Bushmeat hunting, retaliatory killing, habitat degradation and exotic species as threats to Fosa (*Cryptoprocta ferox*) conservation

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Abstract

Large carnivores are in global decline, chiefly resultant of anthropogenic persecution, habitat reduction and disturbance. Fosas represent Madagascar's largest carnivore, occupying much of the island's forest. This thesis examines the threats of bushmeat hunting, retaliatory killing, habitat alteration and exotic species using sociological and remote-sensing methodologies.

Habitat degradation was not associated with reduced fosa occupancy, indicating some resilience within large, contiguous forests. However, competition with exotic species (cats, dogs) was associated with reduced fosa occupancy and potential temporal shifts towards greater nocturnality.

Poor households were more likely to consume protected species. Conversely, wealthier households consumed more fish and eel. This pattern is reflected in Malagasy reported taste preference to consume domesticated animals and certain legally hunted wild species. Protected areas were not associated with reduced protected species consumption.

Fosas' predation was a major cause of rural poultry mortality. Predation was more likely to occur in deciduous forests, in the dry season, during the evening. Fosa predation, and lower education was associated with negative Malagasy attitudes. Wealthy households, and those that had experienced fosa predation were most likely to retaliatory kill a fosa.

Strategies to safeguard fosas' long-term persistence should seek to improve domestic husbandry, build robust coops with the use of watchdogs, promote education, and reduce exotic species abundance.

Contents

Chapter One

Thesis Introduction

Madagascar the threatened "eighth continent"

Madagascar's endemic plant and vertebrate species represent approximately 3.2% and 2.8% of the world's species respectively (Myers et al. 2000). These high levels of endemism, coupled with its rapid decline in forested habitats (Green and Sussman 1990; Harper et al. 2007; Moat and Smith 2007; Allnutt et al. 2013; Zinner et al. 2013; Vieilledent et al. 2017), have led to Madagascar's worldwide recognition as a conservation priority (Brooks et al. 2006; Funk and Fa 2010; Mittermeier et al. 2011; Zachos and Habel 2011).

With a population nearing 25 million, Madagascar is a nation facing severe socio-economic problems. Its population, growing rapidly at 2.7% per annum, is not only one of the highest in the world, but also one of the poorest, recently ranking in the top ten poorest countries by GPD per capita (The World Bank 2016). Consequently, poverty estimates currently define 70% of the population as poor, with the majority of Madagascar's population, approximately 65%, living rurally (United Nations 2015).

Madagascar's continued political instability has hindered the government's ability to support its population and conserve its biodiverse forests. Despite recent democratic elections in 2013 and increased economic growth, the effects of the 2009 *coup d'etat* are still being felt across the island. Corruption is rampant, with Madagascar recently ranked 145 out of 176 countries in 2016 in the Corruption Perception index (Transparency International 2016). This ineffectual governance has ultimately played a significant role in the failure of conservation efforts to slow the deforestation of Madagascar's forests (Casse et al. 2004; Schuurman and Lowry Ii 2009; Randriamalala and Liu 2010; Horning 2012; Gore et al. 2013; Waeber et al. 2016; Remy 2017).

Recent research has estimated deforestation to have reduced Madagascar's natural forest cover to 8.9 million hectares in 2014 (15% of its national territory), with around half of its forest located less than 100 m from the forest edge (Vieilledent et al. 2017). Annual deforestation rates (up to 2010) have consistently recorded annual losses of 1 – 2.5% yr^{-1} varying by forest type and region (Harper et al. 2007; Allnutt et al. 2013; Grinand et al. 2013; Zinner et al. 2013). This deforestation has resulted in highly disturbed, fragmented forests in which anthropogenic disturbance occurs island-wide.

Madagascar's fauna are consequently becoming increasingly threatened in the form of greater exposure to poaching for consumption or trade (Golden 2009; Jenkins et al. 2011; Razafimanahaka et al. 2012; Randriamamonjy et al. 2015; Borgerson et al. 2016), exotic species (Ratsirarson and Goodman 1998; Gerber et al. 2012b; Kull et al. 2014; Farris et al. 2015; Farris et al. 2016) and for carnivores, greater potential for fatal interactions with villagers and their livestock (Hawkins 1998; Jones et al. 2008; Kotschwar Logan et al. 2014). Unfortunately, knowledge of species' response to these anthropogenic disturbances remains poor, with limited research reporting species' reaction to be typically negative, but fluctuate according to taxonomic group, ecoregion and the relative importance of the proximate cause (Irwin et al. 2010). Given Madagascar's wildlife populations are likely to become increasingly exposed to anthropogenic disturbance, it is crucial that we understand the impact humans may have upon Madagascar's forests and its wildlife.

In assessing landscape scale anthropogenic disturbance in Madagascar, the use of an island-wide, large ranging species presents an ideal proxy. This study examines Madagascar's largest carnivore the fosa (*Cryptoprocta ferox*) as a model species in studying the effects of human habitat alteration, disturbance, exploitation and

persecution. Fosas present one of the few native species in Madagascar to be present nearly island-wide and occupy the largest home-range of any terrestrial mammal. Furthermore, fosas' innate biological characteristics (large body size, large home-range, low population density) and conflict prone behavior (predation of livestock) make them particularly susceptible to extinction (Woodroffe 2000; Gittleman 2001; Kruuk 2002; Cardillo et al. 2004; Ripple et al. 2014). Consequently, fosas were used in examining the effects of Madagascar's rapidly altered habitat, invasive species presence, hunting, and retaliatory killing.

The fosa *Cryptoprocta ferox*

Cryptoprocta ferox, Madagascar's largest predator has been labeled a keystone species for its important role atop the food chain (Dollar 2006). Locally known as the fosa[1], it weighs on average 6 - 7 kg, reaching overall lengths of 1.4 m (Hawkins 1998; Dollar 2006), with tail and body of approximately equal length, fosas have evolved to be equally apt in the trees or ground. This arboreal ability even extends to their unusual mating behavior in which females mate with several males in the branches of a large tree over the course of a week (Hawkins 1998). Gestation typically lasts six to seven weeks, with two to four offspring born per litter (Albignac 1973). Females raise young, with juveniles typically independent by age one and sexually mature by the age of three to four years old (Albignac 1975). Females are territorial, with males not maintaining strict territories (Lührs 2012). Most uncommon for a solitary species, male fosas have been observed to create sibling dyads whilst hunting for larger prey, such as sifakas (Lührs and Dammhahn 2009; Luhrs et al. 2012). Given their size and

[1] Previously and more commonly referred to as 'fossa' in English, 'fosa' will be used in this thesis in align with Duckworth et al.'s (2014) attempt to reduce the use of similar common names within the Euplerids.

arboreal capabilities, fosas predominately prey upon lemurs (Hawkins 1998; Dollar et al. 2007) making them the world's only mammalian primate predator specialist. Despite this preference, fosas also maintain a diverse diet (Dollar et al. 2007), exploiting a surprisingly wide range of prey items, largely dependent upon the region's local fauna.

When considering fosa's body size and metabolic requirements, they have been found to occupy disproportionally large home ranges (McNab 1963; Lindstedt et al. 1986; Lührs 2012). Females tend to maintain strict home ranges of 20 km^2, whilst males maintained overlapping home ranges increasing from 40 km^2 to 50 km^2 during the mating season (November to December)(Lührs 2012). Despite being found ubiquitously across Madagascar, previous research has revealed low population densities on the east and west coasts ranging from 0.17 - 0.26 adults per km^2 (Hawkins and Racey 2005; Gerber et al. 2010). To date, much of our current knowledge has been derived from studies investigating fosas' biological, behavioural and sociobiological curiosities, however limited research has examined the threats to the population's long-term viability.

Deforestation and anthropogenic disturbance

Madagascar's original forest cover and subsequent deforestation rates have been a highly controversial topic. Disputes over historical forest cover and the distribution and extent of different vegetation types is still in discussion today (Kull 2000; Klein 2002; Scales 2012; McConnell and Kull 2014). This has made estimations of forest loss difficult (McConnell and Kull 2014) and has plagued dialogue over the drivers of recent and historical deforestation (Scales 2014).

Discourse on deforestation in Madagascar has mostly focused upon the widespread and mostly irreversible effects of swidden agriculture, locally known as 'tavy' (Gade 1996; Kull 2002, 2004; Styger et al. 2007; Klanderud et al. 2010). As a result much of Madagascar's forest loss has largely been blamed upon poverty-driven swidden cultivation (Sussman et al. 1994; Scales 2011; Horning 2012; Zinner et al. 2013; Scales 2014). Despite this, historical reductions in Madagascar's forest may not only be attributed to household subsistence (Green and Sussman 1990), but also to French colonial driven increases in commercial agricultural production of cash crops for export (Randrianja and Ellis 2009; Scales 2014), and timber concessions (Jarosz 1993; Kull 2000). In recent decades too, the important role of cash cropping by the wealthy, by transient migrants, and/or for international export has been associated with deforestation across different regions in Madagascar (Casse et al. 2004; Scales 2012; McConnell and Kull 2014; Scales 2014).

Furthermore, the collapse of democratic governance in 2009 has seen an increase in the rate of loss, and illegal export of forest products (WWF 2001; Randriamalala and Liu 2010). The booming exploitation of precious woods (rosewood and ebony among others) has been widely documented and has reached unheralded and mostly irreversible levels. (Schuurman and Lowry Ii 2009; Randriamalala and Liu 2010). When considering Madagascar's socioeconomic conditions coupled with its ineffective governance, the effects of continued forest exploitation and human encroachment are only likely to worsen. Questions must be asked as to what effect this encroachment has on animal populations, and specifically large-ranging, human-sensitive carnivores like fosas.

With large expanses of Madagascar's forests now fragmented (Harper et al. 2007; Vieilledent et al. 2017), and few unperturbed areas remaining, edge effects are

a pervasive problem (Lehtinen et al. 2003; Watson et al. 2004; Lehman et al. 2006). Exacerbating this issue is Madagascar's mostly rural population, which is frequently located within and around forested regions. This demographic heavily depends upon the forest for its products, including its supplement of food, medical remedies, construction materials, and agriculture.

Unfortunately, our knowledge of the effects of human disturbances upon animal populations in Madagascar is limited (Irwin et al. 2010). Irwin et al.'s (2010) review of species change to disturbed forests found several broad themes. Firstly, overall species response to anthropogenic disturbance tended to be negative, with different taxonomic groups reacting differently to different proximate factors. Furthermore, species' reactions varied across Madagascar's distinct forest types, with highly variable reactions amongst species of lower taxonomic groupings. This review highlights the need for investigation into the effects of human habitat disturbance upon Madagascar's wildlife. Given fosas' island-wide distribution and extinction prone characteristics, they present an ideal model species to examine the effects of island-wide anthropogenic disturbance.

Research has begun to illuminate the effects of anthropogenic habitat disturbance upon Madagascar's understudied carnivores and fosas. Given most of Madagascar's carnivores are elusive and difficult to observe, camera-traps provide an ideal tool for monitoring populations and evaluating patterns of change (O'Connell et al. 2010). Such methods were first used in Ranomafana National Park to examine the impact of logging, and fragmentation on species composition, density and occupancy of several native carnivores and fosas (Gerber et al. 2012b). Findings revealed fewer native species in fragmented than continuous rainforests. Interestingly, fosas were slightly more resilient and were recorded in similar densities in fragments nearer to

the forest (< 2.5km), and in primary and selectively-logged forests, whilst absent from fragments > 15km from contiguous forest. Following Gerber's initial investigation, camera-traps were employed in Madagascar's largest protected park, the northeastern Masoala-Makira complex. Farris et al.'s (2015) study observed clear decreases in native and increases in exotic carnivore occupancy as degradation increased. Feral cats and domestic dogs were also demonstrated to maintain higher rates of occupancy than half of all native species. Expanding upon their initial results, these studies also examined the effect of human and invasive species' presence on carnivore behaviour. Dollar (1999) and Gerber et al. (2012a) noted fosas' to exhibit more crepuscular activity patterns, but overall to display cathemeral patterns in activity. Most notably though, fosas were found to be absent throughout the diel cycle at sites where dogs were most abundant. Likewise, Farris et al.'s (2014) observed similar results with a high overlap between invasive and exotic carnivores, with fosas avoiding humans and dogs across all seasons. Currently only a preliminary study has examined fosas' activity in its deciduous habitat, recording the use of cathemeral activity from radiotelemetry (Rahajanirina 2003). Despite this initial expansion of knowledge little systematic research has been published from Madagascar's western forests compared to its humid counterpart (Waeber et al. 2015).

Madagascar's western forests represent a distinct biome, inhabited by communities living under different cultural and socio-economic conditions. These deciduous forests also represents one of Madagascar's most threatened forest types, with estimated reductions in total forest cover of 97% (Smith 1997; WWF 2001). Considering that Irwin et al.'s (2010) review found variances in species responses to human habitat alteration across Madagascar's distinct forest types, the need for greater geographical scrutiny is vital. Given western Madagascar's highly threatened

habitat is rapidly declining, future research is urgently required into the effects of habitat alteration on its species' occupancy and behavior, most notably, fosas.

Madagascar's wild meat appetite

Whilst the eating of wild animals is nothing new (Barnosky et al. 2004), a burgeoning global population, and greater human encroachment into previously undisturbed forests presents bushmeat consumption as one of the biggest threats to tropical vertebrates (Bennett and Robinson 2000; Brashares et al. 2004; Nasi et al. 2008; Ripple et al. 2016). Consequently, bushmeat consumption has received considerable academic attention worldwide, and in conservation 'hotspots' such as equatorial Africa (Wilkie and Carpenter 1999; Walsh et al. 2003; East et al. 2005; Brashares et al. 2011).

Despite bushmeat's acknowledged threat, its exploration in Madagascar, a conservation priority, has only recently begun gaining momentum. In what was one of the first studies of the hunting of protected species in Madagascar, alarming rates of consumption species' remains were found in a transient raffia harvester's camp (García and Goodman 2003). Most notable was the hunting of large mammals, with a minimum of 32 lemurs and 2 fosas consumed. An ensuing landmark study examined hunting practices in villages nearby the Makira forest in NE Madagascar (Golden 2009). The hunting of 23 mammal species for consumption was found, with 57% of villages having consumed fosas. Furthermore, the modelling of the villages' hunting rates whilst accounting for species' life-history characteristics found hunting practices to be unsustainable. Since this initial research, a number of studies have revealed the illegal consumption of protected species across Madagascar (Jenkins and Racey 2008; Jenkins et al. 2009; Randrianandrianina et al. 2010; Jenkins et al. 2011;

Razafimanahaka et al. 2012; Gardner and Davies 2014; Borgerson et al. 2016; Reuter et al. 2016a; Reuter et al. 2016b).

Despite an increase in the academic examination of bushmeat consumption in Madagascar, few studies have scrutinised its drivers, or its occurrence at a multi-site scale. Several studies have revealed associations between poverty, poor health and the consumption of bushmeat (Jenkins et al. 2011; Golden et al. 2014; Borgerson et al. 2016; Reuter et al. 2016b). Whilst one multi-site study revealed variations in the consumption rates of protected species across eastern and western forests, with consumption of protected species lower in areas where environmental education or enforcement was greater (Razafimanahaka et al. 2012). In light of these significant explorations, no studies have explored the different drivers of the consumption of protected versus unprotected species across forests of varying protection and of different forest types (rainforest versus dry deciduous). When considering Madagascar's immense poverty, booming population and frail political environment, understanding the cultural, socioeconomic and geographical cues of bushmeat consumption are critical in informing effective conservation. Equally important is the evaluation of Madagascar's governmental institutions in curbing hunting practices within protected areas.

Human-carnivore attitudes and persecution

Large carnivore populations are in global decline, largely in the face of widespread persecution (Woodroffe 2000; Ripple et al. 2014). Their biological characteristics lend themselves to 'conflict' with pastoralists (Kissui 2008), with retaliatory killing due to livestock predation a predictable narrative worldwide. Most academic attention has focused upon large carnivore predation of livestock, epitomised by lion's

predation of cattle in Africa (Woodroffe and Frank 2005; Lichtenfeld et al. 2015). Despite the potential for this kind of persecution of carnivores in Madagascar, it has been academically neglected.

Anecdotal reports have cited fosas as a culpable victim of collective group hunting due to their predation of domestic fowl. Given fosas' large home range requirements (Hawkins and Racey 2005; Lührs 2012), in amalgamation with human settlements' continued encroachment on forests, poultry predation by fosas is likely, and known. Furthermore, rural subsistence farmers, Madagascar's poorest demographic, are likely to be most intolerant to harmful impacts upon their livelihoods (poultry theft) with retaliatory killing of fosas a likely repercussion.

Human attitudes towards fosas are equally important variables to be considered when exploring their persecution. In Madagascar, taboos, known as *fady* maintain influence over social norms and attitudes (Van Gennep 1904; Ruud 1960; Lambek 1992; Jones et al. 2008; Sodikoff 2012), and are important in considering their impact upon Malagasy interaction with fosa. Accounts of *fady* in south east Madagascar have been recited, depicting fosas as a threat to lone children in the forest, a livestock predator of piglets, fowl, and to be hated and feared (Ruud 1960). Furthermore fosa are believed to scavenge on the bodies of dead ancestors, and fady prohibiting their consumption has been reported across different regions of the island (Ruud 1960; Jones et al. 2008). Other studies too, have observed fady restricting fosas consumption (Jenkins et al. 2011; Golden and Comaroff 2015). In considering these stories, understanding people's attitudes towards fosas is important given its potential influence on people's propensity to persecute fosa.

In consideration of Golden's (2009) estimation of unsustainable rates of fosa mortality, few annual retaliatory killing events are necessary to have serious

implications for a sub-population's long-term survival. In examining persecution of carnivores in Madagascar, focus upon Madagascar's largest, most conflict-prone native carnivore is a vital first step in uncovering the impacts of persecution in its most widespread form. Furthermore, enumerating fosas killed, and improving our understanding of the drivers of this threat, is critical in providing a holistic representation of the potential threats facing fosas, and many of Madagascar's wildlife as a whole.

Thesis Aim and Overview

This thesis seeks to examine the greatest threats to Madagascar's wildlife, deforestation and habitat alteration, while additionally investigating wildlife persecution in the forms of bushmeat consumption and retaliatory killing. Fosa have been used as a model species to examine these factors in greater detail, and to investigate their effect upon one of Madagascar's most important, widespread and potentially extinction prone species. These topics will be investigated through four interrelated chapters that will ultimately inform our understanding of Madagascar's threatened wildlife, with specific focus upon fosas and the measurement of their conservation status.

Chapter One has discussed Madagascar, and its importance as a conservation priority, whilst considering Madagascar's enigmatic and flagship apex predator, *Cryptoprocta ferox*. A summary of the most significant threats facing 21st century Madagascar was discussed, placing into context their effect on wildlife, and most notably, fosas.

Chapter Two discusses the impacts of anthropogenic habitat alteration upon fosa occupancy. It centres upon a camera-trapping study of two sites of varying anthropogenic disturbance in western Madagascar, Ankarafantsika National Park (ANP) and Andranomena Special Reserve (ASR). Variances in habitat type, as well as human and invasive species presence will be considered as variables impacting fosa site occupancy.

Chapter Three examines the effect of human and invasive species presence upon fosas' temporal activity patterns. Data from chapter two will be used to examine any alteration in fosa behaviour and its potentially damaging effects.

Chapter Four considers the implications of bushmeat hunting in Madagascar and its effect upon fosas. Using household surveys of villages across six forests, it will investigate the species affected and the socioeconomic, cultural and geographical variables that drive its occurrence. Additionally, surveying of six forests of contrasting protected status will allow the consideration of the effectiveness of the Madagascar National Parks (MNP) in their management of illegal activities.

Chapter Five investigates the occurrence of fosa retaliatory killing due to poultry depredation. Seasonal, temporal and poultry ownership practices will be discussed in their potential influence upon poultry depredation. The additional role of socioeconomic, cultural and geographic variables will be discussed as potential drivers of poultry predation, retaliatory killing and Malagasy attitudes.

Chapter Six will consider the thesis' combined results, and their implication for the fosas' long-term persistence. Future conservation strategies are proposed and discussed, based on the data collected during the course of this DPhil.

