit from](#) tourism. Remote poor villages (without access to basic public infrastructure) extend to its north, whilst more prosperous villages flank the route nationale [\(national highway\)](#) to its south.

The southeast province of Fianarantsoa contains several small, important, unprotected fragments of low elevation humid evergreen forests. These comprise the primary forests of Sangasanga, Tsiazonambo, Ambatovaky, Tsitola and Vatovavy, largely surrounded by grassland, agricultural and secondary forests. The commune of Kianjavato is the largest regional village.

### **Sampling strategy and interview protocol**

The research team met the president of each village before the survey to explain the purpose and methods of the study. Permission to survey was granted in all villages. The confidentiality of participants, the research's academic purpose, and the team's total independence from authorities was clearly defined. Household surveys were conducted by a team of Malagasy students, ~~in~~ with the assistance of a local villager fluent in the local dialect and customs. The author participated during initial, and in occasional interviews, to ensure ~~they that interviews~~ were conducted effectively (SDM) (Tourangeau and Yan 2007).

Villages were classified as 'small' or 'large', roughly corresponding to their size as either less than or greater than 100 households. Households located in rural Malagasy villages can be difficult to identify, and logistically difficult to visit (Poudyal et al. 2016). Correspondingly, maps of household locations inside each village (and surrounding hamlets) were created from Google Earth (Version 7.1) satellite imagery, and discussed with the village president. This allowed the representative sampling of remote villages.

~~During surveys of small villages all households were visited~~ All households in small villages were visited during surveys. The head of each household was sought for interview, typically the man and primary hunter (Golden 2009). The study's goals and

structure were explained, including the interviewer and author's academic affiliations, and total independence from any local/national authority (i.e. Madagascar National Parks). Their anonymity was assured, and after any questions were answered, their verbal consent was acquired. If the household head was absent at the time of the first visit, an additional two appointments were scheduled, allowing for a maximum of three opportunities to interview each household in small villages.

In contrast, only a sample of households from large villages was sought for interview. Each large village was divided into quadrants and sampled using East et al.'s (2005) zig-zag method. This requires interviewers to bisect quadrants in a 'zig-zag' trajectory, allowing households located on and off main roads to be visited. Interviewers were instructed to sample every second household, and to visit the next house if the previous tenant was unavailable.

### Questionnaire Design and Implementation

In 2013, a ~~pilot~~ questionnaire was ~~trialled-piloted~~ in ANP; allowing for revision and fine-tuning of the survey used in the current study (Supplementary materials). ~~providing feedback, and the precursor to its current structure.~~

The questionnaire was structured into four segments recording the interviewee's: 1) demographic and socioeconomic information; 2) Livestock ownership practices; 3) ~~dietary patterns~~, preferences and attitudes; and 4) conservation understanding and attitudes. Interviewees remained anonymous, however, household demography, asset ownership, education, and livelihood attainment was recorded to investigate demographic and/or socio-economic drivers of bushmeat consumption (Supplementary materials)-



To measure poverty, six equally weighted indicators were derived from Alkire-Santos Multidimensional Poverty Index (MPI) (Alkire et al. 2015a). Unfortunately, due to questionnaire revisions over the two survey years, only the MPI's most important contributor, the living standard dimension was assessed, missing other recognised dimensions of poverty (health and education) (Ferreira 2011; Alkire et al. 2015b). Consequently, following consultation with Malagasy researcher colleagues we included six relevant living standard indicators: asset ownership (i.e. bicycle, mobile phone); roof material; wall material; floor material; access to electricity; and safe drinking water. These indicators were included in an index and measuring on a scale of increasing poverty from 0 – 1.

The third section examined the interviewee's dietary patterns. Respondent's ~~Data~~ were collected on ~~respondent's~~their: most consumed foods; frequency of domestic and wild meat consumed (number of days per week in which at least one meal that day contains meat); domestic and wild meat preferences and attitudes; frequency, seasonality, method of acquisition (i.e. hunted, bought, gift) and reasons for consuming wild species; ~~recording of hunting~~activities; perceived food insecurity; and wildlife ~~fady~~. Given the four different study regions encompassed humid and deciduous forests that vary vastly in their relative seasonality, Madagascar's two most pronounced seasons (dry from May to November, wet from December to April) that are consistent across all four regions were used for classification. Interviewees were asked to recall the frequency of individual species consumed during their lifetime, previous year and previous week. The final section questioned interviewees about their understanding of environmental conservation, their attitudes and experiences its impact on them of it and attitudes towards it.

Our questionnaire required respondents to directly answer sensitive questions on illegal behaviour (bushmeat consumption). As a result, the data is likely affected by non-responses (Groves and Peytcheva 2008) and social desirability biases (Fisher 1993; King and Bruner 2000), potentially reducing its validity (Solomon et al. 2007; John et al. 2010; Nuno and John 2015). There are techniques, such as the Randomised Response Technique (RRT) (Warner 1965), the Normative Technique (Miller 1984), and the unmatched-count technique (Hubbard et al. 1989) that have been shown to improve reporting of information (John et al. 2010; Razafimanahaka et al. 2012). The potential impact of not applying sensitive question techniques was illustrated by Razafimanahaka et al.'s (2012) study in Andasibe which revealed greater reporting of bushmeat consumption using RRT in areas of greater sensitivity (protected versus unprotected area) than estimates derived from direct questioning techniques. Consequently, several steps were taken to reduce potential biases/non-response, including: assuring interviewee anonymity (Singer et al. 1995); structuring the questionnaire in a decreasing order of intrusiveness (Acquisti et al. 2012); and conducting interviews in a conversational manner, with the inclusion of a local villager (Tourangeau and Yan 2007). Despite this, the potential for underreporting is substantial, and was considered when interpreting bushmeat consumption patterns between protected and unprotected areas.

To assist participants, picture cards with illustrations of livestock and wild animals were used during animal preference/consumption ranking and recall exercises to assist participants.~~To assist participants during animal preference/consumption ranking and recall exercises, picture cards were used to illustrate the domestic and wild animals.~~ During questioning of interviewee taste preferences of domestic and wild animals, respondents were asked to rank: i) domestic; ii) wild; and iii) domestic and

wild animals collectively using picture cards from most to least preferred/consumed.

Likewise, picture cards of a selection of the most common endemic species of each region (including all of the local lemur and carnivore species, several common bird, tenrec and reptile species) were used to assist memory recall for consumption history exercises. ~~picture cards were created of a selection of the endemic species of each focal region, including all of the local lemur and carnivore species, several common bird, tenrec and reptile species.~~ The use of identifiable images of local species also eliminated potential translation issues associated with the nuanced differences in regional Malagasy dialects.