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Chapter Two

Exotic carnivore presence drives endemic carnivore behavioural change and decline in Madagascar's deciduous forests

Abstract

Anthropogenic habitat alteration, and exotic species invasion is threatening carnivores globally. Understanding its impact is critical for creating localised, effective endemic carnivore conservation programs. Madagascar's Eupleridae have been described as the least studied and most threatened group of carnivores worldwide (Brooke et al. 2014). To better understand anthropogenic disturbance's impact, we provide the first multi-region study of one of Madagascar's most imperilled habitat, its deciduous forests. Deforestation, fragmentation, human and exotic species presence were considered as factors affecting the modelled occupancy of Madagascar's largest carnivore, the fosa (*Cryptoprocta ferox*). Two westerly deciduous forests, Ankarafantsika National Park and Andranomena Special Reserve were remotely surveyed using camera-trap grids. Our results revealed no clear patterns between habitat degradation and fosa occupancy. A strong negative association was exhibited between cats and fosas. Dogs were associated with fosa occupancy, however the correlation was at best weak. Cat occupancy was negatively associated with birds, and positively associated with contiguous forest and narrow trails. Conversely, dog occupancy was best predicted by degraded forest, wider trails and exotic civet presence. Our results suggest fosas are capable of navigating degraded landscape and in the short-term, are resilient to disturbance inside contiguous forests. However, high cat and dog occupancy represent a significant source of resource competition through prey exploitation and interference. The spread of disease between exotic species, fosas and their prey may be a considerable risk to their long-term health. Exotic carnivore management strategies should be considered to reduce the widespread predation of endemic species, and the transmission of disease.

Keywords: Madagascar, Eupleridae, deforestation, fragmentation, exotic, feral cat, Menabe, Ankarafantsika.

This chapter forms the basis of a paper prepared for Oryx of which I am the lead author and my co-authors are Luke J Dollar, Cedric Kai Wei Tan and David W Macdonald.

Introduction

Fosas (*Cryptoprocta ferox*) are Madagascar's largest endemic carnivores. They are likely a keystone species (Dollar 2006) and play a critical role in ecosystems across Madagascar as an apex predator of lemurs, small mammals, reptiles and birds (Dollar et al. 2007; Hawkins and Racey 2008). Weighing on average 6-7 kg (Hawkins 1998; Dollar 2006), male fosas have been estimated to occupy large home-ranges of up to 50 km^2 during the mating season, with females maintaining annual ranges of 20 km^2 (Lührs and Kappeler 2013). Despite their wide-ranging behaviour, fosas are locally rare, found at densities of 0.18 – 0.26 km^{-2} in a deciduous forest (Hawkins and Racey 2005) and 0.17 km^{-2} in an eastern rainforest (Gerber et al. 2010). Currently categorized as Vulnerable on The IUCN Red List, fosas face threats from bushmeat hunting (García and Goodman 2003; Golden 2009; Farris et al. 2015b), retaliatory killing due to poultry predation (Hawkins 2016; Reuter et al. 2016), exotic species (Gerber et al. 2012c; Farris et al. 2015c) and island-wide reduction and degradation of habitat (Gerber et al. 2012b; Farris et al. 2015b). Although fosas' geographic range extends across much of the forested landscape, fragmentation means many forests are likely incapable of supporting long-term populations (Hawkins and Racey 2005).

Deforestation has significantly reduced Madagascar's overall forest cover, with much of its remaining forest severely degraded (Harper et al. 2007; Allnutt et al. 2013; Vieilledent et al. 2017). This issue is exacerbated by Madagascar's rapidly growing population at 2.8% p.a., one of the fastest growing and poorest nations on earth (The World Bank 2016). Despite this trend, the effects of anthropogenic disturbance on Madagascar's endemic species has been the subject of little research (Irwin et al. 2010). In addressing these empirical deficits, fosas are of particular interest as focal species for investigating the impacts of human forest disturbance.

Their innate biological characteristics (large body size and home-range, low population density) make them particularly susceptible to extinction in the face of human expansion (Ripple et al. 2014).

Published research documenting fosas' persistence in human disturbed landscapes is limited to studies in Madagascar's eastern rainforests. Gerber et al. (2012b) conducted photographic sampling in author-classified primary, selectively-logged, and fragmented forests of varying distances to intact forest to examine its effect on carnivore composition in Ranomafana National Park (RNP). The study revealed lower endemic carnivore abundance in selectively logged and fragmented forests, with high levels of exotic species in fragmented habitats. Fosas were absent from fragments > 15 km from intact forest. Similarly in Masoala-Makira of northeastern Madagascar comparable results have been found with lower native carnivore and higher exotic carnivore occupancy in more degraded forests (Farris et al. 2014; Farris et al. 2015b). A strong inverse relationship was observed between proximity to village and fosa occupancy (Farris et al. 2014). Despite advances in knowledge of anthropogenic disturbances' effect on rainforest-dwelling fosas, no similar research has yet been published from Madagascar's deciduous forests.

Madagascar's western deciduous forests represent one of its most abundant forest types (Dufils 2003) and globally threatened ecoregions (Janzen 1988; Waeber et al. 2015). Occupying most of the island's west, deciduous forests encompass an array of vegetation types, hosting important biodiversity and many narrow-ranged endemic taxa (Waeber et al. 2015). Deforestation has been particularly devastating, reducing much of the region's existing forest cover (Smith 1997; Scales 2012), with high rates of annual forest loss continuing today (Zinner et al. 2013). Nevertheless, Madagascar's dry forests have been neglected by conservation and research activities

compared to its higher-profile, eastern rainforests (Waeber et al. 2015). This relative deficit in knowledge of Madagascar's dry forest dwelling species' persistence in a now human-dominated landscape inhibits regional conservation efforts. Existing literature reviews have documented Madagascar's endemic species different responses to anthropogenic change in deciduous versus rainforests (Gardner 2009; Irwin et al. 2010). Given this discrepancy, it is critical to understand fosas' response to anthropogenic change inside deciduous forests and provide evidence to inform the management of a keystone species.

This paper presents the first multi-region investigation of the effects of anthropogenic disturbance, in the form of deforestation, as well as the impacts of human and exotic species' on deciduous forest living fosas. Unlike previous single region rainforest studies, two deciduous forests of different regions were chosen, Ankarafantsika National Park in the Marovoay region and Andranomena Special Reserve in Menabe. These two regions encompass a sample of two of Madagascar's most important tracts of deciduous forest, contrasting in levels of forest cover and human occupation. Ankarafantsika contains a mosaic of anthropogenic altered habitats, and human settlements within the park's borders. In contrast, Andranomena encompasses one contiguous forest, with no settlements within its borders. These sites collectively provide a sample of different forms of anthropogenic land-use across western deciduous forests. Our objectives were to examine: 1) The effect of human and exotic species presence on fosa occupancy; 2) The effect of different landscape variables (measures of forest degradation) on fosa occupancy; and 3) The effect of site on fosa occupancy. To fulfil these objectives, a camera-trapping grid was established in each region, and the resulting detection data were used in occupancy modelling.

Methods

Study sites

The northwest Ankarafantsika National Park (ANP) is Madagascar's largest continuous dry deciduous forest (1,350 km^2) (Figure 1). At 37.73 km^2, the site surrounds four villages along the Route Nationale 4 and is characterised by a variety of landscapes from 'old-growth' forest (although not true old-growth, for the purpose of classification, it is defined as contiguous forest that has not been deforested but is currently, or has previously experienced some selective-logging and human disturbance) to savannah, raffia plantations and rice fields. It also contains the park's designated tourist and research trail systems, linked to the local villages. The trails are recurrently used by villagers and frequented by exotic species, such as zebu (*Bos primigenius indicus*), domestic dog (*Canis lupus familaris*), feral cat (*Felis sp.*), bushpig (*Potamochoerus larvatus*) and small Indian civet (*Viverricula indica*). Only one other endemic carnivore occupies ANP, the western falanouc (*Eupleres major*)(Merson et al. 2017).

Andranomena Special Reserve (ASR) is located in the central west region of Menabe. Covering 64 km^2, ASR is largely fragmented from the larger northern Kirindy-Ambadira Forest Complex (Zinner et al. 2013). Two villages delimit ASR's north and southern boundaries. ASR encompasses 35.45 km^2 of contiguous, mostly 'old-growth' forest (defined as in ANP forest), although it has lost many of its local endemics to forest degradation (Smith et al. 1997; Ganzhorn and Schmid 1998). The area is bisected by a grid system of trails established by the former forestry commission (Figure 1). Despite the cessation of commercial logging, evidence of widespread illegal logging was evident throughout the study. ASR contains a second Euplerid, the bokiboky (*Mungotictis decemlineata*).

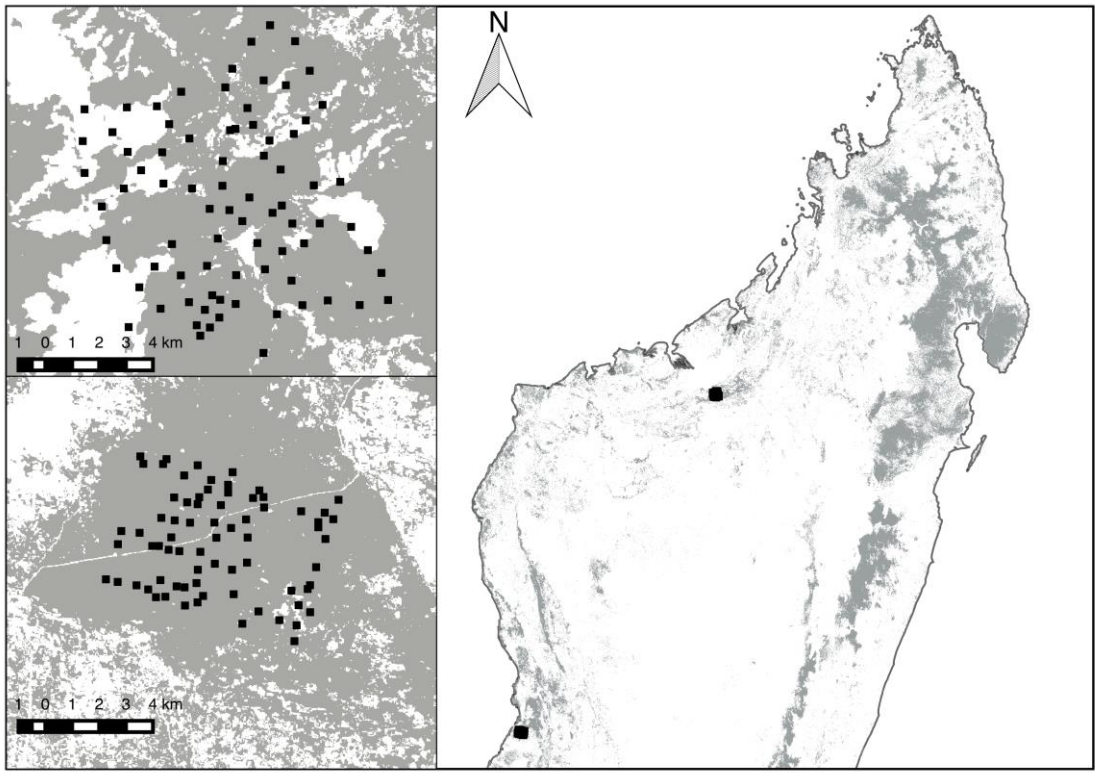

Figure 1. Map of Madagascar and its vegetation cover (in dark grey), inserts display the configuration of our camera-trap grids (cameras denoted by black squares) in Ankarafantsika National Park (top-left) and Andranomena Special Reserve (bottom left).

Camera trap placement

Eighty pairs of camera-traps (Cuddeback Ambush IR 1187, Wisonsin, USA) were placed along trails. Trail systems were chosen as fosas frequently use trails whilst traversing forest (Hawkins 1998; Dollar 2006). In measuring occupancy, it is therefore critical to locate camera-stations as to maximise focal species detection (O'Connell et al. 2010). Additionally, given our interest in examining the effect of humans and exotic species, trails provide the most suitable location to collectively sample all species. Camera-stations were spaced approximately 500m apart, allowing an equal trapping effort across the sampling area. Spacing camera stations closer together also improved the detection of *E. major* and *M. decemlineata*. Across each

site, trapping stations followed the methodology of Farris et al. (2015b) and Gerber et al. (2012b). Pairs of independently operated cameras were placed flanking trails, approximately 20-30 cm above the ground. This method allowed captured individuals to be photographed on both sides, improving species identification (Gerber et al. 2010), whilst accounting for potential camera-trap failure. Camera trap stations operated for approximately 35 – 80 days, as to ensure sufficient data collection, and to minimise violation of the underlying assumptions of occupancy modelling (MacKenzie 2006).

Analysis

Occupancy modelling was used to investigate the effect of camera-station, species and landscape level variables on the probability of fosa presence (MacKenzie and Nichols 2004). Photographic data were converted into detection histories (1 for detection, 0 for non-detection) for fosa, and other species used as covariates. These included exotic species (Dog, Cat, Civet, Pig, Zebu), prey (Lemur, Bird) and humans. All detections within a period of 30 minutes were considered as a single detection (Linkie and Ridout 2011). A complete day was considered when at least one of a station's two cameras was in operation over 24-hours. Capture histories for each species were created through the collapsing of individual days into five-day periods, improving temporal independence and model convergence (Otis et al. 1978). Species-level covariates used the encounter rates of exotics, prey and humans and were calculated by evaluating their Trap Success (TS = Number of detections / Total Days * 100). Two survey covariates were included to account for detection probability, the site surveyed (SITE), and the total days a station was active during each five-day sampling period (EFFORT).

Camera-station level covariates were included to assess the impact of station geography. Previous research indicated the importance of station level metrics (trail width and forest type) on fosa occupancy (Farris et al. 2015b). As a result, the variables Trail Type, Trail Width and Forest Type were included as site covariates. Trail Type was confirmed by a local park/guide. It was categorised as: Madagascar National Park trail (MNP); local – an active villager trail; disused-local – an inactive villager trail; game – an animal trail; logging – an active logger trail; and disused-logging – an inactive logging trail. Trail Width was estimated by averaging the width of the trail at the station and at 10 m either side. Lastly, Forest Type was subjectively and visually classified as either old-growth (discussed previously as intact forest with little disturbance), degraded (low forest cover with few native plant species present), and savannah (anthropogenic grassland).

QGIS (Version 2.12.1-Lyon) and FRAGSTATS (Version 4.2)(McGarigal et al. 2002) were used to create landscape-level covariates. To align with existing Euplerid studies (Gerber et al. 2012b; Farris et al. 2015b) and in the interests of examining the effects of human-settlement, landscape degradation and ecological variables upon fosa occupancy, 13 landscape-level covariates were considered (Table 1). These incorporated various measures of vegetation cover and/or fragmentation, including: the distance to the nearest village, forest-edge, and road; Global Forest Change (GFC); Vegetation Continuous Field (VCF); Total Edge (TE); Total Core Area (TCA); Number of Patches (NP); and Landscape Patch Index (LPI). Potentially important ecological variables also included water source (river or lake), Drainage and Elevation. To assess these metrics, a 500m buffer was created around each camera station and the mean value of the raster cells was calculated for each covariate. Details on each variable are provided in subsequent paragraphs.

Two metrics were used to measure forest cover, GFC (Hansen et al. 2013) and the VCF (DiMiceli et al. 2011). GFC, measured at the 30m resolution allowed the user selection of the percentage forest cover value to be classified as forest. Given the subjectivity of user selection, four levels were chosen (GFC10, 20, 30, 50) and compared within univariate models to find the best performing predictor of fosa occupancy. Alternatively, VCF provides a percentage of forest cover at a 250m resolution. Unfortunately, GFC maps were unavailable for ASR during its survey year, consequently the most recently available 2014 maps were used. These two covariates provided forest cover metrics at contrasting resolutions (30m versus 250m), allowing for the comparison of their respective accuracy in depicting forest cover. We hypothesised that the GFC covariate would perform better within the models due to its higher resolution, providing a more accurate representation of the area's forest cover.

Other measures of fragmentation thought to be important in previous Eupleridae studies (Gerber et al. 2012b; Farris et al. 2015b) were calculated in Fragstats, and included: Total Edge (TE), the sum of all edge segments in the buffer; Total Core Area (TCA) is the sum of core area (m^2) in each patch; Number of Patches (NP) represents the total patches of a class type; and Landscape Patch Index (LPI) equals the percentage of the landscape included in the largest patch.

The two measures of water proximity were calculated using a freely available Madagascar waterway raster (Mapcruzin 2016) and a Digital Elevation Model (DEM) (Jarvis et al. 2008). The Madagascar waterway raster is a freely downloadable raster containing Madagascar's major water sources, rivers and lakes. In contrast, the DEM is a 3D representation of the earth's topography, with areas of lowest elevation assumed to represent points of drainage, and possible seasonal streams (or other water

sources) often overlooked by many freely available rasters. Using the Madagascar waterway raster and the DEM derived drainage raster, the distance to perennial water sources and seasonal streams was calculated. The final ecological covariate Elevation was created from Shuttle Radar Topography Mission's 90m raster (Carroll et al. 2009).

R package 'unmarked' (Version 0.11-0)(Fiske and Chandler 2011) was used to run single species, single season occupancy. Prior to modelling a Pearson's Correlation test was used to eliminate multicollinearity. Correlated continuous predictors with a modulus $r > 0.6$ were removed (that is the predictor that performed worst in the univariate model) and the remaining covariates normalised. A stepwise approach was taken to reduce the total number of competing covariates to be included in the final model. These steps were reproduced for each of the carnivore occupancy models. Firstly, the detection probability was modelled, with the most significant combination of detection covariates selected. Potential covariates were then modelled independently with site covariates, with the best performing uncorrelated covariates retained (Table 1). Akaike Information Criterion (AIC) and model selection was used to rank competing models, and those with an AIC < 2.0 reported. According to Barbieri and Berger (2004), the model containing all covariates with a summed model weight > 0.50 was considered the optimal predictive model. The benefit of this strategy is that its describes the relative importance of each covariate, weighted by the number of times it is included in the top ranking models (those with a delta AIC < 2), and the relative rank of that particular model. However, this strategy may also be its limitation, as given that the models are ranked relative to one another, this strategy does not inform the user if the overall top models are good or appropriate, which can potentially lead to spurious results (Doherty et al. 2012). This may be overcome by

having a good a priori reasoning for the inclusion of each covariate, and their combinations in the model (Burnham and Anderson 2002; Burnham and Anderson 2004). Alternatively, where it may be difficult to identify the best model, model averaging is often employed whereby the weighted average of the parameter estimates are taken from each model (Symonds and Moussalli 2011). However, critics have argued that this approach lacks demonstrable consistent improvements in prediction accuracy (Richards 2005; Richards et al. 2011). Consequently, the summed model weights approach was adopted.

A goodness-of-fit was run to examine the model's likelihood of being correct ($p > 0.05$) and how well the model fit the data (measuring overdispersion as $\hat{c}$). Species occupancy was predicted across both sites in relation to the most important covariates.

Results

Landscape features and site detections

Across both sites a sampling effort of 8,730 nights recorded the presence of a total of three native and three exotic carnivores (Table 1). Unfortunately, camera-trap theft (26 units) in ASR resulted in a shortened survey period (79 days ANP, 36 days ASR). The ANP landscape was overall more degraded with a forest cover of GFC 75.32, with stations located in a mixture of savannah, old-growth and degraded forest. In contrast stations inside ASR were almost exclusively located in contiguous forest (GFC 97.16). The mean distance of stations to the nearest village in ANP (1616.9m), and distance to forest edge (357.5m) was considerably less than ASR (Table 1).

In total 311 independent detections of fosas were recorded (226 ANP, 85 ASR). ANP only other Euplerid, *E. major* was detected only once, likewise ASR's *M.*

decemlineata was detected twice. Small Indian civets were absent from ASR, and were almost exclusively detected at savannah and degraded stations in ANP. These low detections rates prohibited occupancy modelling for the three species. Trap success was higher for dogs (13.66), zebu (18.92) and humans (104.81) in ANP, whilst cats (11.24) and birds (6.58) were higher in ASR (Table 1).

Table 1. The summary statistics of Ankarafantsika National Park and Andranomena Special Reserve. Forest size, camera-trap grid and survey effort, the mean ecological and fragmentation covariates (GFC20 = Global Forest Cover at 20 threshold, VCF = Vegetation Continuous Field), and mean encounter rates (TS = Trap Success) for each site.

Covariates	Ankarafantsika National Park	Andranomena Special Reserve
Forest Size (km^2)	1350.0	64.0
Date	12/04/14 - 12/07/14	20/05/15 - 28/06/15
Camera-trap grid (km^2)	37.73	35.45
Days deployed (SD)	79.14 (9.24)	35,91 (6.18)
Total Stations	79	69
Station Spacing	579.4	464.9
Effort	6252.0	2478.0
Trail Width [1, 2, 3]	3.2	3.1
Habitat Type [2]	Various	Various
Trail Type	Various	Various
Distance to village [1]	1616.9	5113.9
Distance to forest edge [2, 3]	357.5	2489.8
Distance to road [1, 3]	1471.9	1604.9
GFC20 [1, 2, 3]	75.3	97.2
VCF [2, 3]	49.5	48.1
Total Edge [1]	2921.9	1023.3
Total Core Area [1, 3]	30.3	42.6
Number of Patches [2]	7.7	3.0
Landscape Patch Index [2]	1.9	95.4
Distance to water source [1, 3]	2127.1	958.8
Drainage [3]	3348.8	1088.5
Elevation	146.3	26.4
Fosa TS	3.6	3.6
Dog TS [1]	13.7	3.9
Cat TS [1]	3.4	11.2
Civet TS [2, 3]	1.2	0.0
Pig TS [3]	1.81	2.77
Zebu TS [2, 3]	18.9	1.3
Lemur TS [1, 2]	0.3	0.7
Bird TS [1, 3]	3.2	6.6
Villager TS	104.8	32.2

[1, 2, 3] Indicates the best performing uncorrelated covariates included in the final fosa[1], dog[2] and cat[3] occupancy models.

Covariate and model validation

Our two survey covariates (site and effort) were contained in the best performing detection model (Table S1). Consequently, they were included within all subsequent modelling of occupancy with site covariates. Our correlation matrix revealed significant correlations between competing covariates (Table S2). A total of 6 covariates (NP, LPI, VCF, Elevation, Villager and Forest Distance) were discarded from the final fosa occupancy model. The Goodness-of-fit test revealed significant overdispersion, and as a result 5 sites were removed (with a total of 42 detections).

Occupancy

There were no statistically significant differences in occupancy between sites ($p < 0.05$). Fosa occupancy across the landscape was 0.724 and marginally higher in ASR (0.757) than ANP (0.692) (Figure 2) (Chi-squared = 0.003, df = 1, p-value = 0.959). Landscape cat occupancy was 0.736, and marginally higher in ASR (Chi-squared = 2.844, df = 1, p-value = 0.092). Landscape dog occupancy was 0.999 and considerably higher in ANP than in ASR (Chi-squared = 2.306, df = 1, p-value = 0.129).

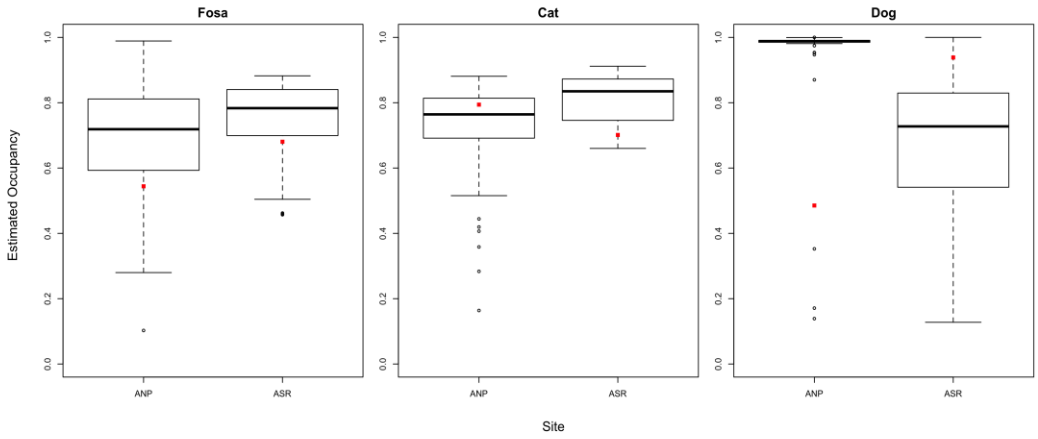

Figure 2. Estimated site occupancy for fosa, feral cat and dogs at Ankarafantsika National Park (ANP) and Andranomena Special Reserve (ASR).

Cat TS, Dog TS, GFC20 and TCA were the most important covariates (Summed Model Weight > 0.5) in explaining fosa occupancy across the landscape (Table 2). Dog TS maintained a weak positive relationship with fosa occupancy, whilst Cat TS, GFC20 and TCA displayed a negative relationship (Table 3).

Dog occupancy was best explained by Civet TS, Forest, NP and TW (Table 3). Civet TS and trail width was positively related to dog occupancy, whilst old-growth, savannah and total patches negatively affected occupancy (Table 3). Finally, cat occupancy was best explained by Bird TS, Trail Width and VCF. A negative relationship was observed between Bird TS, Trail Width and cat occupancy, whist a positive association was recorded with VCF (Table 3).

Table 2. a) Species covariate occupancy models (Ψ) for Fosa, Cat and Dog. Akaike's Information Criterion (AIC_c), relative change in Akaike's Information Criterion from top model (ΔAIC_c), Akaike's Information Criterion weight ($AIC_c wt$), number of parameters (K), and -2 log likelihood. Site covariates included: encounter rates for Cat, Dog, Lemur, Bird, Civet and Zebu; Global Forest Cover at the 20 threshold (GFC20); Total Core Area (TCA); Trail Width (TW); Vegetation Continuous Fields (VCF); Number of Patches (NP), and Forest (old-growth, degraded, savannah). b) The summed model weights for the fosa model.

a)

Species	Ψ Model	AICc	□AICc	AICc wt	K	logLik
Fosa	Cat + Dog + GFC20 + TCA	1195.32	0	0.08	8	-589.11
	Cat + Dog + GFC20	1195.54	0.22	0.07	7	-590.34
	Cat + GFC20	1195.81	0.49	0.06	6	-591.59
	Cat + Dog + TCA	1195.85	0.53	0.06	7	-590.5
	Cat + Dog + GFC20 + TCA + TW	1196.2	0.89	0.05	9	-588.41
	Cat + Dog + Road + TCA	1196.3	0.99	0.05	8	-589.6
	Cat + Dog + GFC20 + TW	1196.41	1.09	0.04	8	-589.65
	Cat + Dog + GFC20 + Lemur	1196.44	1.12	0.04	8	-589.67
	Cat + Dog + GFC20 + Lemur + TCA	1196.49	1.17	0.04	9	-588.55
Cat	Bird + TW + VCF	1558	0	0.23	7	-771.59
	Bird + TW	1558.33	0.33	0.2	6	-772.86
Dog	Civet + Forest + NP + TW	1288.57	0	0.1	9	-634.55
	Forest + Lemur + NP + TW	1288.68	0.11	0.09	9	-634.61
	Civet + TW + VCF	1289.17	0.6	0.07	7	-637.14
	FD + Forest + Lemur + NP + TW	1289.46	0.89	0.06	10	-633.83
	Civet + FD + Forest + NP + TW	1289.51	0.94	0.06	10	-633.85
	Forest + NP + TW + Zebu	1289.56	0.99	0.06	9	-635.05

b)

Covariate	Weight
Cat TS	0.94
Dog TS	0.77
GFC20	0.69
Total Core Area	0.57
Lemur	0.25
Trail Width	0.23
Road Distance	0.08
Village Distance	0.07
Total Edge	0.07

Table 3. Species covariate occupancy models (Ψ) for Fosa, Cat and Dog including all best performing, uncorrelated covariates.

Model	Covariate	Estimate	SE	z	P (>|z|)
Fosa	**(Intercept)**	**1.023**	**0.414**	**2.471**	**0.014**
	Trail Width	-0.331	0.281	-1.177	0.239
	Cat TS	**-0.915**	**0.429**	**-2.134**	**0.033**
	GFC20	-0.986	0.895	-1.102	0.271
	TE	-0.542	0.505	-1.074	0.283
	TCA	-0.658	0.383	-1.719	0.086
	Village Distance	0.252	0.406	0.621	0.534
	Dog TS	0.891	0.585	1.524	0.127
	Lemur TS	-0.352	0.303	-1.160	0.246
	Water Distance	0.138	0.302	0.456	0.648
	Road Distance	-0.071	0.496	-0.143	0.887
	Bird TS	-0.262	0.353	-0.741	0.459
Cat	**(Intercept)**	**1.080**	**0.593**	**1.823**	**0.068**
	Trail Width	0.012	0.228	0.050	0.960
	Bird TS	-0.615	-0.325	1.892	0.059
	Civet TS	-0.664	-0.374	0.483	0.629
	VCF	0.434	0.273	1.588	0.112
	Forest Distance	0.082	0.482	0.171	0.865
	Drainage	0.111	0.355	0.314	0.754
	Zebu TS	0.030	0.340	0.088	0.930
	Water Distance	0.336	0.274	1.227	0.220
	Pig TS	0.654	0.536	1.219	0.223
	Road Distance	0.048	0.263	0.181	0.857
	TCA	-0.092	-0.257	0.359	0.720
Dog	**(Intercept)**	**17.252**	**18.983**	**0.909**	**0.363**
	Trail Width	0.459	0.575	0.798	0.425
	Civet TS	2.682	5.059	0.530	0.596
	Lemur TS	2.578	6.223	0.414	0.679
	Zebu TS	1.336	2.638	0.506	0.613
	Forest Distance	-0.472	1.152	-0.410	0.682
	LPI	-0.973	0.875	-1.111	0.266
	Forest-Primary	-8.321	12.923	-0.644	0.520
	Forest-Savannah	-6.867	13.027	-0.527	0.598
	VCF	1.588	1.232	1.289	0.197
	NP	-1.498	1.102	-1.359	0.174
	Trail-Game	7.043	152.808	0.046	0.963
	Trail-MNP	-4.115	13.577	-0.303	0.762
	Trail-OLT	3.699	65.202	0.057	0.955
	Trail-Villager	-4.241	13.580	-0.312	0.755

* TS: Trap Success, Global Forest Cover 20 (GFC20), Total Edge (TE), Total Core Area (TCA), Vegetation Continuous Field (VCF), Landscape Patch Index (LPI), Number of Patches (NP), Madagascar National Park Trail (Trail-MNP), Old-logging Trail (OLT).

Discussion

Our findings unveiled a mixed relationship between fosas, landscape degradation and exotic species. No clear trends were apparent between fosas and degradation, however a clear negative relationship existed between fosas and cats, with no discernable pattern between fosas and dogs. Cats were negatively associated with birds, and detected more frequently in contiguous forest with narrower trails. Alternatively, dogs preferred degraded landscapes (but not savannah), with larger trails and in positive association with civets. These results mostly conform to previous rainforest studies of exotic species' negative effect upon Madagascar's endemic carnivores (Gerber et al. 2012b; Farris et al. 2015b; Farris et al. 2016). They suggest that fosas, capable of traversing through degraded landscape, are more resilient to habitat disturbance within contiguous forests than other Euplerids. However, the significant reduction and fragmentation of forest across Madagascar likely inhibits their long-term persistence across the landscape. Furthermore, the high prevalence of feral cats and dogs across our sites present considerable competition with fosas through the consumption of shared prey (Gould 1996; Brockman et al. 2008), and exclusion from habitat. The spread of disease, such as toxoplasmosis (Pomerantz et al. 2016), between exotic species, fosas and their prey is of concern, imperilling the fosas' long-term population health.

Exotic species impact upon fosa occupancy

Cats had the most pronounced negative association with fosa occupancy, likely underpinned by inter-guild competition. Cats have been globally acknowledged for their devastating effects on native wildlife through predation, competition, hybridization and disease (Dickman 1996; Phillips et al. 2007; Medina et al. 2011). In

Madagascar, predation by cats on lemurs has been recorded (Sauther 1989; Goodman et al. 1993; Brockman et al. 2008), and was also witnessed at ASR with a station photographing a cat having killed a red-fronted brown lemur (*Eulemur rufus*)(Figure 3). Predation of smaller species, such as birds, mammals and reptiles is common, evident by the killing of a speckled hognose snake (*Leioheterodon geayi*)(Figure 3).

Figure 3. Rare photographs of feral cats having captured and killed a *Eulemur rufus* and *Leioheterodon geayi* inside Andranomena Special Reserve.

In addition, cat occupancy was strongly associated with negative bird trap success, and with this relationship also documented previously in Masoala-Makira (Farris et al. 2015b). These results support the likely negative effect their unabated predation is having upon endemic species abundance. Gerber at al. (2012b) and Farris et al. (2015b) did not observe a negative association of cat presence on fosas but did record negative associations of cats with other rainforest dwelling Euplerids, *Galidia elegans* and *Fossa fossana*. Nevertheless, cats' uninhibited predation of fosas' prey supports exploitation competition as a contributing mechanism of fosa's reduced occupancy.

Within our sites, fosas and cats occupied similar, mostly nocturnal periods of activity. Their temporal overlap is in contrast to previous rainforest studies in which cats were recorded to be nocturnal and fosas crepuscular (Gerber et al. 2012c) or cats diurnal and fosas nocturnal (Farris et al. 2015a). These previous patterns suggest that where cats and fosas occupy similar temporal and/or geographical niches, cats may exert a negative effect upon fosas. In understanding the mechanism of competition, feral cats weigh considerably less than adult fosas (Brockman et al. 2008), suggesting interference competition to be less likely. However, juveniles and sub-adult fosas are of comparable weight to cats (Rahajanirina 2003), potentially permitting resource interference between smaller fosas and adult cats.

In concordance with previous rainforest studies, Dog TS did not have a negative association with fosa occupancy (Gerber et al. 2012b; Farris et al. 2015b). This is distinct from dogs' reported impact on another Euplerid *Galidictis fasciata* (Gerber et al. 2012b) and incongruous with dogs' globally damaging affect (Hughes and Macdonald 2013). However, activity pattern analyses have found fosas to display temporal activity shifts towards greater nocturnality, and/or absence from sites with higher dog detections (Gerber et al. 2012a; Farris et al. 2015a. Considering dogs' significantly larger size (Dollar Unpublished) and pack sociality, they represent a more significant source of interference competition. Fosas' adoption of greater nocturnality is presumably to avoid inter-specific aggressions and has been recorded amongst intra-guild carnivores of smaller size (Harrington et al. 2009). This temporal partitioning may be obscuring dogs' affect in occupancy models. In reality, dogs' underlying impact upon fosa through temporal exclusion is likely significant, reducing access to important diurnal prey species (such as the larger-bodied lemurs).

Whilst potentially not as effective as a resource competitor as cats, dogs' greater predatory impact upon Madagascar's ecosystem is still significant.

Disease transmission between cats, dogs, and endemic species may have a potential lethal impact through their widespread prevalence across the landscape. Fatal cases of *Toxoplasma gondii* infection have been recorded in captive fosas (Corpa et al. 2013) and lemurs (Spencer et al. 2004; Juan-Sallés et al. 2011; Siskos et al. 2015), highlighting their vulnerability to lethal infections. Field research of exotic and introduced carnivores in western Madagascar (including Ankarafantsika) has revealed a raft of viruses and parasites, including canine parovirus and herpesvirus, feline calicivirus and *T. gondii* (Pomerantz et al. 2016). The latter was prevalent in > 93% of captured fosas. These high infection rates are disconcerting when considering fosas and lemurs' fatal infection to *T. gondii* in captivity. It could then be expected, that similar to worldwide species reductions to disease (Pedersen et al. 2007) that these high infection rates have the potential to result in wild fosa mortalities and at the very least, a negative impact on an infected individual's long-term health.

Habitat degradation impact on fosa occupancy

Fosa occupancy was greater in ASR, likely associated with its greater forest cover, and lower dog and human presence. However, within our models fosa occupancy was not influenced by habitat degradation. This unclear trend in the association between habitat degradation and species occupancy was also recorded with fosas and other Euplerids in Madagascar's easterly rainforests (Gerber et al. 2012b; Farris et al. 2015b). Despite this carnivore presence surveys have recorded fosa absence from landscapes > 5 km (Kotschwar Logan et al. 2014) and forest fragments > 2.5 km from the nearest contiguous forest (Gerber et al. 2012b). This suggests, that despite fosas'

resilience to habitat degradation within contiguous forest, they are unable to persist far from intact forest. When considering Madagascar's highly disturbed and severely fragmented forests (Harper et al. 2007), it is likely that many are of insufficient size to support long-term, sustainable fosa populations (Hawkins and Racey 2005).

Cat occupancy was greater in ASR, and positively linked to higher vegetation cover and weakly associated with narrow trails. This could be attributed to their avoidance of larger carnivores (dogs/fosas) and humans, whilst using trails frequented by smaller species and prey. Farris et al. (2015b) found similar positive associations with forest cover, likely confirming their preference to areas of greater prey abundance.

Dogs recorded the highest landscape occupancy. In contrast to cats and fosas, dogs displayed greater occupancy in ANP, and a positive association with large trails, civets, and a negative association with old-growth forest, and savannah. Dogs' positive association with trail width is likely due to their positive correlation with humans, accompanying them during forest activities. Likewise their negative association with old-growth forest and savannah implies their use of degraded habitat, also frequented by humans. This supports the dogs' positive association with Ankarafantsika's third exotic carnivore, the civet, which was rarely detected inside old-growth forest.

Despite no association between habitat degradation and cat occupancy, dogs were indirectly associated with degraded forest. This is in concordance with recent easterly occupancy studies that revealed greater exotic carnivore presence in more degraded landscapes. Stations located in ANP encompassed a mixed matrix of savannah, and degraded forest, typically representative of forests surrounding rural villages. Ankarafantsika recorded considerably high trap success of humans and other

exotics such as zebu and civet (absent from ASR), with half the number of birds detected of ASR.

ASR was selected to represent a contiguous deciduous forest, of less anthropogenic disturbance than ANP. However despite less fragmentation than ANP, it was experiencing severe levels of illegal selective-logging at the time of surveying. These high levels of unanticipated disturbance undoubtedly affected the overall modelling of occupancy, reducing the distinctiveness of habitats degradation metrics. Future surveys of Madagascar's western forests must seek greater disparities in landscape degradation to fully reveal its affects. Furthermore, stations were originally spaced in anticipation of documenting the region's other Eupleridae, the falanouc and bokiboky. However, this spacing came at a cost, with occupancy estimates potentially inflated due to fosas' large ranging, theoretically permitting the traverse of several stations in one day. In an ideal scenario, future camera-trap grids would be larger, with greater spacing between individual stations, so as to be more ecologically representative, encompassing more individual home-ranges and thus producing a more accurate occupancy estimate (O'Connell et al. 2010).

Long-term implications

This research has contributed to our knowledge of the affects of anthropogenic disturbance in Madagascar's deciduous forests. Multi-year studies over greater spatial scales are required to unravel the 'snapshot' view of single-season occupancy models. Recent research on Madagascar's eastern coast documented the first multi-year study of these affects and revealed decreases in endemic species and replacement by exotic carnivores (Farris et al. 2016). Fosas displayed stable occupancy during this period, however their occupancy equilibrium fell below observed occupancy, indicating a

declining population. This supports our results reporting their apparent and at least short-term resilience to habitat degradation inside contiguous forests. Despite this, their long-term population decline is clear (Hawkins 2016). This is largely the result of the severe reduction and fragmentation of Madagascar's forests, the killing of fosas' for bushmeat and poultry depredation, and the rise in abundance of dogs and cats, stoking competition and disease transmission. The potential impact of exotic species was largely the focus of the discussion, and steps must be taken to mitigate their impact upon fosas and the ecosystem as a whole. Cat and dog sterilisation programs have been operating in rural villages surrounding ANP by author L. Dollar, and more recently in Ranomafana National Park by the Mad Dog Initiative. Such programs, in align with the culling of feral cats/dogs should be trialled, with their effectiveness evaluated in reducing exotics, and improving native species abundance. If effective at both the operational, and ecosystem level, we propose the incorporation of these programs into an island-wide forest management strategy.