## Analysis

Three response variables were modelled to identify the predictors of a household's: 1) consumption of protected species (C1); 2) consumption of unprotected species (C4); and 3) consumption of fish and eel (usually wild caught, potentially aquaculture reared). Species protection status was defined in alignment with Madagascar's National Classification for Animal Species (Rakotoarivelo et al. 2011). This report classifies species into one of three categories.

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Category 1 (C1) contains protected species, which is split into Class 1 (C1C1) those that are strictly protected (i.e.g. lemurs) and Class 2 (C1C2) those that may be hunted under authorisation, commercial, sport or regulatory conditions (e.g. fosas may be killed in defence of livestock). For analysis we grouped all Category 1 protected species together into our first response variable (C1).

Category 2 (C2) species (i.e.g. bushpig) are defined as pest species that may be hunted at all times, whilst Category 3 (C3)(i.e.g. tenrec) are game species permissibly hunted under license. For analysis we grouped pest, game, and species unlisted under

Malagasy law (i.e. small Indian civet) into our second response variable (C4). These were grouped to represent unprotected species as in reality, despite certain legislative protection for game species, hunting is not known, monitored or followed (Keane et al. 2011; Rakotoarivelo et al. 2011).

Our final response variable included both fish and eel species (Tilapia, Carp and Anguila spp.). These species are often rurally wild-caught-wild-rurally, but may also be reared through aquaculture, and thus represent a transitory group between wild and domestic species and -despite the protection of some eel and fish species, only unprotected species were recounted by interviewees. This animal grouping was included in bushmeat preference rankings but modelled as a distinct response variable.

Six variables were considered as potential predictors of bushmeat consumption, including, Forest Size, Village Size, Household Distance, Household Education, Poverty and Conservation Benefit (Table S1). Region was included as a fixed blocking factor to encompass geographic variation. Village was included as a random effect to allow for the nesting of households within villages. Continuous predictors were standardised to z-scores to allow comparison and interpretation of predictors.

Forest size was included to examine the possible effect of larger forests (known to have greater species diversity and abundance) (Burkey 1989) on hunting opportunities. Likewise, Household distance to forest edge was included to assess the possible impact of forest access. Village size was included as larger villages are typically wealthier, and better endowed with infrastructure and access to markets, affecting a household's need for alternate livelihoods. Household poverty was measured on a continuous scale of increasing poverty from 0 – 1. Household education was included to examine the impact of higher education on a household's consumption of protected species. They were defined (with their Malagasy equivalent in brackets)

as: No Education; Primary School (EPP); Junior Secondary (CEG); Senior Secondary (Lyceé publics); and Tertiary (Université). Finally, the interviewee's perceived benefit (binary) from conservation was incorporated to assess the role of conservation in reducing bushmeat consumption. It was expected that interviewees who said they benefited from localised conservation would be less likely to disobey conservation legislation.

Protected species were consumed by a minority (31.8%) of households, so zeroes (non-consumption) dominated this response. We hypothesized that different processes might affect whether households consumed any protected species, compared with those that affected the quantity consumed by households that reported having consumed at least one animal. To account for this, a hurdle approach was adopted (Zuur et al. 2012). This involved two steps, firstly the modelling of the response variable as a binary variable using a generalised linear mixed model where the levels of the binary response were consumption of no protected species, and consumption of *at least one*. Secondly, the modelling of those households that reported consuming at least one species (as a zero-truncated distribution). Zero-inflated generalised linear mixed effect models (GLMMs) were conducted in R (Version 0.99.902) using the MCMC package (Version 0.9-4)(Martin et al. 2017). This package fits models using a Bayesian framework. We used uninformative priors for parameter estimates, and 80,000 iterations with a burn-in of 2000 and thinning of 10.

Model 1 examined which of the six variables is a significant predictor of a household's consumption of protected species (C1). Model 2 and Model 3 examined the predictors for the consumption of legally hunted species (C4) and the predictors for the consumption of fish and eel. For each binary and Poisson model, two models were run for each of the three response variables (protected, unprotected, fish/eel). Firstly, a

global model comprising all of the predictors was created, and then a reduced model was produced containing only the significant predictors (these are reported in Tables S3, S4, S5).

For the binary models, the response variable recorded whether households had consumed any individuals of that species' category (1/0). The response variable for the Poisson models was measured as the total individual animals reported to have been consumed by the household during the previous year. Annual quantity was used instead of mean weekly frequencies to account for seasonal and/or rare events (Golden et al. 2013b). For Poisson models, some outliers with implausible reported consumption rates were removed (~ 6 - 9% of households).

## Research approval

Ethical clearance and research approval was granted by The University of Oxford's Central University Research Ethics Committee (Number: SSD/CUREC1A/14-010) and the Madagascar Government (Permit:107/14-109/15/MEEMF/SG/DGF/DCB.SAPT/SCB).

## Results

During the successive austral winters of 2014 - 2015, a total of 1746 households were interviewed (1325 males, mean age  $42.4 \pm 13.3$  years; 410 females,  $38.8 \pm 13.9$  years). 565 households surrounded unprotected forests, 456 surrounded reserves, whilst 725 surrounded national parks (Table 1). Most (77.5%) of interviewees described their principal livelihood to be derived from farming. Primary school (43.6%) was and junior secondary (24.6%) were the most common educational level, whilst whilst a substantial

~~minority~~ similar numbers of interviewees reported having attained a junior secondary education (24.6%) or (22.5%) had no formal education.

### Domestic and wild meat eating habits and preferences

The primary source of meat for the majority (57.9%) of respondents' primary meat source was from domestic animals/livestock. Members of households consumed the meat of livestocking an average of  $1.46 \pm 1.13$  days during the prior /week. Conversely, 28.6% primarily consumed wild meats ( $3.07 \pm 1.63$  days/week), and 13.5% consumed domestic and wild meats equally. Most (95.2%) of interviewees reported experiencing food shortages, with 65.4% reporting food shortages during the wet season, 14.8% during the dry season ~~or~~ and 19.8% all entire-year (19.8% respectively). Interviewees reported experiencing/perceiving food shortages on average for  $2.7 \pm 1.8$  SD months/year.

Chicken (52.7% of respondents), cow (zebu) (26.3%) and pigs (26.3%) were interviewees' favourite domestic meats. They were primarily favoured for their good taste (79%), nutrition (6.5%), and purely out of habit (5.1%).

Almost all (98.1%) respondents had~~ve~~ consumed bushmeat during their lifetime. Respondents' favourite bushmeat ~~were~~as fish (26%), tenrec (21%), helmeted guineafowl (20%), eel (16%), bushpig (11%), lemur (2%), and bat (1%). These animals were preferred for their taste (42.7%), consumed out of habit (22.4%), easily captured (11.7%) and locally sold (10.4%).