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Appendices

Appendix Table S1. Detection probability (*p*) models for fosa. Akaike's Information Criterion (AIC_c), relative change in Akaike's Information Criterion from top model (ΔAIC_c), Akaike's Information Criterion weight (AIC_cwt), number of parameters (K), and -2 log likelihood.

***p* models**	**AIC_c**	**ΔAIC_c**	**AIC_cwt**	**K**	**-2 log likelihood**
p (site + effort)	1038.16	0	0.71	4	-514.93
p (effort)	1041.22	3.06	0.15	3	-517.52
p (site)	1042.1	3.93	0.1	3	-517.96
p (.)	1044.07	5.91	0.04	2	-519.99

Appendix Table S2. Correlation matrix of occupancy model covariates (correlated covariates denoted in bold).

	Road Dist.	Elevation	Water Dist.	Village Dist.	GFC20	VCF	Forest Edge Dist.	Drainage	TE	TCA	NP	LPI	Villager TS	Dog TS	Cat TS	Zebu TS	Bird TS	Civet TS	Lemur TS
Road Dist.	1	0.124	0.18	0.364	-0.338	-0.353	-0.116	-0.103	0.142	0.094	0.007	-0.213	-0.037	-0.089	0.162	-0.061	0.033	0.084	0.129
Elevation	0.124	1	0.447	**-0.695**	-0.527	-0.041	**-0.742**	**0.693**	0.347	-0.101	0.318	-0.469	0.206	0.16	-0.393	0.078	-0.271	0.155	-0.098
Water Dist.	0.18	0.447	1	-0.352	-0.517	-0.32	-0.481	0.182	0.346	-0.026	0.275	-0.414	0.277	0.093	-0.27	0.268	-0.173	0.228	-0.184
Village Dist.	0.364	**-0.695**	-0.352	1	0.249	-0.233	**0.753**	**-0.741**	-0.415	0.292	-0.509	0.316	-0.338	-0.271	0.401	-0.214	0.269	-0.137	0.147
GFC20	-0.338	-0.527	-0.517	0.249	1	**0.706**	0.467	-0.454	-0.528	-0.034	-0.271	**0.777**	-0.085	-0.045	0.25	0.039	0.159	-0.328	0.129
VCF	-0.353	-0.041	-0.32	-0.233	**0.706**	1	0.01	0	-0.315	-0.172	0.013	0.54	0.073	0.091	0.026	0.177	0.009	-0.235	0.071
Forest Edge Dist.	-0.116	**-0.742**	-0.481	**0.753**	0.467	0.01	1	**-0.62**	-0.531	0.269	-0.557	0.529	-0.387	-0.293	0.277	-0.204	0.189	-0.218	0.083
Drainage	-0.103	**0.693**	0.182	**-0.741**	-0.454	0	**-0.62**	1	0.247	-0.072	0.237	-0.358	0.044	0.053	-0.255	-0.034	-0.237	0.256	-0.085
TE	0.142	0.347	0.346	-0.415	-0.528	-0.315	-0.531	0.247	1	-0.542	**0.869**	**-0.789**	0.305	0.186	-0.312	0.047	-0.018	0.238	-0.068
TCA	0.094	-0.101	-0.026	0.292	-0.034	-0.172	0.269	-0.072	-0.542	1	**-0.617**	0.256	-0.247	-0.216	0.144	-0.269	-0.052	-0.026	-0.019
NP	0.007	0.318	0.275	-0.509	-0.271	0.013	-0.557	0.237	**0.869**	**-0.617**	1	-0.501	0.3	0.209	-0.261	0.12	-0.073	0.136	0.007
LPI	-0.213	-0.469	-0.414	0.316	**0.777**	0.54	0.529	-0.358	**-0.789**	0.256	-0.501	1	-0.213	-0.111	0.326	0.044	0.015	-0.34	0.146
Villager TS	-0.037	0.206	0.277	-0.338	-0.085	0.073	-0.387	0.044	0.305	-0.247	0.3	-0.213	1	0.667	0.006	0.508	-0.025	0.074	-0.128
Dog TS	-0.089	0.16	0.093	-0.271	-0.045	0.091	-0.293	0.053	0.186	-0.216	0.209	-0.111	**0.667**	1	-0.009	**0.608**	-0.093	0.142	-0.059
Cat TS	0.162	-0.393	-0.27	0.401	0.25	0.026	0.277	-0.255	-0.312	0.144	-0.261	0.326	0.006	-0.009	1	-0.093	0.098	-0.108	0.042
Zebu TS	-0.061	0.078	0.268	-0.214	0.039	0.177	-0.204	-0.034	0.047	-0.269	0.12	0.044	0.508	**0.608**	-0.093	1	-0.088	0.138	-0.051
Bird TS	0.033	-0.271	-0.173	0.269	0.159	0.009	0.189	-0.237	-0.018	-0.052	-0.073	0.015	-0.025	-0.093	0.098	-0.088	1	-0.022	0.078
Civet TS	0.084	0.155	0.228	-0.137	-0.328	-0.235	-0.218	0.256	0.238	-0.026	0.136	-0.34	0.074	0.142	-0.108	0.138	-0.022	1	-0.059
Lemur TS	0.129	-0.098	-0.184	0.147	0.129	0.071	0.083	-0.085	-0.068	-0.019	0.007	0.146	-0.128	-0.059	0.042	-0.051	0.078	-0.059	1

* Dist.: Distance, TS: Trap Success, Global Forest Cover 20 (GFC20), Vegetation Continuous Field (VCF), Total Edge (TE), Total Core Area (TCA), Number of Patches (NP), Landscape Patch Index (LPI).

Chapter Three

Activity patterns of sympatric living exotic and endemic carnivores (the fosa) in Western Madagascar's deciduous forests

Abstract

Western Madagascar's deciduous forest is an important, threatened habitat to little-known Eupleridae, such as the fosa *Cryptoprocta ferox*. Using camera-trap grids established in two important deciduous forests, Ankarafantsika National Park and Andranomena Special Reserve we report the impact of the activity of exotic carnivores on that of the fosa. Three methodologies, kernel density, circular and wave analysis were used to evaluate the activity pattern overlap between exotic Feral cats *Felis* sp., domestic dogs *Canis familiaris*, exotic small Indian civets *Viverricula indica*, and the endemic fosa. Our results showed fosas to be cathemeral, peaking in activity in the evening and at dawn. Cats were nocturnal, whilst also highly active at dusk. Civets did not display a dominant period of activity, but were relatively more active in the night, and at dusk. In contrast, dogs were diurnal, and also active at dawn, in alignment with human activity. Fosa activity significantly overlapped with the nocturnal cat and civet, whilst being distinct from the diurnal dog and humans. Our results suggest there is potentially a competitive impact of exotic feral dogs and cats when present across fosas' dry forest habitat. This highlights the need for further examination into the impact of Madagascar's exotic carnivores, and the experimental trial to investigate the impact of their removal (or reduced abundance) on Madagascar's wildlife.

Keywords: Activity patterns, Madagascar, Eupleridae, Fosa, *Cryptoprocta ferox*, deforestation, invasive species, Menabe, Ankarafantsika.

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Introduction

Interspecific competition has been demonstrated to strongly influence the behaviour, abundance and distribution of sympatric-living carnivores (Creel and Creel 1996; Fedriani et al. 2000; Berger and Gese 2007). To facilitate coexistence, competing carnivores typically define their niche through the distinction in diet (Bothma et al. 1984; Almeida Jácomo et al. 2004), space (Vanak et al. 2013) and/or temporal activity patterns (Carothers and Jaksić 1984; Kronfeld-Schor and Dayan 2003; Hayward and Slotow 2009).

Understanding sympatric species' activity patterns is important, as it may have evolutionary significance, ecological and physiological ramifications (Kronfeld-Schor and Dayan 2003). The partitioning of species' activity patterns may be shaped by two species driven processes, exploitation and interference competition (Carothers and Jaksić 1984; Kronfeld-Schor and Dayan 2003). Exploitation competition involves the reduction of a shared resource between two organisms. In contrast, interference competition exists when one organism reduces another's ability to access a shared resource. However, interspecies competition is not the only process to shape a species' activity but equally important is the influence of other abiotic mechanisms, such as the lunar cycle (Owings and Lockard 1971; Cozzi et al. 2012). Given today's endemic species widely occupy disturbed landscapes (Haddad et al. 2015), potentially competing with a host of new exotic competitors, understanding activity patterns is now increasingly important.

Fosas (*Cryptoprocta ferox*, and commonly known as fossa, will be henceforth described as 'fosa' in alignment with Duckworth *et al*. (2014) to reduce the usage of similar common names in the Eupleridae) are Madagascar's largest carnivore and the world's only mammalian primate predator specialist (Dollar et al. 2007; Hawkins and

Racey 2008). Occupying much of forested Madagascar, fosas are the country's most widely distributed carnivore, and are currently listed as 'vulnerable' by the IUCN Red List (Hawkins 2016). Fosas are threatened by deforestation (Hawkins and Racey 2005; Gerber et al. 2012b), bushmeat consumption (Golden 2009; Farris et al. 2015b), retaliatory killing (Kotschwar Logan et al. 2014), and exotic carnivores (Gerber et al. 2012c; Farris et al. 2015b).

Recent research has documented the potential impact of exotic carnivores on Madagascar's endemic carnivores' spatio-temporal activity. These temporal impacts have been well documented in eastern Madagascar, with studies in Ranomafana National Park and Masoala-Makira reporting fosas to display cathemeral and nocturnal activity, depending on the study and year (Dollar 1999; Gerber et al. 2012a; Farris et al. 2015a). In western Madagascar, a deciduous forest radio-telemetry study in Tsimaloto northwest Ankarafantsika National Park provided some evidence for cathemeral activity as fosas' principal behaviour in an area absent of dogs (Rahajanirina 2003). Across deciduous forests and rainforests, fosas' spatial sensitivity to dogs has also been reported, with fosas notably absent at sites where domestic dogs were abundant (Dollar 2006; Barcala 2009; Gerber et al. 2012a; Farris et al. 2015a). However, despite Rahajanirina's (2003) preliminary insight into the activity of the fosa in northwest Ankarafantsika, a systematic investigation of exotic and endemic carnivores temporal activity in deciduous forests is otherwise lacking.

Deciduous forests comprise some of the world's most threatened forests (Janzen 1988). In fact, the highest rates of deciduous deforestation in Africa were recorded in Madagascar from 1980 – 2000 (Miles et al. 2006). It has previously been estimated that only 3% of Madagascar's deciduous forests remain (Smith 1997; WWF 2001), with its current cover likely much lower (Zinner et al. 2013). Unfortunately

research on deciduous forests has largely been neglected in favour of research activities on Madagascar's eastern rainforests (Waeber et al. 2015). Given activity patterns are dictated by a combination of biotic (e.g. inter-species competition) and abiotic (e.g. temperature, lunar cycle) factors (Kronfeld-Schor and Dayan 2003; Vieira et al. 2017), it is necessary to understand a species' temporal use of space throughout its major habitats. Nevertheless, there has been little research documenting the competitive effects of exotic species in one of the fosas' major habitats and one of Madagascar's most threatened regions, its deciduous forests. As such, empirical study is warranted to understand the extent of exotic-endemic species competition across Madagascar's landscape.

This study provides the first examination of fosas and exotic carnivores' use of the diel period in two different deciduous forested regions. Our objectives were to: i) identify the major patterns of sympatric living exotic and endemic carnivore temporal activity; ii) examine patterns of temporal overlap, or segregation; and iii) examine differences in carnivore activity between the two study sites. Three contrasting methodologies, kernel density analysis, wave, and circular analysis were used to examine the principal periods of carnivore activity and periods of overlap or segregation. Given previous studies use of kernel density analysis and resource selection (Gerber et al. 2012c; Farris et al. 2015a) to examine activity patterns of Madagascar's carnivores, a comparison of all three methods will provide greater scrutiny of each species' activity pattern. This research provides much needed evidence of the effects of exotic species on mammals occupying western deciduous forests, and reports their impact across the fosas' westerly range.

Methods

Sites

Two deciduous forests typical of Madagascar's western landscape were identified in the regions of Marovoay and Menabe. Located in the north-western region of Marovoay, Ankarafantsika National Park (ANP) is Madagascar's largest contiguous deciduous forest (1,350 km^2). The forest contains a variety of endemic species, including two euplerids, the vulnerable fosa and the endangered Western Falanouc *Eupleres major* (Merson et al. 2017). The camera-trap grid in ANP encompassed 37.73 km^2 of habitat containing a mixture of old-growth forest, degraded forest, and savannah surrounding three rural villages.

Madagascar's western Menabe region contains some of the largest fragments of deciduous forest. It is one of Madagascar's most important landscapes, supporting high levels of regional and local endemism, coupled with high annual deforestation (Zinner et al. 2013). Covering 64 km^2, Andranomena Special Reserve (ASR) is situated approximately 30 km north of Morondava. Two species of euplerids persist, the fosa and the endangered Bokiboky *Mungotictis decemlineata* (Hawkins 1998; Razafimanantsoa 2003). The camera-trap grid in ASR covered 35.45 km^2 of mostly contiguous forest, although sections of ASR were experiencing high levels of illegal logging during surveys.

Camera-trap placement

ANP and ASR were surveyed for 35 and 80 days respectively during April – June 2014, and May - June 2015. Approximately 80 pairs of camera-traps (Cuddeback Ambush IR 1187, Wisonsin, USA) were spaced approximately 500 meters apart within each site. Camera-stations were established on trails to improve detection of

focal carnivores species, the fosa (Dollar 2006), falanouc, bokiboky and exotic carnivores (feral cat *Felis* sp., domestic dog *Canis familiaris*, exotic small Indian civets *Viverricula indica*). Cameras were programmed to take only photos, every five seconds, and were placed approximately 30 cm above ground, flanking trails to improve species detection and account for potential camera-trap failure. Camera-stations were in operation for 24 hours per day, allowing the detection of individual species throughout the diel period, thus permitting the analysis of species' temporal activity.

Analysis

Any detection of a species within a thirty-minute period was recorded as a single event (Linkie and Ridout 2011). In examining the dominant period of each species' activity, the 24-hour period was separated into dawn, day, dusk and night. Dawn and dusk (crepuscular) were classified as one hour before and after sunrise and sunset respectively. Day (diurnal) was considered as the period between these hours, and night (nocturnal) classified as the period outside. For each category of period, we calculated the number of counts expected under an even distribution of counts throughout the day, i.e. total counts divided by 24 multiplied by the number of hours in that period. Thereafter, a chi-squared test (or Fisher exact test for the civet due to low counts), and a post-hoc chi-squared test were performed against this even distribution to determine if a species' exhibited a dominant period of activity (dawn, day, dusk, night).

Three statistical methods, kernel density, circular and wave analysis were employed to examine the difference in activity pattern between two species. Given previous studies of Madagascar's rainforest dwelling carnivore activity patterns have

employed only kernel density analyses (Gerber et al. 2012a; Farris et al. 2015a), our comparison of the three methodologies will provide greater scrutiny of each carnivore's activity pattern. Data collected from both sites (ANP and ASR) were combined for all analyses except for the investigation of differences in inter-site species activity patterns.

Analyses were conducted in R (Version 3.2.4). A species' time of detection (t) was measured separately for each method, and converted into radians ($\Theta = 2\pi t/24$). Kernel density t was equal to the proportion of hours and minutes in one day. Circular t was equal to the hour and minute (in proportion of an hour) of detection, and Wave t was equal to the detection time rounded to the nearest hour.

Kernel density analysis presumes that individual detections represent a random sample of the underlying distribution, with this probability density function representing a species' true activity pattern (Ridout and Linkie 2009). A measure of overlap was calculated using program 'overlap' in R (Package 0.2.6)(Meredith and Ridout 2014). The coefficient of overlap (Δ) was calculated on a scale of 0 – 1 ($\Delta = 1$ indicating an identical density distribution)(Weitzman 1970). Several coefficient measures were available, however Δ_1 was chosen given its superiority for smaller sample sizes (Ridout and Linkie 2009).

A species' diel period activity represents a circular distribution (24 hour clock), ideal for circular statistics (Zar 2010). A circular ANOVA was performed, testing for significant difference in the mean activity time between different species. An equal kappa test was performed to ensure homogeneity of concentration amongst samples, and if the assumption was violated a non-parametric Watson-Wheeler test was used (Pewsey et al. 2013). The circular analysis was conducted in R package 'circular' (3.2.2 Version)(Agostinelli and Lund 2013).

The final method, wave analysis, involves the prediction of daily activity as a function of continuous trigonometric predictor variables (Zar 1996). Based on the observed activity, four wave models were constructed representing the predicted daily activity as one and two full 24-hour cycles (SinΘ, CosΘ, Sin2Θ, Cos2Θ). We then tested for significant differences in periodicity between two species using the interaction term between the particular wave and species. (SinΘ * Species; CosΘ * Species, Sin2Θ * Species, Cos2Θ * Species). Species is a categorical factor with the two species as separate levels. The model with the highest adjusted R^2 was selected, and the significance of the interaction between the wave and species reported.

Results

ANP and ASR camera grids were in operation for 79 ± 9.2 and 36 ± 6.2 days respectively (camera theft reduced the ASR survey's length). This resulted in a total sampling effort of 8,730 nights. All locally present endemic and exotic carnivores were photographed, however the falanouc (Merson et al. 2017) was detected only once and the bokiboky twice, hence we excluded these species from analysis. Fosas were independently detected on 311 events (226 ANP, 85 ASR), dogs 942 (850 ANP, 92 ASR), and cats 477 (209 ANP, 268 ASR). Civets were only detected in ANP and in total 75 times.

Fosas were cathemeral with no significant periodicity in activity (Chi-squared = 7.7392, df = 3, p-value = 0.05172), however there was a trend for increased activity in the evening and at dawn (Table 1)(Figure 1). Civets displayed a significant periodicity in activity (Fisher's exact test, p = 0.042), with predominant activity at dusk and in the evening (Figure 1). However, the post-hoc Fisher's exact test revealed no significant difference between each period (Table 2). Cats were significantly more

active at dusk and in the evenings (Table 2)(Figure 1). Lastly, dogs were active diurnally and at dawn (Table 2)(Figure 1), in alignment with human activity.

Table 1. The dominant period of carnivore and human activity, measured by the proportion of counts within each period, and the observed counts per available hours, and the expected number of counts per available hours.

Species	Dawn	Day	Dusk	Night
Fosa				
Proportion	0.113	0.117	0.09	0.68
Observed counts/hr (expected)	17.5 (12.8)	14 (12.8)	3.6 (12.8)	21 (12.8)
Cat				
Proportion	0.078	0.145	0.12	0.657
Observed counts/hr (expected)	6.9 (19.8)	28.5 (19.8)	18.5 (19.8)	31.2 (19.8)
Civet				
Proportion	0.013	0	0.16	0.827
Observed counts/hr (expected)	0.5 (3.1)	0 (3.1)	6 (3.1)	6.2 (3.1)
Dog				
Proportion	0.139	0.777	0.024	0.06
Observed counts/hr (expected)	66 (39.5)	73.7 (39.5)	11.5 (39.5)	5.7 (39.5)
Human				
Proportion	0.087	0.852	0.038	0.023
Observed counts/hr (expected)	328.5 (313.2)	640.1 (313.2)	143 (313.2)	17.2 (313.2)

Table 2. Post-hoc chi-squared tests (or for *V. indica* fisher-exact) examining differences between time periods for each species.

Period Comparison	Fosa	Cat	Dog	Civet
Dawn vs. Dusk	0.8041	0.4625	< **0.001**	0.2727
Dawn vs. Day	0.1016	0.241	0.7792	1
Dawn vs. Night	0.8041	0.4225	< **0.001**	0.2727
Dusk vs. Day	0.2286	**0.0256**	< **0.001**	0.2727
Dusk vs. Night	0.8041	0.8398	0.3553	1
Day vs. Night	0.1002	**0.0256**	< **0.001**	0.2727

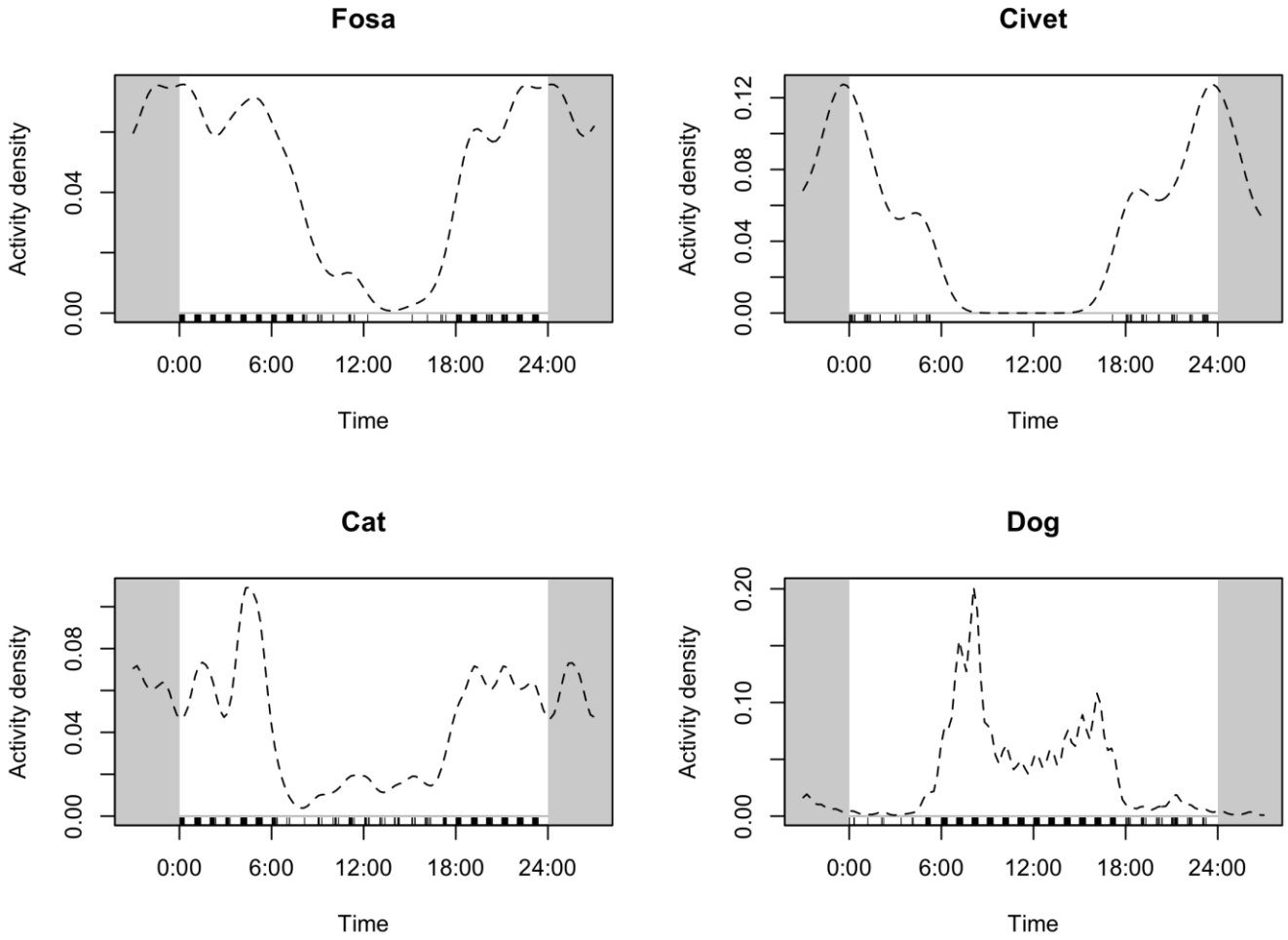

Figure 1. The 24-hour activity patterns (measured as a kernel density) of *C. ferox*, *V. indica*, *Felis* sp., and *C. familiaris*.

Nocturnally active species', fosas, cats and civets overlapped to a large extent in their activity patterns (Table 3)(Figure 2). Conversely, diurnally active dogs overlapped minimally with fosas, cats and civets, but highly overlapped with humans. Dogs and humans (ANP 0.8676 Δ_1), fosas/cats (ASR 0.8196 Δ_1) and fosas/civets (ANP 0.8153 Δ_1) had the highest overlaps in activity (Table 3)(Figure 2). Despite mostly congruous results across the three analyses, differences were evident with kernel density correlation coefficients reporting a high temporal overlap for fosas/civets (0.8153), whilst wave and circular analyses reported significant differences in activity patterns ($p < 0.05$ & 0.01). Similar discrepancies between analyses were found for other species' pairings such as fosa/cat, cat/civet and dog/human (Table 3).

Marginal temporal differences in species overlap were observed between sites. The overlap in fosas' and dogs' activity in ASR (Δ_1 =0.3835) was higher than that in ANP (Δ_1 = 0.2942) (Table 3). Cats also showed a similar trend in overlap with dogs across both sites. Fosas', cats' and dogs' temporal overlap with humans' activity appeared relatively similar between sites.

Wave analysis revealed no significant differences in species' activity patterns between sites (Fosa $p = 0.166$, Cat $p = 0.794$, Dog $p = 0.857$). However, fosas did exhibit greater (marginally non-significant) crepuscular and diurnal activity in ASR than in ANP (Figure 3, kernel density analysis). Conversely, cats had high densities of dawn activity in ANP, whereas dogs' activity was relatively consistent between sites (Figure 3).

Table 3. Species' pairing overlap estimators for kernel density (correlation coefficient Δ_1), wave (cox1 model) and circular methods for Ankarafantsika National Park and Andranomena Special Reserve.

Species Pairing	Ankarafantsika National Park					Andranomena Special Reserve				
	Kernel Density	Wave (cosx1)		Circular		Kernel Density	Wave (cosx1)		Circular	
	Δ_1	Adjusted R^2	p (t)	R^2	p (F)	Δ_1	Adjusted R^2	p (t)	R^2	p (F)
Fosa / Cat	0.8019	0.5222	0.469 (0.730)	0.0014	0.3664 (0.8177)	0.8196	0.6956	0.0019 (-3.3)	0.01381	0.0063 (7.574)
Fosa / Dog	0.2942	0.5282	< 0.001 (7.456)	0.2823	< 0.001 (788.1)	0.3835	0.2361	< 0.001 (4.058)	0.2823	< 0.001 (788.1)
Fosa / Civet	0.8153	0.6727	0.0313 (-2.225)	0.0195	0.0016 (10.17)	NA	NA	NA	NA	NA
Fosa / Human	0.2432	0.6261	< 0.001 (-8.994)	0.0683	< 0.001 (653.4)	0.2949	0.403	< 0.001 (-5.505)	0.1341	< 0.001 (165.4)
Cat / Dog	0.2704	0.3849	< 0.001 (-5.651)	0.2275	< 0.001 (469.3)	0.3713	0.6957	< 0.001 (-4.401)	0.2708	< 0.001 (312.4)
Cat / Civet	0.7623	0.6249	0.0117 (2.63)	0.0016	0.2607 (1.268)	NA	NA	NA	NA	NA
Cat / Human	0.2295	0.4759	< 0.001 (-6.631)	0.0534	< 0.001 (500.4)	0.2784	0.7002	< 0.001 (-4.669)	0.2903	< 0.001 (600.4)
Dog / Civet	0.1775	0.5491	< 0.001 (-7.67)	0.1716	< 0.001 (296.1)	NA	NA	NA	NA	NA
Dog / Human	0.8676	0.4873	0.6 (-0.529)	0.0004	0.0456 (3.996)	0.8130	0.444	0.37 (-0.899)	0.0064	0.0099 (6.677)

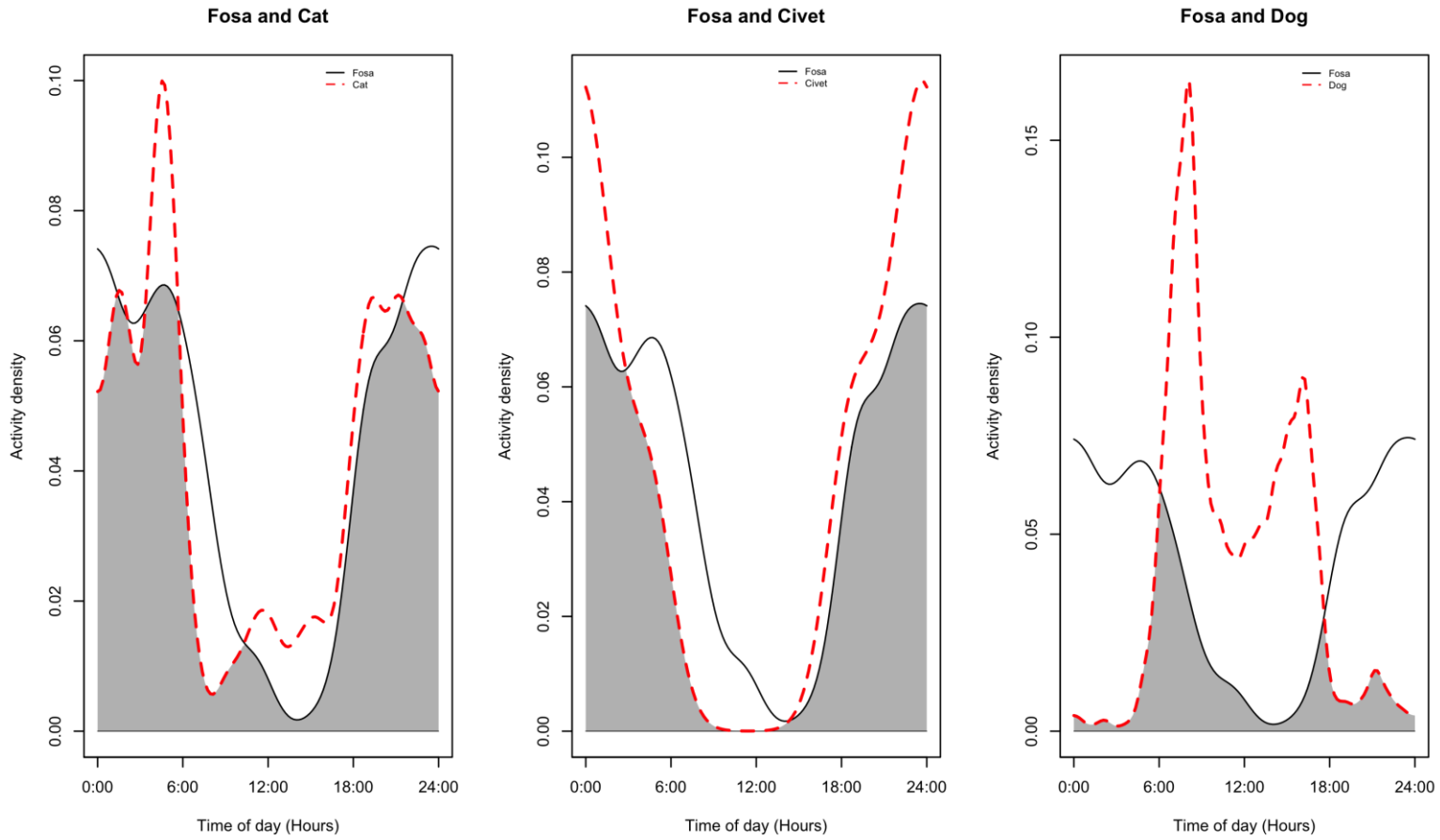

Figure 2. *Cryptoprocta ferox* overlap in temporal activity with the three observed invasive carnivores across both sites, as measured by the kernel density across the 24-hour period.

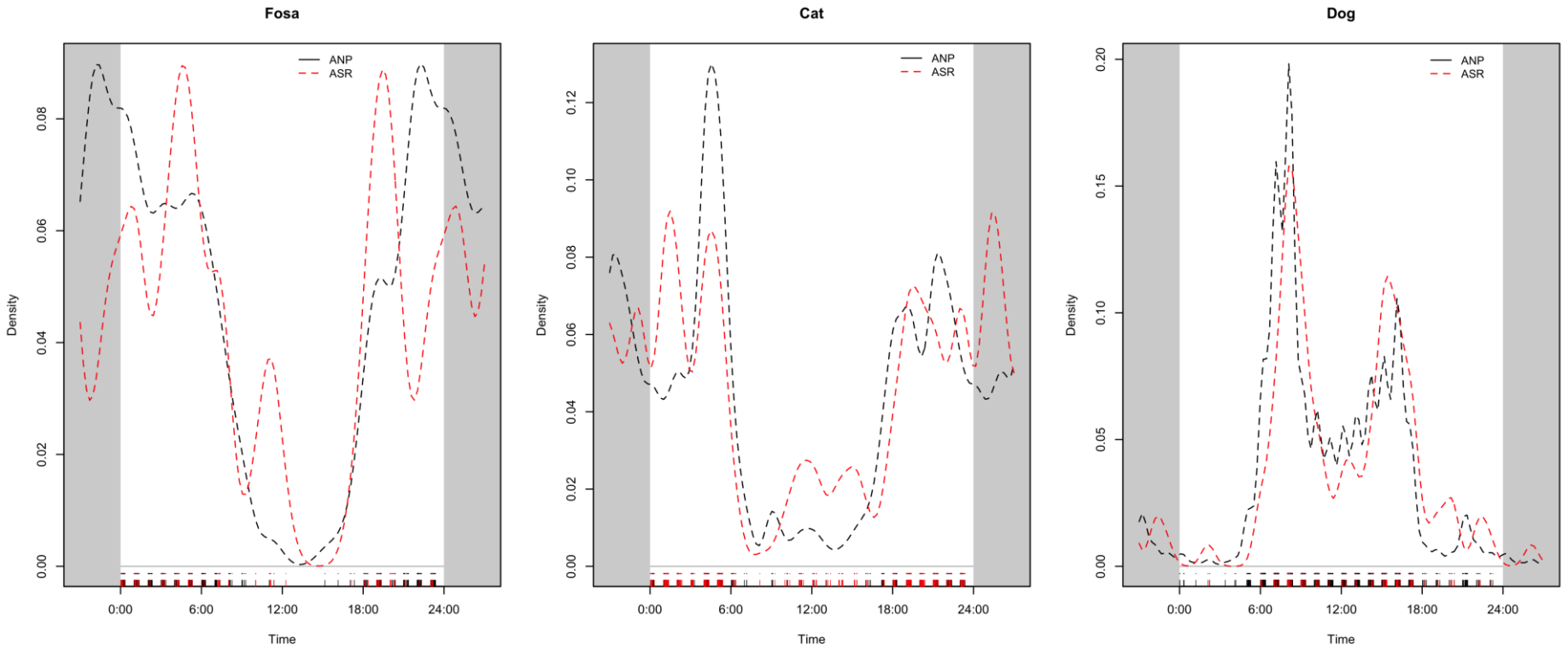

Figure 3. Differences in temporal activity (measured by the kernel density across the 24-hour period) between the two study sites, Ankarafantsika National Park (ANP) and Andranomena Special Reserve (ASR) for the three carnivore species sufficiently detected at both sites.

Discussion

Fosas' highly overlapped in activity with nocturnal cats and civets, while markedly distinct from diurnal dogs and humans. The three methodologies were mostly consistent, with higher kernel density overlap coefficients corresponding to significant difference in activity patterns detected by wave and circular analyses. Our results were mostly similar to previous rainforest studies in Ranomafana and Masoala-Makira whereby fosas were observed to be cathemeral, but most active in the crepuscular hours (Dollar 1999; Gerber et al. 2012a), or nocturnal (Farris et al. 2015a). Fosas' activity pattern overlap with cats and civets, and fosas' temporal avoidance of dogs mirrored the results of previous rainforest studies. Previous research in (then) dog-absent areas of ANP (Rahajanirina 2003) observed higher nocturnality than estimated in our (dog present) ANP site, potentially suggesting greater fosa nocturnality in association with increased dog presence. This association could be confounded with other unaccountable factors, however, this behaviour has been previously observed in Masoala-Makira (Farris et al. 2015a).

Carnivore overlap and competition

Fosas have previously been observed to display higher levels of diurnal activity in sites absent of dogs (Dollar 1999; Rahajanirina 2003). Of particular comparative interest was the study by Rahajanirina (2003) conducted in a remote section of our shared ANP site. This site is devoid of human settlements inside the forest. In contrast, our surveys documented fosas' activity in an area of ANP with considerable human activity and its associated dog presence. Previous ANP fosa trapping studies have also observed a dramatic decrease in fosa captures (to zero) in association with an increase in domestic dog captures. Following the euthanisation of captured dogs,

there was a subsequent rebound in fosa captures (Barcala 2009). The impact of dogs (humans too) was also noticeable in examining differences in overlap between our two sites. In ANP, fosas and cats overlapped less with dogs and humans compared to ASR, with cats exhibiting a considerably higher capture rate in ASR. This is likely a result of higher dog and human presence in ANP, evident by the tripled detection rates of dogs and humans in ANP compared to ASR. Similar patterns have been recorded in Masoala-Makira whereby fosas' were observed to display greater nocturnality at sites where human and dogs were most active, and greater diurnality at sites where human and dogs were rare (Farris et al. 2015a). Likewise, Gerber et al., (2012a) observed fosas to mostly be absent at sites where dogs were most abundant and active throughout the diel cycle, although other anthropogenic disturbances such as forest degradation and fragmentation were likely influential too.

Domestic dogs represent a significant interspecific competitor to fosas. They are considerably larger, and live in groups (Kleiman and Eisenberg 1973), having been detected within the forest in pairs, and often accompanying humans during forest-related activities. This is evident in our study where we found high degree of overlap between dogs and humans in both study sites. Considering that dogs are a prolific worldwide invasive predator (Hughes and Macdonald 2013), their potential depletion of fosas' prey is highly probable. However, dogs not only represent a source of exploitation competition, but studies suggest a potential source of interference competition too. Temporal niche shifts to maintain access to a species' habitat, whilst avoiding interspecific aggression has been observed between similar-sized invasive and endemic carnivores (Harrington et al. 2009). Given dogs' larger size and sociality, fosa behavioural changes to greater nocturnality is a likely strategy to reduce aggressive encounters whilst maintaining use of its habitat.

Fosas, cats and civets displayed the greatest temporal overlap, creating potential for exploitation and interference competition. Of particular concern are feral cats, a formidable worldwide invasive predator (Medina et al. 2011; Nogales et al. 2013) and a recognised predator of lemurs (Brockman et al. 2008) and other endemic species. At ANP, feral cats have been recorded to weigh 2.9 – 5.5 kg (Brockman et al. 2008), significantly larger than local domestic cats and less than the average adult 6 – 7.4 kg female and male fosa (Hawkins 1998; Dollar 2006). Presumably, fosas' larger size would mostly prohibit interference competition, with male adult fosas (weighing up to and over 11 kg) potentially capable of consuming smaller cats. In contrast, sub-adult fosas are of comparable weight (Rahajanirina 2003; Dollar 2006), making inter-species aggression and interference competition possible. Interestingly, a study of fosa occupancy at our study sites, revealed that a higher presence of cats is negatively associated with fosa presence. This negative association could potentially be an artefact of shared temporality, with fosas detected less frequently at stations where cats were active and/or abundant. Regardless of the underlying driver (interference and/or exploitation competition), these occupancy and activity pattern results show the potential negative impact that cats shared temporality is having on fosas.

Deciduous forest living civets recorded similar activity to that of their rainforest counterparts (Gerber et al. 2012c; Farris et al. 2015a). Despite temporal overlap with fosas, civets' relatively small size and their preference for less forested habitats means their direct competition with fosas is less likely. Civets however, are a successful invasive carnivorous predator in islands across the Indian Ocean and parts of Africa, capable of depleting shared smaller prey such as birds, reptiles and mammals (Duckworth et al. 2015). Consequently, their predatory impact on

Madagascar's endemic species should be evaluated, and strategies for their control examined.