Aquatic species (44%)(fish and eel) ~~were~~as the most highly preferred and highly ranked bushmeat category, with tenrec (21%), birds (20%) and bushpig (12%) the other highly preferred first ranking animals (Fig. 2). The most highly preferred rank ~~five~~5 and ~~six~~6 animals were lemurs and carnivores, whilst bats were the lowest ranked group.

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Aquatic animals were the overwhelmingly most consumed animal group (Fig. 2). Birds, bushpig and tenrecs were the other most consumed animals, whilst carnivores, lemurs and bats were the least consumed species.

Domestic poultry (43.5%), ungulates (26%), and wild aquatic animals (15.7%) were the most preferred wild and domestic species when collectively ranked (Fig. 3). However, tenrecs, lemurs, bushpigs and birds became more preferred within the interviewees' ranks four to ten.

#### **Wild species consumed**

In the year before interviews, 35.7% of villages (collective household results) consumed bat, 78.6% consumed bird, and 71.4% consumed tenrec (Table 2). Approximately half of villages had consumed a lemur or carnivore.

In the year before interviews, 84.8% of households had consumed fish, 47.2% consumed tenrec, 46% consumed bird and/or eel, and 29% consumed bushpig (Table 2). A small proportion of households had consumed a species of bat (10%), lemur (6%) and/or carnivore (3.1%).

During the year before interviews, fish, tenrec, eel and bird were consumed in the highest number (Table 2). Fish and birds were most consumed during the previous week, with bats, carnivores and eels equally consumed. Tenrecs were the only species consumed with any conspicuous seasonal patterns, with their consumption being confined to the wet season. Carnivores, lemurs, birds, and tenrecs were primarily hunted. In contrast, bushpigs, fish and eel were commonly purchased.

Households located inside rainforests reported higher rates of consumption of C1 (protected) species than households located inside deciduous forests, 4.87 and 1.48 individuals/households, respectively (Table 3). They also consumed higher rates of C3



(game) and unlisted species. The unprotected rainforest Vatovavy-Fitovinany consumed the most Category 1 Class 2, Category 3, and unlisted animals. However the most Category 1 Class 1 strictly protected species (i.e. lemurs) were consumed in the rainforest National Park (Moramanga).

71 different species were consumed (Table S2). 33 strictly protected, 12 protected, 1 pest, 12 game, and 7 unlisted species. The most frequently consumed game species were *Tenrec ecaudatus* (2293 last year; 740 households), *Echinops telfairi* (856 last year) and *Pteropus rufus* (481 last year). Strictly protected species of bird such as the *Lophotibis cristata* (330 last year) were frequently consumed, whilst *Mungotictis decemlineata* (C1C1) was the most consumed Euplerid (163 last year). *Avahi laniger* (62 last year), *Propithecus verreauxi* (80 last year) and *Microcebus rufus* (205 last year) were the most frequently consumed lemurs.

Commented [SD6]: Include per household number

### Drivers of protected species consumption

The binary model of protected species consumption provided evidence that Region (Vatovavy-Fitovinany), Household Distance, and Household Education were associated with protected (C1) species consumption (Table S3). There was weak evidence ( $p < 0.10$ ) that probability of consumption was lower for respondents who reported a positive Conservation benefit. Households with higher education were more likely to consume any protected species.

Region, Poverty and Forest Size were associated with greater protected species consumption (Poisson model, Table S3). Households in Moramanga and Vatovavy-Fitovinany, those that were poor, and those living near large forests consumed more individuals of protected species. The effect of poverty on protected species consumption was more marked in Moramanga than elsewhere (Fig. 4).

421

#### 422 **Drivers of unprotected species consumption**

423 Region and Household Education were significant predictors ( $p < 0.001$  and  $p < 0.05$   
424 respectively) of a household's reported binary consumption of an unprotected (C4)  
425 species (Table S4). Households with higher levels of education and those from  
426 Moramanga were less likely to consume unprotected species.

427 Forest Size was a significant predictor of greater unprotected species  
428 consumption, with more individuals of unprotected species consumed by households  
429 located nearer to larger forests (Table S4).

430

#### 431 **Drivers of fish/eel consumption**

432 The significant predictors for the (binary) consumption of fish and eel included Region,  
433 Poverty, Forest Size and Household Distance (Table S5). Households from the region's  
434 Moramanga and Vatovavy-Fitovinany, those adjacent to larger forests, those at greater  
435 distances from the forest ( $p < 0.05$ ), and those that were wealthy were more likely to  
436 have consumed a fish/eel ( $p < 0.10$ ) (Table S5).

437 The Poisson model of the significant predictors of fish/eel consumption reported  
438 significant effects of poverty and household distance in align with the binary model  
439 (Table S5)(Fig. 4). Households that perceived a benefit from conservation reported  
440 consuming lower quantities of fish/eel ( $p < 0.10$ ).

441

#### 442 **Discussion**

443 The poorest households consumed protected species in the greatest quantities.  
444 Conversely, highly favoured fish/eel were more likely to be consumed by wealthier  
445 households, and when they were, they were consumed in greater quantities. Protected

areas were not associated with lower consumption of protected species, with Moramanga households reporting the highest rates of strictly protected species consumption. Households located in rainforest regions had higher consumption rates of wild species from all categories (protected, game, pest, unlisted). These results reflect interviewees' reported preference for consuming ~~domestic animals~~livestock – they suggest that when households are sufficiently wealthy ~~domestic animals~~livestock are consumed in preference to protected wild species. Unlisted, pest and game species were the most favoured wild animals. Our results suggest that the high preference for domestic and unprotected species has potentially created a price barrier for poorer households. Future efforts to reduce the consumption of protected species ~~consumption~~ should focus on improving accessibility and reducing domestic meat cost in rural Madagascar. Given benefits of conservation from protected area (PA) management may be unevenly distributed depending on the location of the village (within or outside of PA), and the presence of PA staff (Aymoz et al. 2013), these programmes should uniformly focus on villages within and surrounding protected areas. Ensuring greater distribution of other benefits from PAs (e.g. tourist revenue from PA entry fees) is equally important in encouraging greater ownership, and rule following by villages in PAs.