Analytical differences in methodologies

The kernel density overlap coefficient, and the circular and wave analyses' significance tests were mostly congruous in their conclusion, i.e. high coefficient of overlap (kernel density) was associated with an insignificant difference in activity patterns (wave and circular). For species activity pattern comparisons including the civet, a sample size effect could be applicable due to their low capture rate. Some other differences did exist, potentially explained by circular/wave's measurement of a species' peak times in activity, compared to kernel density's measurement of overlap. This means that species that significantly overlapped in activity, but maintained different peaks in their activity, may result in contradicting results between kernel density and wave/circular methodologies. Furthermore, there were also some differences between the circular and wave analyses (i.e. wave estimated no significant difference in human and dog activity, whilst circular estimated a significant difference). These methodological differences could be the result of several factors. Firstly, the circular method examines differences between mean peaks, while assuming equal variance in time detected between species. Consequently, when activity patterns are not unimodal, the circular approach could be misleading. In contrast, the wave analysis examines differences between the peaks and troughs in a species' activity, accounting for the difference in variance in activity between species. In conclusion, when examining a species' activity pattern, an ecologist's choice of a particular statistical model should depend upon the objective of their research, with

the various models providing different insight into the distinct, often enigmatic, aspects of a species temporal activity.

Conclusion

Our research provides evidence for shared temporality between fosas and exotic carnivores. Shared temporal activity has the potential to create alternative forms of intra-guild conflict in competition for resources. Consequently, sterilisation of domestic carnivores (dogs/cats) and euthanisation of feral exotic species should be considered as a potential strategy to reduce their impact upon Madagascar's endemic species. Such programs have been enacted by the Mad Dog Initiative in Ranomafana, and explored in Barcala's (2009) study in Ankarafantsika, where associations have been observed between reduced dog and increased fosa trapping success. Support for sterilisation programs has been reported in Ranomafana National Park, where 90% of villagers' approved the use of neuter programs if freely available (Valenta et al. 2016). If local sentiment is similar across Madagascar, the efficacy of such programs should be studied to examine the relationship between exotic and endemic carnivore abundance. With the control of exotic species (such as the feral cat) already a global conservation priority, the efficacy of such programs is urgently needed to warrant their implementation, and to ensure the integrity and continuance of Madagascar's biodiversity across its most important remaining habitats.

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Chapter Four

Poverty and low taste preference drives the consumption of protected species in Madagascar

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-hunted wild species, or examined its variance across Madagascar's forests and protected 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 protected habitat (National Park, Reserve, Unprotected). 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 modelled. We found that poorer households reported consuming greater quantities of protected species whereas wealthier households reported consuming greater quantities of fish and eel. There was no evidence that consumption of protected species was lower in protected areas, with households located inside Andasibe-Mantadia National Park, Madagascar's most visited protected area, reported as consuming the greatest quantities of protected species. Malagasy most favoured meat was from domestic animals, and fish. The consumption pattern of wild species reflected interviewees' high preference for specified unlisted, pest and game species. Most protected species (such as lemurs and carnivores) were interviewees' least favoured wild foods. 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 will reduce the consumption of protected species.

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

This chapter forms the basis of an article prepared for Animal Conservation of which I am the lead author and my co-authors are Luke Dollar, Paul Johnson and David Macdonald.

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 to reduce its impact on wildlife populations, and to ensure the livelihoods of those human populations who 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). In a protected area in northwest Madagascar, wild species are reportedly an important source of nutrition for rural households (Golden et al. 2011), with similar patterns of rural household dependence on bushmeat observed across Africa (Brashares et al. 2011). Recent research has shown the consumption of protected animals to be widespread (García and Goodman 2003; Randrianandrianina et al. 2010; Razafimanahaka et al. 2012; Golden et al. 2013b), with its occurrence principally driven by poverty and poor health (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). Little research has examined its drivers across large geographical areas, with current research almost exclusively focused on single sites or single regions. Furthermore, our understanding of the potential different drivers of the consumption unprotected versus protected species across Madagascar's protected and unprotected forests is unclear. Given Madagascar's rural population occupy an extremely diverse landscape, surrounding forests of different protected 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 species and protected area planning more widely.

Madagascar's legislation permits seasonal hunting of specified endemic species, and unrestricted hunting of pests. This legislation is mostly in align with the IUCN Red List and CITES (Rakotoarivelo et al. 2011), and forbids the hunting of most 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 developing and enforcing Madagascar's protected species framework.

Madagascar's biodiversity is characterised by large abiotic and biotic variation both between and within regions (Vences et al. 2009). This geographic variation influences the species that are consumed across Madagascar's different regions. However, it has also been documented that the consumption of different species across Madagascar is 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). Research has highlighted the importance of understanding tribal cultures, but its value for conservation has been disputed (Horning 2003; Golden and Comaroff 2015a; Golden and Comaroff 2015b). Furthermore, presumed generational erosion of *fady* (Jenkins et al. 2011) may not be the ultimate cause, with inter-regional migration reported to decrease adherence to local taboos (Golden and Comaroff 2015b), supporting the need for multi-region bushmeat studies.

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). Recently, Madagascar's protected area's effectiveness in reducing deforestation has been estimated to only marginally decrease deforestation once accounting for other confounding factors (Eklund et al. 2016). In examining protected area's efficacy in reducing wildlife consumption, Razafimanahaka et al. (2012), reported the frequency of consumption of different protected species (sifaka, brown lemur, fosa) to be lower in areas of greater conservation awareness and protective legislation. Furthermore, the use of the randomised response technique (a specialised method for investigating sensitive behaviours) yielded higher estimates of bushmeat consumption in areas of greater sensitivity (the implications of not using such techniques will be discussed in the methods). Despite these advancements, there is still a lack of understanding of what drives the consumption of protected and unprotected species across forests of varying protection.

We document findings from the first comparative study of protected and unprotected species consumption 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 Sites

Four sites were chosen to incorporate Madagascar's two most abundant forest types (deciduous and rainforest), and their protected status. Madagascar has adopted a categorical system of protected areas incorporating: Category 1 Strict Nature 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). Whilst these regions were selected to represent a sample of Madagascar's protected areas and its major forest types, there selection was constrained by the requirements of finding a suitable site for a camera-trapping study (Chapter Two/Three).

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

Forest Type	Region	Protection Status	Forest Size (km^2)	Total Villages	Households Interviewed
Deciduous	Marovoay	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

Covering approximately 1350 km^2 Ankarafantsika National Park (ANP) is Madagascar's largest contiguous deciduous forest (Figure 1). Located in the

northwest (16°S, 46°E), 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 savannah, rice fields, or is otherwise severely degraded.

The central western region of Menabe is a recognised conservation hotspot due to high regional endemicity, 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^2 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 align with the expansion of the nearby Lambokely settlement (Zinner et al. 2013).

Encompassing approximately 155 km^2 of humid rainforest, Andasibe-Mantadia National Park (AMNP)(18°S, 48°E) is Madagascar's most visited protected area. Its largest village Andasibe commune is the focus of tourism. Remote poor villages extend to its north, whilst more prosperous villages flank the route nationale 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, Tsiazonamboa, Ambatovaky, Tsitola and Vatovavy, largely surrounded by grassland, agricultural and secondary forests. The commune of Kianjavato (21°S, 47°E) is the largest regional village.

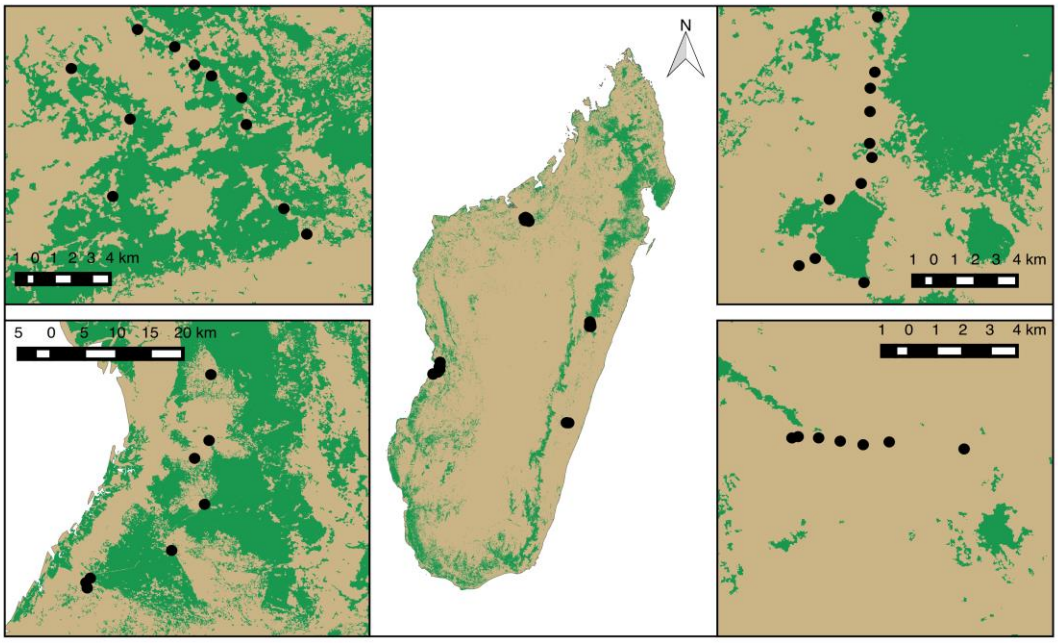

Figure 1. The four study regions, Marovoay, Moramanga, Vatovavy-Fitovinany and Menabe, with forest cover represented in green (clockwise from top-left with village location inserts).

Sampling strategy and interview protocol

Prior to surveying, the research team met with the president of each village, and our study was explained. 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 assistance of a local villager fluent in the local dialect and customs. The author participated during initial, and in occasional interviews, to ensure they were conducted in a conversational manner (Tourangeau and Yan 2007). However, the author was overall infrequently present, to ensure interview privacy (Aquilino et al. 2000). Due to the questionnaire's length, refreshments were provided as a small token of gratitude/compensation. Permission was always granted by the village president before commencing interviews.

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, as many are often not be located nearby the village centre, and may be located in distant hamlets (Poudyal et al. 2016). Given these logistical difficulties, maps of household locations inside each village (and surrounding hamlets) were created from the most recently available Google Earth (Version 7.1) satellite imagery. In particularly remote locations, interviewers stationed themselves inside distant hamlets to obtain a representative sample. The location of these remote households was also confirmed with each village president, and local guide. Furthermore, during surveys, the potential for prolonged household (interviewee) absence was possible, due to the use of distant seasonal accommodation during periods of intensive farming. This issue was discussed with the president of each village, and where possible, villagers were asked to be available for interview during certain days of the week. These methods were incorporated to establish a systematic sampling strategy to reduce potential biases borne by the unrepresentative sampling of certain demographics bound by location or profession (most commonly, farmers).

During surveys of small villages all households were visited. 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 conduct a household interview within 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 of approximately 30 households was trialled in ANP, providing the precursor to its current structure. The questionnaire underwent several phases of revisions and improvements prior to household surveys in 2014/15. Experience from this pilot questionnaire was used to train interviewers, ensuring the core of each question was understood, and asked correctly, eliminating any translation misunderstandings.

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 (Figure S1; S2). 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.

To measure poverty, six equally weighted indicators were derived from Alkire-Santos Multidimensional Poverty Index (MPI) (Alkire et al. 2015a). This

index assesses poverty through three dimensions (health, education and living standards), and has been adopted by the United Nations Development Program in assessing poverty and development in Madagascar. Whilst it is the most popular poverty index, critics have questioned the appropriateness of any single index, and the composition of various indicators (Ravallion 2011; Dotter and Klasen 2017). Despite this, the MPI has been illustrated to be robust measure of acute poverty in over 100 countries (Alkire and Santos 2014). Unfortunately, due to data-collection discrepancies, only the MPI's most important contributor, the living standard dimension was assessed, missing other important dimensions of poverty (Ferreira 2011; Alkire et al. 2015b). Consequently, we included six of its indicators: asset ownership (i.e. bicycle, radio, TV, mobile phone); roof material; wall material; floor material; access to electricity, and safe drinking water. These indicators were considered appropriate in the context of the trial survey, and through discussion with team members, but overall were found to be reliable between study sites.

The third section examined the interviewee's dietary patterns. Data were collected on respondent's: most consumed foods; frequency of domestic and wild meat consumed; 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 hunter activities, and wildlife *fady*. Given the four different study regions encompassed humid and deciduous forests that vary in their relative seasonality, Madagascar's two most pronounced seasons (dry from May to November, wet from December to April) 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 conservation, their attitudes and experiences of it.

Participants were asked to describe their general attitudes towards conservation (or fosa, Chapter 5). In examining these relationships, we considered Eagly and Chaiken's (1993) definition of attitude as a '*psychological tendency that is expressed by evaluating a particular entity with some degree of favour or disfavour'*. This chapter seeks to understand the relationship between people's attitude as a potential driver of their behaviour, be that, consuming protected species, or killing a fosa in retaliation (Chapter 5). In understanding this relationship, it's worth considering the theory of planned behaviour, the now most popular social-psychological theory (Hardeman et al. 2002). It stipulates that behaviour is influenced by attitude, subjective norms, and perceived behavioural control, with their relative importance varying by behaviour (Ajzen 1991). In considering these potential drivers of behaviour, knowing general attitudes alone, isn't necessarily useful in predicting a particular behaviour, as people often perform behaviours that contradict a particular attitude (St John et al. 2011). Consequently, care must be taken when interpreting interviewee's general attitudes as predictors of particular behaviours.

Our questionnaire required respondents to directly answer sensitive questions on potentially illegal (bushmeat consumption), and/or sensitive behaviours (retaliatory killing of fosa, Chapter 5). As a result, the collected data is likely affected by non-response (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 popular 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). These techniques assure anonymity to the interviewee, and estimate a

proportion of the population participating in a sensitive behaviour. Regression techniques have also developed to examine the relationships between covariates and the information derived from sensitive questioning methods such as RRT (van den Hout et al. 2007), or the unmatched count technique (Imai 2011). Despite this, these techniques were not implemented into our questionnaire due to the large sample sizes required to negate the large sampling variances inherit within these methods (Lensvelt-Mulders et al. 2005). This comes at a cost, with the potential impact of not using sensitive question techniques illustrated by Razafimanahaka et al. (2012). This study demonstrated a greater reporting of bushmeat consumption using RRT in areas of greater sensitivity (protected versus unprotected area) than estimates derived from direct questioning techniques. The potential for this underreporting must be considered when interpreting patterns of bushmeat consumption between different regions.

To reduce potential biases/non-response, several methods were implemented to increase interviewee responsiveness. Firstly, anonymity was assured, which has been shown to improve responsiveness (Singer et al. 1995). Secondly, the questionnaire was structured in a decreasing order of intrusiveness (i.e. first asking accounts of other people's killing of fosas), which has been demonstrated to illicit more truthful responses (Acquisti et al. 2012). Thirdly, interviews were conducted in a conversational manner, and with the inclusion of a local villager. This was hoped to reduce intrusiveness, and reduce the perceived threat of disclosure of interviewee activities to authorities (Tourangeau and Yan 2007).

To assist participants during animal preference/consumption ranking and recall exercises, picture cards were used to illustrate different 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, 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 different regional Malagasy dialects.

Several steps were taken to prepare the contents of our extensive questionnaire for dataset entry and analysis. Firstly, the questionnaire was administered and recorded in Malagasy, and contained open-ended questions that required coding. Consequently, coding was typically conducted at the end of each survey day by individual interviewers (at least one was fluent in English) as a team exercise under supervision of the lead author. This method ensured that responses were coded correctly, and in unison. Lastly, as a result of the questionnaire's structure (to reduce intrusiveness), the ordering of several questions may have been influential on the interviewee's subsequent response. Specifically, when eliciting the interviewee's attitude towards fosas, their stated response is potentially affected (negatively/positively) by the questions preceding it. Only one such response was explored in detail (interviewee attitude towards fosa), and this effect was taken into account in the interpretation of interviewees' attitudes in Chapter 5).

Analysis

Three response variables were modelled to identify the best predictors of a household's: 1) consumption of protected (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.

Category 1 (C1) contains protected species, which is split into Class 1 (C1C1) those that are strictly protected (i.e. lemurs) and Class 2 (C1C2) those that may be hunted under authorisation, commercial, sport or regulatory conditions (i.e. 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. bushpig) are defined as pest species that may be hunted at all times, whilst Category 3 (C3)(i.e. 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 species were grouped together to represent unprotected species, as in reality, despite certain legislative protection (i.e. game species), these hunting regulations are unlikely to be 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 sp.). These species are often wild caught in rural areas, but may also be reared through aquaculture, and thus represent a transitory group between wild and domestic species. 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. 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 anticipated 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. 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 only households to have consumed 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 discussed (i.e. Forest Size) 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 second model was produced containing only the significant predictors reported from the global model. These significant predictors are reported (Table 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 species counts were 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). To maintain interviewee anonymity, individual villages will not be named in the results or discussion.

Results

During the successive austral winters of 2014 - 2015, a total of 1746 households were interviewed (1325 males, mean age 42.4 ± 13.3 years; 410 females, 38.8 ±13.9 years). 565 households surrounded unprotected forests, 456 surrounded reserves, whilst 725 households surrounded national parks (Table 1). 77.5% of interviewees described their principal livelihood to be derived from farming. Primary school (43.6%) and junior secondary (24.6%) were the most common educational level, whilst a substantial minority (22.5%) had no formal education.

Domestic and wild meat eating habits and preferences

The majority (57.9%) of respondents' primary meat source was domestic animals, consuming an average of 1.46 ± 1.13 days/week. Conversely 28.6% primarily consumed wild meats (3.07 ± 1.63 days/week), and 13.5% consumed domestic and wild meats equally. 95.2% of interviewees experience food shortages, with 65.4% during the wet, dry season or entire year (19.8% respectively). Interviewees reported experiencing/perceiving food shortages on average for 2.7 ± 1.8 SD months/year.

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

Almost all (98.1%) respondents have consumed bushmeat during their lifetime. Respondents' favourite bushmeat was 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) was the most highly preferred and highly ranked category, with tenrec (21%), birds (20%) and bushpig (12%) the other highly preferred first ranking animals (Figure 2). The most highly preferred rank 5 and 6 animals were lemurs and carnivores, whilst bats were the lowest ranked group.

Aquatic animals were the overwhelmingly most consumed animal group (Figure 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 (Figure 3). However tenrecs, lemurs, bushpigs and birds became more preferred within the interviewees' ranks four to ten.

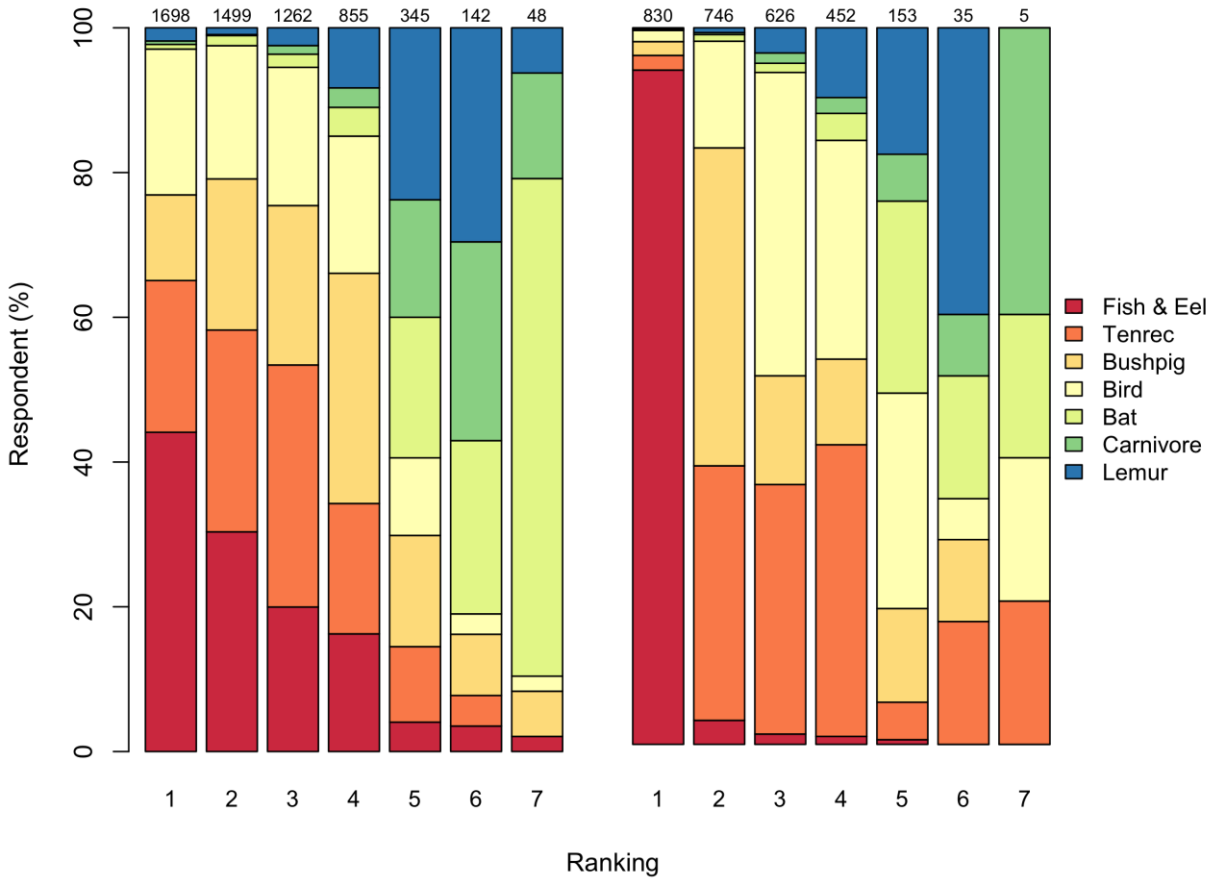

Figure 2. Total respondents' proportional bushmeat preference (left bar chart) and consumption frequency rankings (right bar chart). The total respondents to have stated a ranking is atop each bar. Note: not all respondents listed 7 species, hence the decline in total respondents in higher rankings.

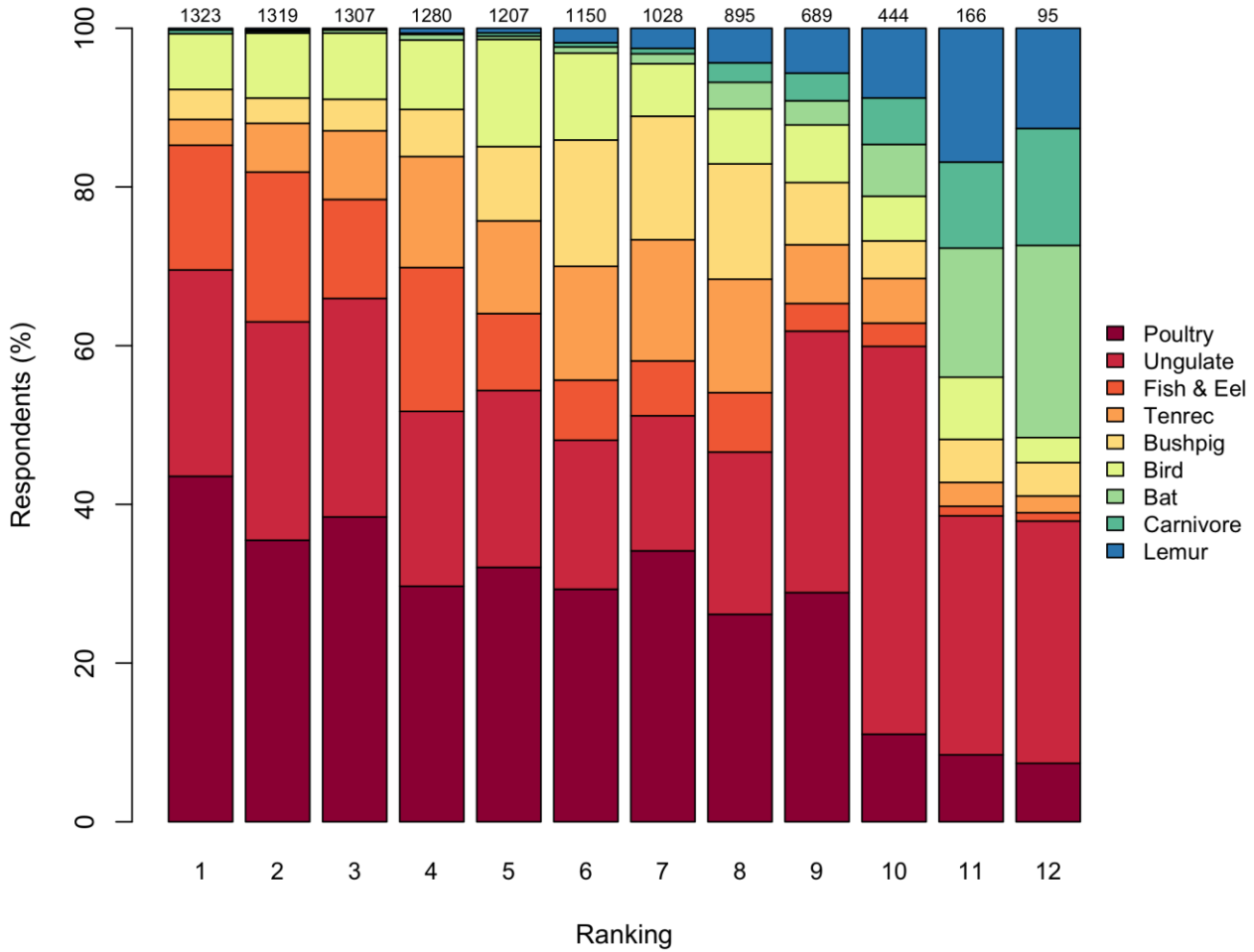

Figure 3. Total respondents' proportional domestic (poultry – chicken, duck, turkey; ungulate - zebu, pig, goat, sheep), fish & eel and bushmeat preference ranking. The total respondents to have stated a ranking is atop each bar.

Wild species consumed

Each village had consumed (over lifetime) at least one species of wild bird, fish, tenrec and bushpig (Table 2). 89.3% and 85.7% of villages' had also consumed lemurs and eels. During the previous year, birds (78.6%), fish (71.4%) and tenrec (71.4%) were consumed the most consumed animals. Approximately half of the villages had consumed a lemur or carnivore.

Within households, fish, tenrecs, birds and bushpigs were the most consumed animals (Table 2). Only 14% and 7.6% of villagers had consumed lemurs and carnivores. During the previous year, approximately 84.8% of households had consumed fish, and approximately half had consumed birds, eel and/or tenrecs. A minority had consumed a species of bat (10%), lemur (6%) and/or carnivore (3.1%).

During the previous year, fish, tenrec, eels and birds were the most consumed wild animals (Table 2). Fish and birds were most consumed during the previous week, with bats, carnivores and eels consumed in equally. Tenrecs were the only species consumed seasonally, 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.

Table 2. The total number of individual animals consumed by grouping, and proportionally by village, household, season, and method of acquisition (B & H = bought and hunted).

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

Households located inside rainforests consumed higher rates of Category 1 strictly protected animals than deciduous forests 4.87 individuals/household (1.48 in deciduous)(Table 2). They also consumed higher rates of Category 3 and unlisted animals. 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), *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.

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 endangered species consumption (Table S3). Conservation benefit (a positive benefit) was weakly significant ($p < 0.10$). Conversely households with higher education were more likely to consume any protected species.

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

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

The Poisson model found evidence for effects of Region, Poverty and Forest Size to be associated with the number of individuals of protected species consumed (Table S3). Households in Moramanga and Vatovavy-Fitovinany, those that were poor, and those living near large forests consumed more protected species. Poorer households consumed more individuals of endangered species, with this effect more marked in Moramanga than elsewhere (Figure 4).

Drivers of unprotected species consumption

The second binary model examining household consumption of unprotected species revealed Region and Household Education to be significant predictors ($p < 0.001$ and $p < 0.05$ respectively)(Table S4). Households with higher levels of education and those from Moramanga were less likely to consume unprotected species.

The final Poisson model provided evidence that Poverty and Forest Size were significant predictors of the consumption of unprotected species. Despite a weak significant negative association between poverty and unprotected species consumption in the global model ($p < 0.10$), it was not found to be a significant predictor in the final model (Figure 4)(Table S4). However, Forest Size was a significant predictor, with greater unprotected species consumed in larger forests.

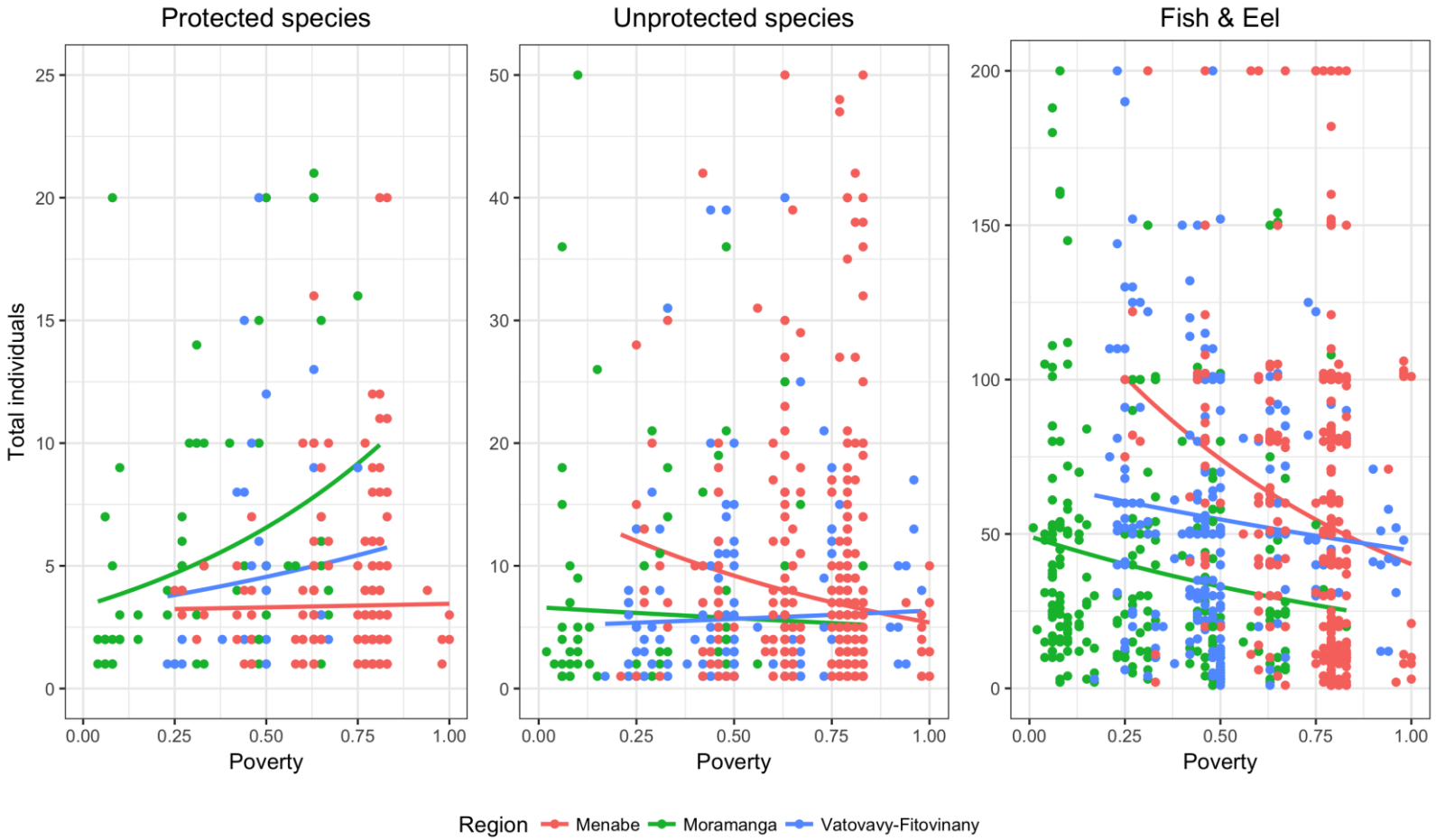

Figure 4. The relationship between total animals consumed and a household poverty index, sorted by region. The left and right plots display patterns of protected, and unprotected species consumption

Drivers of fish/eel consumption

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

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

Discussion

The poorest households consumed protected species in the greatest quantities. Conversely unprotected species were more likely to be consumed by wealthier households, and where 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 – they suggest that when households are sufficiently wealthy domestic animals are consumed in preference to endangered bushmeat 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 protected species consumption should focus on improving accessibility and reducing domestic meat cost in rural Madagascar.

Domestic species favoured

Our respondents' stated preferences for domestic animals 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 the 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. 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 reported higher rates of household lemur consumption in Masoala-Makira where up to 50% of households had consumed some species of lemur (Golden 2009; Borgerson et al. 2016). Likewise, in our same study site (Andasibe), Razafimanahaka et al. (2012) found household lemur consumptions rates of >10% (varying by species), suggesting lemur consumption occurs significantly less in Andasibe than Masoala-Makira. In comparing discrepancies between our research, and previous studies in Andasibe, temporal differences in annual consumption rates may be possible. However, what is more likely is underreporting due to the use of direct questioning. The potential for underreporting was demonstrated in Razafimanahaka et al.'s (2012) estimates of the proportion of their Andasibe population to have consumed sifaka (*Propithecus diadema*), where RRT produced an estimate of nearly four times that of direct questioning.

In our study, the rainforest regions reported higher wild species consumption rates. This could be reflected by higher overall species abundance and diversity in tropical forests (Wilson 1999), presenting greater hunting opportunities. These results do however contrast with Razafimanahaka et al. (2012) who reported higher

consumption rates of several species (sifaka, brown lemur, whistling duck, flying fox) in deciduous forests compared to a rainforest. This could be due to the significant variability between the different regions, and/or communities surveyed. This highlights the need for greater sampling coverage (and indeed greater replicates over time), improving the analyses' robustness, and the interpretation of regional consumption 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. 2004).

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 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. Tenrecs were the only wet-season hunted species, with their vulnerability to opportunistic

hunting 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 during the wet season. Conversely, consumption of carnivores (particularly fosas) has been known to occur in response to retaliatory killing during the dry season.

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. Alarmingly, 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, with previous studies reporting individual species consumption rates to be up to four times higher through the use of sensitive questioning techniques (Razafimanahaka et al. 2012).

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. There was little evidence for a poverty effect, though there was an 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' 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, in reality, other more likely explanations include, 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 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 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 species), 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 as a protein source. In contrast with 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. tenrec).

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. Poorer households were more likely to have consumed greater quantities of protected species, wealthier household's (albeit weakly significant in the global model) were more likely to consume unprotected species and very significantly likely to consume fish/eel. This pattern reflects Malagasy taste preference rankings and shows more desirable species are consumed by the wealthy, with less desirable species consumed by the poor.

Household's 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 common market sold animals. Likewise, Forest Size was reflective of greater fish/eel consumption and presumably underpinned by previously outlined reasons. Unsurprisingly larger villages with more developed markets and often wealthier 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 understand, and unlikely of any significant value in reality.

Conclusion

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. These projects have potential, and their long-term success must be monitored and evaluated (Van Vliet 2000; Roe at 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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Appendices

Appendix Figure S1.

Human-Wildlife Relationship Questionnaire Interviewer Name:

Please read to participants the study information and ensure verbal consent is given. Follow instructions in italicised Text. Please complete entire questionnaire.

Part One: Demographic: Q1. Respondent Information.

Date:		Household #	
Interview Start/Finish:		GPS S GPS E	
Village		Sub-Village	
Sex		Age (years)	
Marital Status		Ethnicity	
# People living in household >18yrs M/F		# Children (<18yrs) M/F	
Land > 500M		* Household-head Education level	
** Pets		Religion	

* [*For Education ask if highest level is: none, primary, secondary or tertiary*] ** [*What type of pet, and how many?*]

Q2. Are you from this village originally? YES NO

If NO, where? _____ How many years have you lived here? _____

Household-head Job: _____ Number of children <18 in school? _____

Q3. Do you grow crops? YES* NO *If Yes, type:

1. _____ 2. _____ 3. _____ 4. _____ 5. _____

Q4. Do you own an ox-cart? YES NO If so, how many? _____

Q5. What type of cooking material do you typically use? _____Q6. What kind of light do you use in your home? _____ Q7. How happy are you with this method in lighting your home?

VERY HAPPY QUITE HAPPY NEUTRAL QUITE UNHAPPY VERY UNHAPPY

Q8. How do you acquire your drinking/cooking water? _____

Q9. Assets. ELECTRICITY [*If so, please circle assets owned*] TV RADIO FRIDGE

CAR MOTORCYCLE/SCOOTER BICYCLE WATCH MOBILE PHONE

Q10. How many rooms do you have in your household? _____ Q11. How many people sleep per room? _____

Roof Material [*observe*] RAFFIA METAL GRASS PALM OTHER: _____

Wall Material [*observe*] MUD BAMBOO WOOD BRICK CEMENT-BLOCK

Floor Material [*observe*] EARTH TREE-BARK WOODEN-PLANK CEMENT CERAMIC TILES

Part 2: Wildlife-livestock relationship

Q1. If you own livestock, what breeds and how many do you own? *[If no skip to Q16*]

	Quantity	Protected Y/N?	How?
1. Adult Chicken 2. Chick			
Duck			
Turkey			
Goat			
Pig			
Zebu			
Other			

Q2. Do you allow your poultry to ALWAYS roam freely? YES NO

[If yes, skip to Q11. If no, please continue with the next question. Please tick multiple boxes if participant stores poultry in more than one place/time.]

Q3. What poultry do you store? CHICKEN DUCK TURKEY OTHER: _____

Q4. Where do you store your poultry? COOP INSIDE-HOUSE OTHER: _____

Q4a. Ranking of coop quality (1 = Very weak, 5 = Very Strong)? _____ Photo number: _____

Q5. What time of day do you store your poultry? MORNING MIDDAY AFTERNOON EVENING

Q6. What time of year do you store your poultry? DRY WET BOTH

Q7. Why do you store your poultry? _____

_____

Q8. Do you set up snares to protect your poultry? YES NO [*If no, skip to Q11*]

Q8a. Where do you set up your snares? _____

_____

Q9. Have you ever found any animals in your snares? YES NO [*If yes, fill in box below*]

What type of animal did you find?	How many times in your lifetime?	How many times since last year?	What time of year? (dry/wet/both)	** What time of day?	What did you do with the animal?
Wild cat					
Fosa					
Small Indian civet					

[* *Since local event ** Morning/Midday/Afternoon/Evening*]

Q10. Has anyone else in your village ever found an animal caught in a snare protecting their poultry coup? YES NO [*If yes complete table below*]

Who/where? [*use spatial/temporal cues*]	Did you see it?	What animal snared?	How many times in lifetime?	How many last year?	** What time of day?	What time of year? (dry/wet/both)	What did they do with it?

[* *Since local event* ** *Morning/Midday/Afternoon/Evening*]

Q11. Do you know of anyone whose livestock has been killed by a fosa? YES NO *[If yes continue, if no please skip to Q17]*

Who/where? [*use spatial/temporal references*]	Did you see it?	Poultry breed?	Cost?	Lifetime	Number during last year?	What time of year? (dry/wet/both)	What time of day?	What did they do with it?	What did they do to prevent future attacks?

[** *Morning/Midday/Afternoon/Evening*]

Q12. Do you know of anyone else who has ever hunted fosas in retaliation for killing their poultry or for any other reason? YES NO

Q12a. Did you see it? YES NO [*If No, please skip to Q14*].

Q12b. When? *Year* ____ ____ *Season* ____ ____ Q12c. Why did they kill it?_____

Q12d. How many times? ____ *ID*: ____ Q12e: How did they hunt it? _____

Q13. Were they successful in hunting it? YES NO [*If No, please skip to Q14*] Q13a. If so, how many fosas have they killed? _____

Q13b. Where? _____ Q13c. What did they do with them? _____

Q14. Have any of your poultry ever disappeared? YES NO How many last year?_____ Have you seen any of your poultry being killed, if so what?