### **Domestic species favoured**

Our respondents' stated preferences for ~~domestic animals~~livestock and fish confirms previous observations across Madagascar (Randrianandrianina et al. 2010; Jenkins et al. 2011; Gardner and Davies 2014; Golden et al. 2014a; Golden et al. 2014b; Reuter et al. 2016b). Unlike continental Africa where wild species are often a favoured meat variety (Njiforti 1996; East et al. 2005; Schenck et al. 2006), it is clear in Madagascar

that domestic meat is preferred. This suggests their consumption is likely regulated by price and accessibility (Wilkie and Godoy 2001; Milner-Gulland and Bennett 2003; Wilkie et al. 2005).

### **Bushmeat consumption**

71 wild species were documented as consumed in this study. Patterns roughly reflected preference rankings and Malagasy law with the unprotected/favoured species most consumed. The most highly consumed (and favoured) endemic species were those from Tenrecidae. Although hunting of tenrecs is supposedly regulated, conflicting laws dictate different regulations for individual species. For instance, *T. ecaudatus* (game) is seasonably huntable under license, whereas *H. semispinosus* (Class 2 protected) is permissibly hunted under quota. Unfortunately hunters are unlikely to know and follow these regulations (Keane et al. 2011; Rakotoarivelo et al. 2011), with hunting of tenrecs realistically unregulated. For instance, although most tenrecs are hunted with dogs, this method is banned even with a permit. Currently, little research has examined the sustainability of harvest rates, with few reports linking overhunting to localised decline (Ganzhorn et al. 1990; Nicoll 2003). Given tenrecs are one of the few preferred endemic species, future examination of our data would be useful in evaluating the sustainability of current harvest rates considering species' life-history data.

In total, 31 strictly and 12 protected species were consumed. 23 species of lemurs were eaten, including three of the five most consumed previous year species. This included the vulnerable *Microcebus rufus*, the endangered *Propithecus verreauxi*, and the critically endangered *Eulemur mongoz* (205, 80, 79 individuals). Although lemurs were consumed by fewer than 10% of households, consumption occurred in over half of villages. Previous research has typically reported higher rates of household

496 lemur consumption (in the previous year) in different areas of Madagascar, including:  
497 Masoala-Makira where up to 50% of households had consumed some species of lemur  
498 (Golden 2009; Borgerson et al. 2016); Betampona strict nature reserve where up to 17%  
499 of households consumed lemur (Golden et al. 2014b); and Lac Alaotra, where 2.5% of  
500 households consumed lemurs at lower rates (Borgerson et al. 2018b). Likewise, in two  
501 of our same-study sites (Vatovavy-Fitovinany and Moramanga, respectively),  
502 (Andasibe), Borgerson et al. (2018a) found household consumption rates in forests  
503 surrounding Kianjavato to be slightly higher at 2%, whilst Razafimanahaka et al. (2012)  
504 found household consumptions rates in Andasibe-Mantadia of >10% varying by lemur  
505 species. This suggests that the consumption of lemurs occurs significantly less in  
506 Andasibe compared to Masoala-Makira. In comparing discrepancies in our study to  
507 Razafimanahaka's, temporal differences in annual consumption rates, and/or potential  
508 underreporting due to the use of direct questioning of a sensitive behaviour may be  
509 responsible (Razafimanahaka et al. 2012).

510 In our study, the rainforest regions reported higher wild species consumption  
511 rates. This could be reflected by higher overall species abundance and diversity in  
512 tropical forests (Wilson 1999), presenting greater hunting opportunities. These results  
513 do however contrast with Razafimanahaka et al. (2012) who reported higher  
514 consumption rates of several species (sifaka, brown lemur, whistling duck, flying fox)  
515 in deciduous forests compared to a rainforest. This could be due to the significant  
516 variability between the different regions, and/or communities surveyed. This highlights  
517 the need for greater sampling coverage (and indeed greater replicates over time),  
518 improving the analyses' robustness, and the interpretation of regional consumption  
519 patterns.

Madagascar's carnivores, the family Eupleridae, were some of the least consumed mammals. However, one Euplerid, the endangered *Mungotictis decemlineata* was one of the five most consumed protected species. Besides *M. decemlineata*, the low consumption likely reflects most Euplerid's unattractiveness as bushmeat and their opportunistic consumption from both snaring, and retaliatory killing during poultry predation (Golden 2009; Kotschwar Logan et al. 2014).

Few species were purchased, with the majority hunted by the interviewee. Purchasing of preferred species (fish and bushpig) was common, whilst the least preferred (lemur and carnivores) were mostly acquired by hunting. Previous research has reported the trading of bushpig (Golden et al. 2014b), but has suggested opportunistic hunting of wild species (Gardner and Davies 2014; Golden et al. 2014b). Reuter et al.'s (2016a) study reported hunting to be conducted mostly informally, however purchases through restaurants, markets, and travelling merchants were more formalised than previously estimated. Although protected species are primarily hunted, our research supports recent suggestions of a potentially more formalised, albeit small bushmeat trade and/or greater rule breaking.

The majority of wild species were reportedly hunted all year, likely reflected in an amalgamation of opportunistic hunting and persistent species presence of certain species. Tenrecs were the only species ~~wet season~~-hunted species in the rainy season, with their vulnerability to opportunistic hunting is at least partially reduced during their austral aestivation (Gould and Eisenberg 1966; Lovegrove and Génin 2008; Golden et al. 2013a). Carnivores and bats were primarily consumed during the dry season. Consumption of bats has previously been linked to periods of food shortages (Goodman 2006; Jenkins and Racey 2008), although our respondents typically experienced food shortages typically during the wet season. Conversely, consumption of carnivores

(particularly fosas) has been known to occur in response to retaliatory killing during the dry season. These results are similar to seasonal hunting patterns in Masoala peninsular where austral winter hunting of bushpig, tenrec and lemur, and austral summer hunting of carnivores was reported (Borgerson 2016; Brook et al. 2019). Behavioural-physiological characteristics of prey are similarly purported as drivers of hunter behaviour (Borgerson 2016).

### **Major drivers of protected species consumption**

The most likely explanation for the consumption of higher quantities of protected species was poverty. Although the relationship between poverty and bushmeat is complex, varying culturally and geographically, recent inter-country research has revealed poorer rural households to consistently consume more bushmeat (Brashares et al. 2011). In Madagascar, poverty, poor health and child malnutrition has been shown to drive rural lemur consumption (Borgerson et al. 2016). Other research has also drawn parallels between wealth, food insecurity and meat consumption (Golden et al. 2011; Jenkins et al. 2011; Golden et al. 2014a; Reuter et al. 2016b). Given the majority of consumed protected species were of low preference, poorer households are more likely to consume them out of food insecurity.

Consumption of strictly protected species was most prevalent in the Moramanga region. This region encompasses Andasibe-Mantadia National Park, Madagascar's most visited national park. Despite significant tourism revenue (Newsome and Hassell 2014), its distribution is uneven, with isolated villages typically financially neglected. Without greater park intervention and support, protection status alone is unable to reduce protected species consumption by poor households. Alarming, Andasibe-Mantadia likely represents the most sensitive area for reporting

bushmeat consumption, due to its high exposure to the MNP, tourism and local NGOs. Consequently, interviewee underreporting was potentially significant across this region.

Our observations on what drives the likelihood of consuming *any* protected species were inconclusive. Households further from the forest, and those with higher education were more likely to consume protected species. In practice this is unlikely, and the direction of this reported effect is not well understood, however it could be the result of risk of reporting, with these households less fearful of reporting their consumption than those living near protected areas. There was little evidence for a poverty effect, though there was a significant association with poverty among the subset of households reporting some consumption – the poorest of these families consumed more individuals of protected species. Households’ from Vatovavy-Fitovinany, a region encompassing unprotected, fragmented rainforests were less likely to consume protected species, but those that did, were more likely to have consumed larger quantities of protected species. A local NGO, the Madagascar Biodiversity Partnership (MBP), collaborates with households in reforestation and livelihood improvement schemes, which may positively influence the likelihood of households’ not participating in bushmeat consumption. This negative association (albeit statistically small) was reported between interviewee’s that perceived a conservation benefit and their reported consumption of bushmeat. This could explain why households overall consume less, but those that don’t receive conservation benefit consumed higher quantities of protected species. However, there are many other potentially confounding explanations including, reduced overall consumption due to, decreased hunting opportunities in Vatovavy’s small forest fragments, supporting less abundant



biodiversity; and underreporting from households that participate with (or are aware of) the MBP, and are less likely to reveal their hunting activities.

Forest ~~s~~Size was a significant predictor of protected species consumption in the final Poisson model, with households near larger forests consuming more individuals. This could be explained by the association of larger forests with greater species diversity and abundance (Burkey 1989), consequently providing greater opportunities for the hunting of wild species.

### **Major drivers of unprotected species consumption**

Although ~~p~~Poverty was an insignificant predictor, it did display a negative association, with this pattern worth discussing. Firstly, unlisted (helmeted guineafowl), pest (bushpig) and game species (tenrec) are highly preferred over protected species. Secondly, they are legally hunted and therefore commonly sold in Malagasy restaurants and markets. The amalgamation of a legal marketplace and higher preference drives price increases, ultimately limiting accessibility to wealthier households. This phenomenon has been reported for tenrec and helmeted guineafowl, noted for their high preference and cost in western Madagascar (Randrianandrianina et al. 2010).

Regionally, households from Moramanga were less likely to have consumed an unprotected species. This could be due to the conservation value of certain endemic species (tenrec and bird), and the significant MNP and NGO (Association Mitsinjo) presence. Furthermore, despite the legality of consuming most game species, the question is still likely sensitive in villages nearby these conservation centres, which could have resulted in lower reporting. Furthermore, much of the region is relatively wealthy due to the park's tourism value, with households potentially more financially able to afford higher preferred ~~domestic animals~~ livestock as a protein source. However,

when considering the higher consumption of greater quantities of protected species in Moramanga, this pattern is still not well understood, and could be reflective of the widespread consumption of unprotected species, making modelling of the predictors of binary consumption difficult.

Households with higher education were less likely to have consumed an unprotected species. The underlying mechanism for this is not fully known, however it could be associated with a greater knowledge of the moral (social norms) or ecological consequences of the unsustainable consumption of certain unprotected endemic species (i.e. g. tenrec). However, if this was the reason, it would be assumed that household education would have had a negative association with the consumption of protected species in the C1 models.

### **Major drivers of fish/eel consumption**

Wealthier households were more likely to have consumed a fish/eel and to have consumed greater quantities. This pattern reinforces poverty's role as a major driver of wild species consumption. It reflects Malagasy taste preference rankings and shows more desirable species are consumed by the wealthy, with less desirable species consumed by the poor.

Households from Moramanga and Vatovavy-Fitovinany, two rainforest regions, and relatively wealthier regions than the baseline deciduous forest region of Menabe consumed more fish/eel. Food security within Menabe is poor, with the region suffering serious food production shortages, and its relative dry nature (lack of water sources) likely underpins the association of greater fish/eel consumption in the two rainforest regions.

Households further from the forest were more likely to have consumed fish/eel, likely reflective of low access to forest dwelling species and greater dependence upon animals sold more commonly in markets. Likewise, Forest Size was reflective of greater fish/eel consumption and presumably underpinned by previously outlined reasons (more biologically productive areas). Unsurprisingly, larger villages with more developed markets and typically wealthier residents consumed more fish/eel. Surprisingly households that perceived benefitting from conservation consumed smaller quantities of fish/eel, the direction of association between these variables is not well understood, and unlikely of any significant value in reality.

## Conclusions

This research provides strong evidence that poverty is the principal driver of protected species consumption in Madagascar. It supports a growing (Golden et al. 2014a; Borgerson et al. 2016) body of literature documenting the consumption of endangered mammals by Madagascar's poorest and most food insecure. Given bushmeat is considered undesirable compared with domestic meat, and that there is no clear cultural affinity for it, our results suggest that improving domestic animal availability would be a promising mechanism for decreasing the hunting of threatened species. This could be achieved through improved poultry production programs, targeting disease reduction (e.g. Newcastle's disease), and improved husbandry techniques. Such alternative livelihood approaches have been implemented with mixed success (van Vliet 2000; Roe et al. 2015; Wicander and Coad 2015; Wright et al. 2016). Currently in NE Madagascar, programs aiming to improve Malagasy nutrition and reduce bushmeat consumption through village poultry health improvement programs are being trialled and implemented by MAHERY. These projects have potential, and their long-term success

must be monitored and evaluated (van Vliet 2000; Roe et al. 2015). Furthermore, the local context of bushmeat consumption, the applicability of the program across households/communities, and the scalability of the intervention must be considered (Wright et al. 2016). Such measures are needed to implement effective programs, to ultimately protect Madagascar's threatened species, and to alleviate poverty, food insecurity and potential zoonotic disease transmission.

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895

896 **Figure Captions**

897 **Fig. 1** The four study regions, MarovoayBoeny, Moramanga, Vatovavy-Fitovinany and Menabe, with forest cover represented in green  
898 (clockwise from top-left with village location inserts).

899

900 **Fig. 2** Total respondents' proportional bushmeat preference (left bar chart) and consumption frequency rankings (right bar chart). The total  
901 respondents to have stated a ranking is atop each bar. Note: not all respondents listed 7 species, hence the decline in total respondents in higher  
902 rankings.

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904 **Fig. 3** Total respondents' proportional domestic (poultry – chicken, duck, turkey; ungulate - zebu, pig, goat, sheep), fish & eel and bushmeat  
905 preference ranking. The total respondents to have stated a ranking is atop each bar.

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907 **Fig. 4** The relationship between total animals consumed and a household poverty index, sorted by region. The left and right plots display  
908 patterns of protected, and unprotected species consumption.

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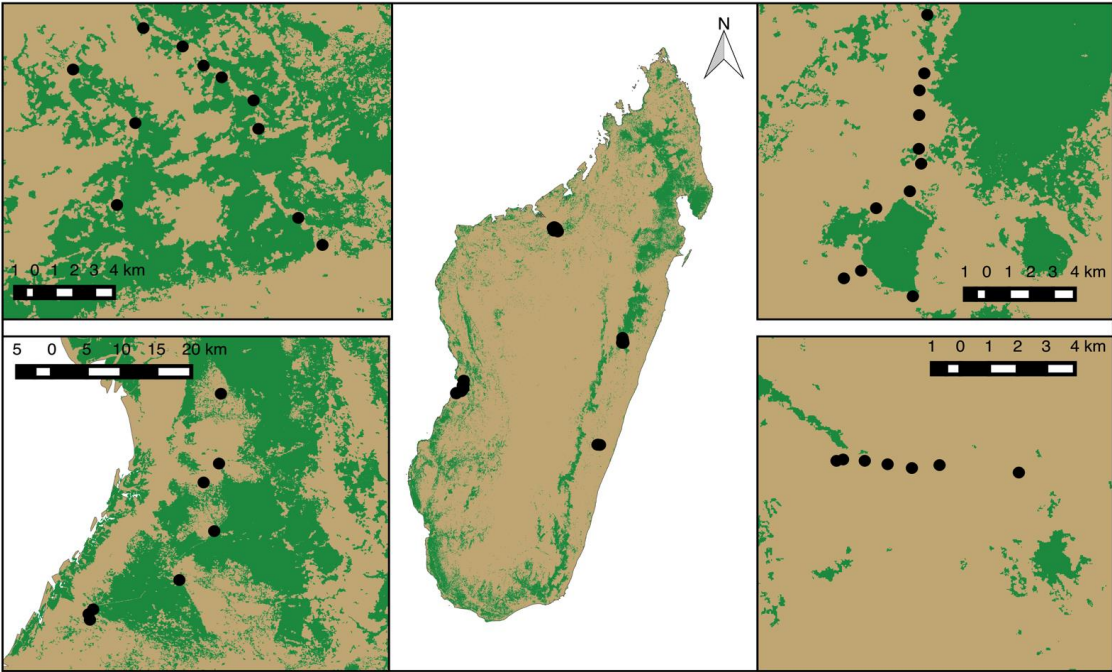
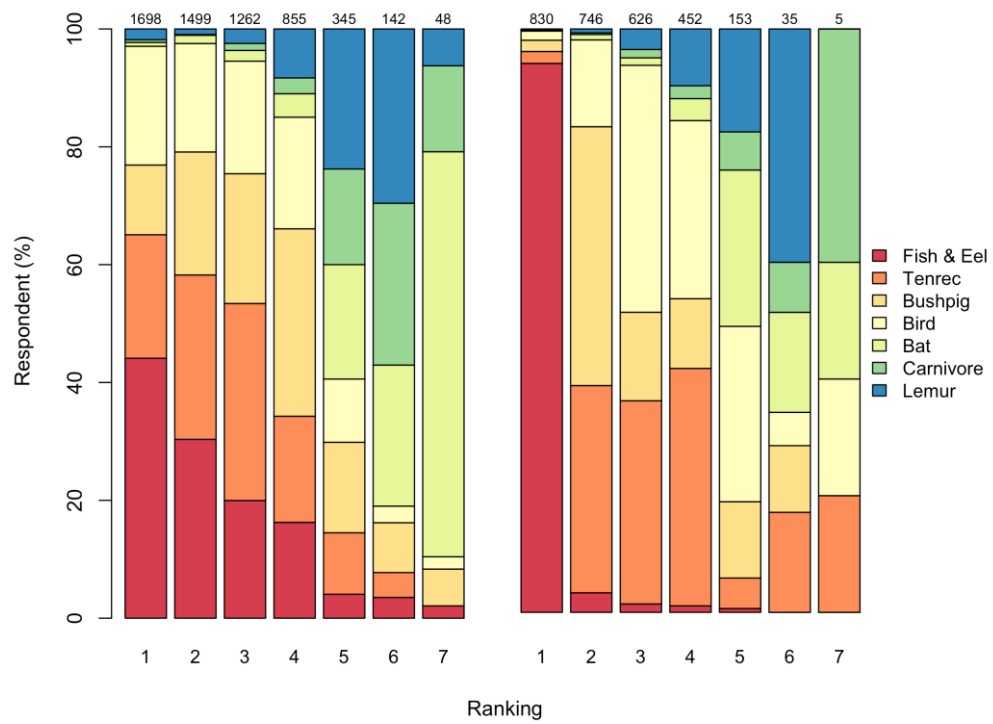
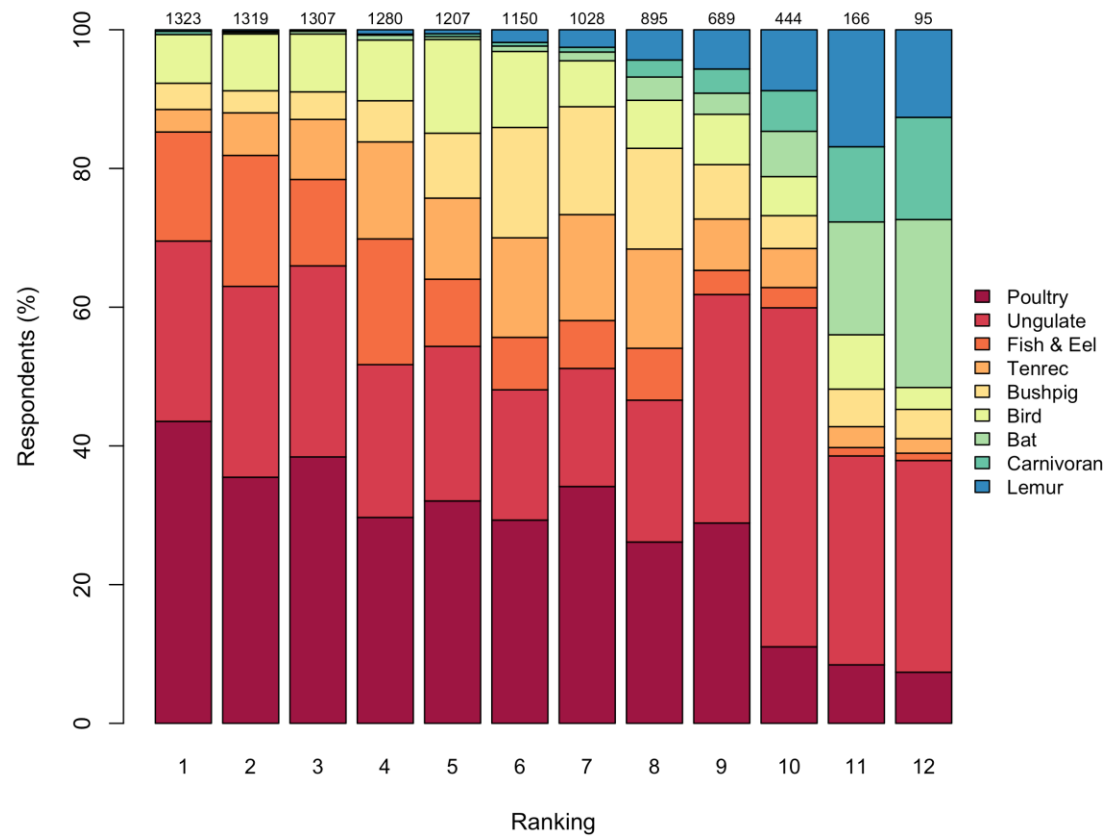


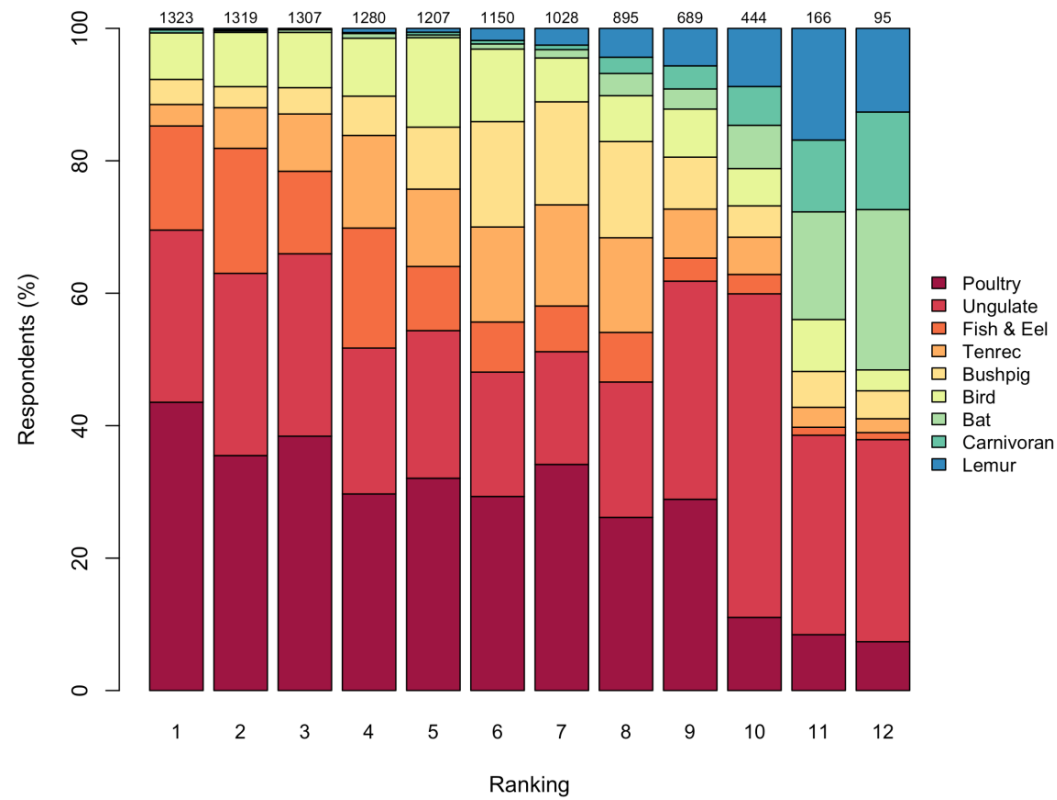
Fig. 1

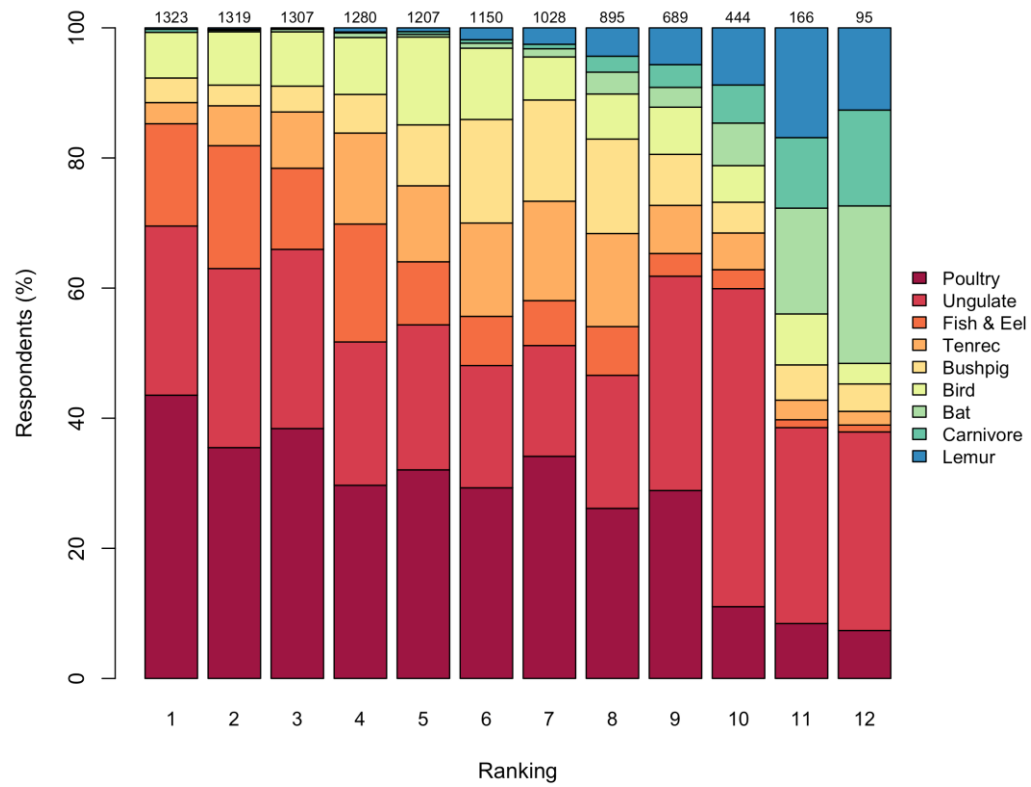






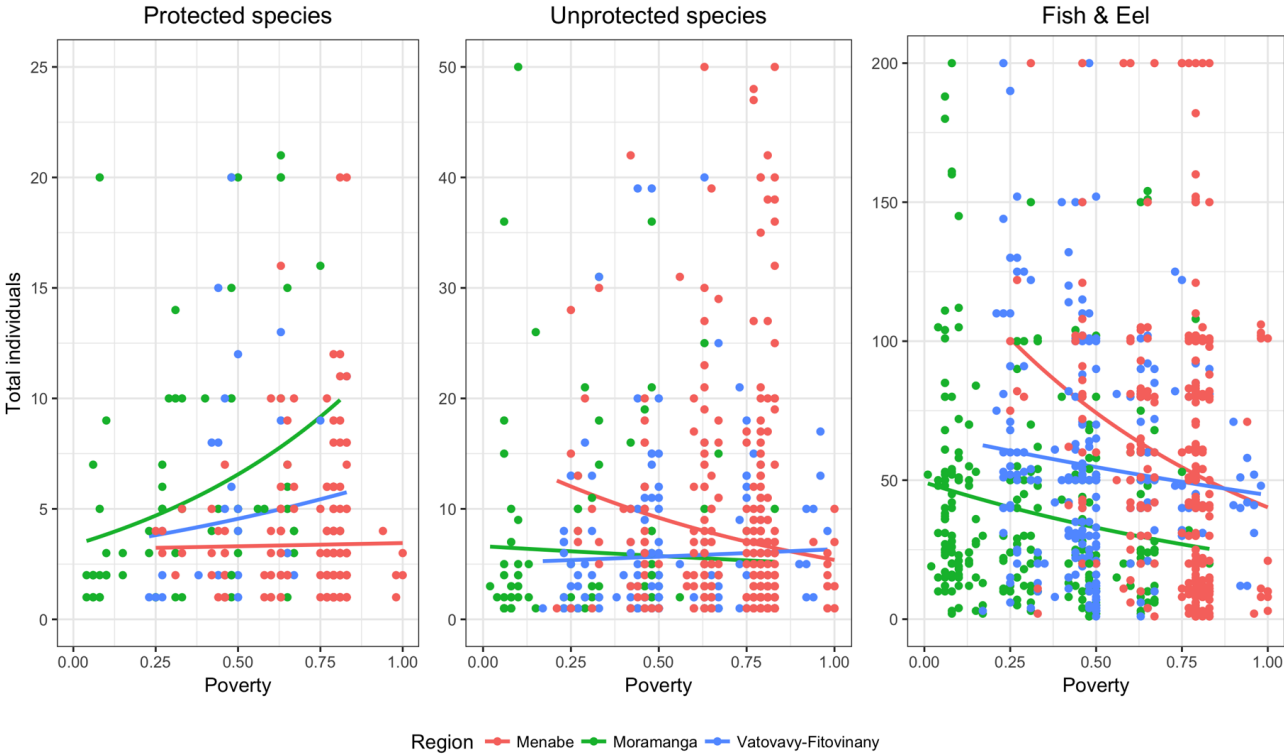
**Fig. 2**





**Fig. 3**

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Fig. 4

927 **Table 1.** The four study regions, detailing their forest type, protection status, total villages and households visited.

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Forest Type	Region	Protection Status	Forest Size (km <sup>2</sup> )	Total Villages	Households Interviewed
Deciduous	<del>Mareo</del> Boeny	Ankarafantsika National Park	1,350	8	363
	Menabe	Andranomena Special Reserve	64	2	190
	Menabe	Kirindy Private Reserve	710	2	266
	Menabe	Unprotected	710	1	206
Rainforest	Moramanga	Andasibe-Mantadia National Park	155	6	362
	Vatovavy-Fitovinany	Unprotected	< 10	5	359

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941 **Table 2.** The total number of individual animals consumed by category, and proportionally by village, household, season, and method of  
 942 acquisition (B & H = bought and hunted).  
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Animal	Total Consumed		Village Last year (%)	Household Last year (%)	Season Consumed (%)			Acquisition Method (%)			
	Last year	Last week			Dry	Wet	Both	Bought	Hunted	B & H	Gift
Bat	569	71	35.7	10.0	49.1	15.2	35.7	38.2	50.2	4.3	7.3
Bird	4160	198	78.6	46.0	45.8	4.7	49.5	23.2	65.1	8.5	3.1
Carnivore	256	71	50.0	3.1	44.7	15.5	39.8	11.6	68.3	9.1	11.0
Eel	4489	60	67.9	46.0	28.1	29.0	42.8	44.2	45.7	8.1	1.3
Fish	79852	7784	71.4	84.8	8.1	18.7	73.2	50.7	39.0	9.4	0.2
Lemur	727	32	53.6	5.7	43.2	7.6	49.2	20.5	64.8	3.2	10.3
Tenrec	6165	0	71.4	47.2	10.0	67.0	22.9	27.5	63.0	6.6	2.7
Bushpig	1043	1	67.9	22.9	37.3	5.5	57.1	59.7	29.9	7.0	3.3

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952 **Table 3.** Previous year household consumption rate (individual animals per household) of species by protection classification, forest type and  
953 protected areas.

Forest	Protection	Category 1	Category 2		Category 3	Not Listed	TOTAL
			Class 1	Class 2			
Deciduous		<b>1.48</b>	<b>0.89</b>	<b>0.59</b>	<b>1.20</b>	<b>43.11</b>	<b>47.27</b>
	National Park	NA	NA	NA	NA	NA	<b>NA</b>
	Reserve	2.17	1.28	0.89	1.83	70.80	<b>76.98</b>
	Unprotected	2.54	1.58	0.96	1.93	57.75	<b>64.75</b>
Rainforest		<b>4.87</b>	<b>1.03</b>	<b>3.84</b>	<b>2.37</b>	<b>60.68</b>	<b>72.79</b>
	National Park	3.80	1.63	2.17	1.90	49.74	<b>59.24</b>
	Reserve	NA	NA	NA	NA	NA	<b>NA</b>
	Unprotected	5.95	0.42	5.53	2.85	71.70	<b>86.45</b>
TOTAL		<b>2.88</b>	<b>0.95</b>	<b>1.93</b>	<b>1.69</b>	<b>50.36</b>	<b>57.81</b>

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