[*Ask if the following killed their poultry and list any other, find out specifics of each*] *[If No please skip to Q16]*

What killed your poultry?	What kind of poultry?	What was the cost of the animal?	How many killed over lifetime?	How many killed since last year?	* What time of year?	** What time of day does this mostly occur?	Do you usually see it happen?	If so, what do you typically do?	What have you done to prevent it happening in the future?
Car									
Bird of Prey									
Fosa									
Disease									
Snake									
Wild Cat									

** Wet/Dry/Both **Morning/Midday/Afternoon/Evening*

Q15. Have you (or anyone in your household) ever hunted fosas in retaliation for killing your poultry or for any other reason? YES NO [*If No, please skip to Q17*]

Q15a. When? *Year* ____ ____ *Season* ____ ____ Q15b. Why? _____

_____

Q15c. How many times? _____ Q15d: How do you hunt fosas? _____

_____

Q16. Were you (or anyone in your household) successful in hunting fosas? YES NO [*If No, skip to Q17*]

Q16a. If so, how many fosas have you killed? _____ Q16b. Where? _____

Q16c. What did you do with it? _____

Q17. How do you feel about the fosa?

STRONGLY DISLIKE QUITE DISLIKE NEUTRAL QUITE LIKE STRONGLY LIKE

Q18. Why do you feel this way? _____

_____

Q19. Does the fosa provide any benefit to you? YES NO What benefit/why no benefit?

_____

Q20. Does the fosa provide any benefit to the ecosystem? YES NO What benefit/why no benefit?

_____

Q21. Why do you think the fosa wants to eat your poultry? _____

Q22. Are you scared of the fosa for your own safety? YES NO Why? _____

_____

Q23. Are you scared of the fossa for your poultry? YES NO Why? _____

_____

Q24. Do you think the fosa's population should be controlled? YES NO Why? _____

_____

Q25. Do you believe in any taboos relating to the fosa? YES NO If so, what taboos? _____

_____

Part 3: Diet

Q1. What are your household's five most consumed foods (could you please rank them in most eaten)?

1. _____ 2. _____ 3. _____ 4. _____ 5. _____

Q2. Do you consume these foods seasonally or perennially? [*Please list*]

DRY:_____

WET:_____

BOTH:_____

Q3. What are your household's five most accompaniments to rice/maize (could you please rank them)?

1. _____ 2. _____ 3. _____ 4. _____ 5. _____

Q4 What are your household's five most consumed fruits (could you please rank them)?

1. _____ 2. _____ 3. _____ 4. _____ 5. _____

Q5. What is your primary source of meat? DOMESTIC ANIMAL WILD ANIMAL

Q6. On average how many days per week does at least one meal contain meat? Dom ___ Wild ___ None __

Q7. Is there a period of the year in which you have don't have enough food?

Season: _____ From: _____ To: _____ #Months:_____

Q8. What is your favourite domestic meat? _____ Why? _____

Q8a. TEST. Which of those animals have you ever seen in the forest? _____

Q8b. Please rank in order of preference (only ranking what you have eaten):

Zebu ____ Duck ____ Goat ____ Chicken ____ Turkey ____ Pig ____ Sheep: ____ Other: _____

Q8c. Why did you rank the animals in this order? _____

_____

Q8d. Please rank in order of most consumed (only ranking what you have eaten):

Zebu ____ Duck ____ Goat ____ Chicken ____ Turkey ____ Pig ____ Sheep: _____ Other: _____

Q8e. Why do you choose to eat domestic meat? _____

_____

Q9. Have you ever eaten any of these animals before during your lifetime? YES NO

[*If yes, please answer Q9a, If no please skip to Q12*]

Q9a. What is your favourite wild meat? _____ Why? _____

Q9b. Please rank in order of preference (only ranking what you have eaten):

Lemur ____ Bird ____ Tenrec ____ Reptile ____ Pig ____ Carnivore ____ Aquatic ____ Bats ____

Q9c. Why did you rank the animals in this order? _____

_____

Q9d. Why do you choose to eat wild meat? _____

_____

Q10. Please rank in order of preference (only ranking what you have eaten):

Lemur ____ Bird ____ Tenrec ____ Reptile ____ Pig ____ Carnivore ____ Aquatic ____

Bats ____ Zebu ____ Duck ____ Goat ____ Chicken ____ Turkey ____ Pig ____

Q11. In your lifetime have you ever eaten?

Animal	Species	How many times eaten during lifetime?	How many times during previous year?	How many times in the last seven days?	Which season do you most commonly eat (wet/dry/both)?	How did you acquire it? (Bought/Hunt/Gift)	Where Bought/Hunted and/or who gave?	If bought, cost per kg or animal?	Why buy (cheap/tasty?) /hunt (i.e. opportunistic, specific) /gift (special occasion)?	How hunted?

Q12. Have you ever hunted and sold?

Animal	Species	How many times during lifetime	How many times during last year?	How many times on average do you hunt per week?	How do you hunt it?	Which season do you most commonly sell?	On average how many individuals do you catch per hunt?	Where do you hunt it?	Where do you sell it?	How much do you sell it for per kg/animal?	Why do you hunt and sell?

Q13. What type of wild animals have you tried to hunt for most in your life?

_____

Q13a. Please rank in order hunting success (only animals that you have hunted).

Lemur __ Bird __ Tenrec __ Reptile __ Pig __ Carnivore __ Aquatic __ Bats __

Q13b. What animal was easiest to catch? _____ Why? _____

_____

Q14. Are there any taboos relating to any wild animals in this area? YES NO

What?_____

Part 4. Wildlife conservation

Q1. What do you think wildlife conservation is? _____

_____

Q2. Why would we conserve wildlife? _____

_____

Q3. Who do we protect wildlife for? _____ Why do you feel this way? _____

_____

Q4. Do you like wildlife conservation?

STRONGLY LIKE QUITE LIKE NEUTRAL QUITE LIKE STRONGLY LIKE

Q4a. Why do you feel this way? _____

_____

Q4b. Do you receive any benefit from conservation? YES NO

What?_____

Q5. Do you know that this is a protected (or unprotected) area? YES NO

Q5a. What does this mean? _____

Q6. Why do you think the forest was protected? _____

_____

Q7. How do you feel about this forest being established as a protected (or unprotected) area?

STRONGLY LIKE QUITE LIKE NEUTRAL QUITE LIKE STRONGLY LIKE

Q7a. Why do you feel this way? _____

Q7b. Do you receive any benefit from this forest? YES NO

What? _____

Q8. Has anyone ever spoken to you about conservation? YES NO

How many times? _____ Job? _____ Who did they work for? _____

Where were they from? _____

What did they tell you? _____

_____

Did this change your perception of wildlife conservation? YES NO

WHY?_____

Appendix Figure S2.

Fanontaniana Fanadihadiana momba ny fifandraisan'ny olombelona sy ny zavaboahary

Anaran'ny mpanadihady:

Vakio amin'ny olona hadihadianao ity alohan'ny hametrahanao fanontaniana aminy ary anontanio raha manaiky ny handray anjara izy. * Araho tsara ny fanoroana voasoratra toy ny soratanana . Vitao hatramin'ny farany ny fanadihadiana.

Fizarana 1: Filazana ankapobeny: Q1. Momba ny hadihadiana:

Daty:		Laharan'ny tokantrano#	
Ora fanombohan'ny fanadihadiana/ famaranana:		GPS S GPS E	
Fokontany		Tanàna	
Lahy sa Vavy		Taona	
Manambady sa tsia/Maty vady sns..		Foko	
# Isan'olona isan-tokantrano >18 taonz. #Lehilahy/Vehivavy		# Ankizy (< 18 taona) #Lehilahy/Vehivavy	
Tany > 500m2		* Fari-pianaran'ny loham-pianakaviana	
** isan'ny biby		Finoana	

* [*tsy nianatra, ambaratongs voalohany, faharoa, fahatelo, ambony*] ** [*karazam-biby, firy?*]

Q2. Teraka teto ve ianao? ENY TSIA

Raha tsia, avy aiza? _____ Hafiriana ianao no nipetraka teto? _____

Asan'ny filoham-pianakaviana: _____ Isan'ny ankizy mianatra <18 taona i?: _____

Q3. Mamboly ve ianao? ENY* TSIA *Raha Eny, inona? _____

1. _____ 2. _____ 3. _____ 4. _____ 5. _____

Q4. Manana sarety ve? ENY TSIA Firy? _____

Q5: Inona no fomba fahandroana sakafo fampiasa ao an-trano? _____

Q6. Inona ny jiro fampiasa ao an-trano? _____Q7. Afa-po ve ianao amin'io karazanjiro io?

TENA FALY FALY TSISY AMBARA FALIFALY TSY FALY

Q8. Aiza no maka rano hosotroina/ ahandrahoana? _____

Q9. Kojakoja ananana HERINARATRA [*Ataovy anaty boribory*] TV RADIO FRIGO

FIARA MOTO/SCOOTER BISIKILETA FAMANTARANANDRO FINDAY

Q10. Efitrano firy no misy ao an-tokantrano? _____ Q11. Olona firy isan'efitra no miara-matory? _____

Tafon-trano [*jereo*] RAFIA FANITSO BOZAKA SATRANA HAFA: _____

Rindrina [*jereo*] TANY BARARATA HAZO BIRIKY SIMENITRA

Gorodona [*jereo*] TANY TREE-BARK HAZO SIMENITRA CARREAUX

Fizarana 2: Firandraisan'ny zavaboahary sy ny biby fiompy

Q1. Inona avy ny karazam- biby fiompy anananao ary firy? [*raha tsia dia dingano hatrany amin'ny Q16*]

	Isany	Arovanao ve izy ireo? ENY/TSIA	Fomba ahoana?
1-Akoho 2- Zanak'akoho			
Gana/Dokotra			
Vorontsiloza			
Osy /bengy			
Kisoa /Lambo			
Omby			
Hafa			

Q2. Avelanao handehandeha FOANA ve ny akoho amam-borona? ENY TSIA

[Raha Eny dia dingano hatrany amin'ny Q11. Raha tsia dia tohizo ny fanontaniana manaraka Mariho daholo raha mametraka ny akoho amam-borona amin'ny fotoana /toerana samihafa izy.]

Q3. Inona no avy no tsy alefa mandehandeha?

AKOHO GANA/DOKOTRA VORONTSILOZA HAFA: _____

Q4. Aiza no apetrakao ny akoho amam-borona? FISOKO AO AN-TRANO HAFA: _____

Q4a. Hamafin'ny fisoko (1 = TSY MAFY, 5 = TENA MAFY)? _____ Sary # : _____

Q5. Amin'ny fotoana manao ahoana no hidiana ny akoho amam-borona?

MARAINA ATOANDRO HARIVA ALINA

Q6. Amin'ny vaninandro inona no tsy avela hivoaka ny akoho amam-borona?

MAINTANY FAHAVARATRA IZY ROA

Q7. Maninona no hidianao ny akoho amam-borona? _____

Q8. Mametraka fandrika hiarovana ny akoho amam-borona ve ianao?

ENY TSIA [*Raha tsia , dingano hatramin'ny Q11*]

Q8a. Aiza no asianao fandrika? _____

Q9. Efa nahatratra biby tamin'ny fandrika ve ianao? ENY TSIA [*Raha eny dia fenoy ny tabilao eo ambany*]

Inona ny biby efa tratranao/azonao?	Impiry teo amin'ny fiainanao ?	Impiry tanaty ny herintaona?	Tamin'ny fotoana? (maintany/orana/izy roa)	** Tamin'ny fotoana inona?	Nataonao inona ilay biby?
Kary					
Fosa					
Jaboady					

** (Maraina,/Antoandro/Tolakanadro/Hariva)

Q10. Efa nisy olona teo an-tanana ve nahita biby tratra tao anaty fandrika natao hiarovana akoho amam-borona? ENY TSIA [*Raha eny dia fenoy ny tabilao eo ambany*]

Iza/taiza? [*toerana/fotoana*]	Hita nao ve?	Biby inona	Impiry teo amin'ny fiainanao?	Impiry tao anaty ny herintaona?	** Amin'ny fotoana inona?	Amin'ny vaninandro inona? (maintany/avy orana /izy roa)	Nataon'izy ireo inona ilay biby rehefa maty?

[***Maraina/Atoandro.Hariva/Alina*]

Q11. Mahalala olona izay nanana akoho amam-borona efa novonoin'ny fosa ve ianao? ENY TSIA *[Raha eny dia tohizo, raha tsia dia dingano hatrany amin'ny Q17]*

Iza/Taiza? [*toerana/fotoana*]	Hita nao ve?	Karazam-borona inona?	Ohatrinona no tokony ho vidiny?	Impiry teo amin'ny fiananao no nisehoan'iz any?	Impiry no niseho tanaty ny herintaoan?	Amin'ny vaninandro inona?	Amin'ny fotoana inona ?	Nataon'izy ireo inona ilay biby rehefa maty?	Inona no nataon'izy ireo mba tsy hisehoan'izany intsony amin'ny ho avy?

Q12. Mahalala olona hafa efa nihaza fosa ve ianao satria namomo ny akoho amam-boronao izy na noho ny antony hafa? ENY TSIA [Raha tsia, dingano hatramin'ny Q15]

Q12a. Hitanao ve? ENY TSIA (Raha tsia, dingano hatramin'ny Q14) Q12b: Oviana no nitranga? Taona: _____ _____ _____ Vaninandro: _____ _____ __ ___

Q12c: Raha Eny, nahoana? _____Q12d. Impiry? _____ ID: __

Q12e: Ahoana no nihazany fosa? _____

Q13. Nahavoa ve izy nihaza fosa? ENY TSIA [Raha tsia, dingano hatramin'ny Q15] Q13a. Raha eny, fosa firy no voavono? _____

Q13b. Taiza? _____ Q13c.Natao inona ny fosa maty avy eo? _____

Q14. Efa nanana akoho amam-borona maty/ voavono na tsy hita izay nalehany ve ianao? ENY TSIA Firy tamin'ny taon-dasa? _____

Firy no nanjavona tsy hita, firy no hita fa maty?

[Raha tsia, dingano hatrany amin'ny Q16][Anontanio raha ireto biby manaraka ireto no namono ny akoho amam-borona, Inona raha tsy amin'ireo, *anontanio ny mombamomba ny tsirairay*]

** Avy orana/Maintany/Izy roa ** Maraina/Antoandro/Tolakandro/Hariva* [*Raha tsia dia dingano hatrany amin'ny Q17*]

Inona no namono ny akoho amam-borona?	Biby inona no maty?	Ohatrino na no tokony ho vidiny?	Firy ny akoho amam-borona maty teo amin'ny fiainanao?	Firy no maty tanaty ny herintaona?	* Tamin'ny fotoana inona?	** Amin'ny fotoana inona no tena isehoany?	Hitanao ve ny nisehoany?	Raha eny inona no nataonao?	Inona no nataonao mba tsy isehoan'iznay intsony amin'ny ho avy?
Fiara									
Voromahery									
Fosa									
Aretina									
Bibilava									
Kary									

Q15. Efa nihaza fosa ve ianaoa na ny olona ao an-tranonao satria namono ny akoho amam-boronao izy na noho ny antony hafa? ENY TSIA

Q15a. Oviana? Taona: ____ ____ ____ Vaninandro: ____ ____ ____ Q15b. Raha eny, nahoana? _____

Q15c. Impiry? _____ Q15d: Ahoana no nihazanao ny fosa? _____

Q16. Nahavoa ve ianao na ny olona ao an-tokantranonao? ENY TSIA [*Raha tsia , dingano hatrany amin'ny Q17*

Q16a. Raha eny, firy ny fosa efa novonoinao? _____ Q16b. Taiza no nitranga? _____

Q16c. Nataonao inona ilay fosa rehefa maty? _____

Q17. Manao ahoana ny fahitanao ny fosa?

TENA TIANAO TIANAO TSISY AMBARA TSY TIANAO TENA TSY TIANO

Q18. Inona no anton'izany? _____

_____

Q19. Aminao, misy tombontsoa azo avy amin' ny fisian'ny fosa ve? ENY TSIA Inona ny tombony/

Nahoana no tsy misy tombony? _____

Q20. Aminao, misy tombony ho an'ny forest tontolo iainana ve ny fosa? ENY TSIA Inona ny tombony/ Nahoana no tsy misy tombony?_____

Q21. Aminao, inona ny antony mety mahatonga ny fosa hininana ny akoho amam-boronao?_____

_____

Q22. Matahotra fosa ve ianao sao dia mandratra mamono anao izy? ENY TSIA Nahoana?_____

_____

Q23. Matahotra fosa ve ianao sao dia mihinana ny akoho amam-borona izy? ENY TSIA Nahoana?_____

_____

Q24. Aminao, tokony ho ferana ve ny isan'ny fosa anaty ala? ENY TSIA Nahoana?_____

_____

Q25. Mino ny fady mifandray amin'ny fosa ve eto amin'ity tanàna ity? ENY TSIA

Raha eny dia inona avy? _____

Fizarana 3: Fihinanana hena

Q1. Inona no tena sakafo haninareo matetika ao an-trano? (afaka alahatrao ve?)

1. _____ 2. _____ 3. _____ 4. _____ 5. _____

Q2. Misy fotoana ve ny fihinananareo azy ireo sa mandava-taona (Mba tanisao azafady)

Maintany:_____

Fahavaratra:_____

Izy roa:_____

Q3. Inona no laoka tena fihinanareo ao an-trano? (Alaharo azafady)

1. _____ 2. _____ 3. _____ 4. _____ 5. _____

Q4. Inona no voankazo tena fihinanareo ao an-trano? (Alaharo azafady)

1. _____ 2. _____ 3. _____ 4. _____ 5. _____

Q5. Inona no hena tena fihinanareo? AVY AMIN'NY BIBY FIOMPY BIBY DIA (TSY OMPIANA)

Q6.Impiry isan-kerinandro ny sakafonareo no misy hena? Biby fiompy: _____ biby dia: _____ Tsy misy: _____

Q7. Isantaona, misy fotoana ahatsapanao tsy fahampiana ara-tsakafo ve ato an-tokantrano? ENY TSIA

Fotoana inona? _____Volana inona? _____hatramin'ny_____

Q8. Inona ny hena avy amin'ny biby fiompy tena tianao? _____ Nahoana? _____

_____

Aseho ny sary

Q8a. Iza amin'ireo biby ireo no efa hitanao tao anaty ala? _____

_____

Q8b: Alaharo araka ny itiavanao azy ny hena efa nohaninao?

OMBY: ____ GANA/DOKOTRA: ____ OSY/BENGY: ____ AKOHO: ____

VORONTSILOZA/KOLOKA: ____ KISOA/LAMBO: ____ ONDRY: _____ HAFA: _____

Q8c. Inona no anton'ny nandaharanao azy toy izao?_____

_____

Q8d. Please rank in order of most consumed (only ranking what you have eaten):

OMBY: ____ GANA/DOKOTRA: ____ OSY/ BENGY: ____ AKOHO: ____ VORONTSILOZA/ KOLOKA: ____

KISOA/ LAMBO: ____ ONDRY: _____ HAFA: ____

Q8d. Inona no mahatonga anao hihinana hena avy amin'ny biby fiompy? _____

_____

Q9. Efa nihinana 'biby dia' araka tahaka ireto amin'ny sary ireto ve ianao teo amin'ny fiainanao? ENY TSIA

[*Raha eny, valio ny Q9a, raha tsia , dingano hatrany amin'ny Q12*]

Q9a. Inona no biby dia tena tianao? _____ Nahoana? _____

_____

Q9b. Mba alaharo araka ny fitiavanao azy (ireo izay efa nohaninao ihany): Varika: ___ Vorona: ___

Trandraka: ___ Bibilava: ___ Lambo: ___ Biby mpihinan-kena (fosa, sns.): ___ Hazandrano: ___ Ramanavy: ___

Q9c. Inona no antony nandaharanao toy izao? _____

Q9d. Inona no mahatonga anao hihinana hena avy amin'ny biby dia? _____

Q10. Mba alaharo araka ny fitiavanao azy (ireo izay efa nohaninao ihany) Varika/Gidro: ___ Vorona: ___

Trandraka: ___ Bibilava: ___ Lambo: ___ Biby mphinan-kena hafa (Foasa, sns): ___ Hazandrano: ___ Ramanavy: ___

Omby: ____ Gana/Dokotra: ____ Osy: ____ Akoho ____ Vorontsiloza: ____ Kisoa: ____

Q11. Inona avy ny biby efa nohaninao tamin’ny fiainanao?

Biby	Karazam-biby	Impiry teo amin’ny fiainanao?	Impiry tao anatiny’ny taona lasa teo?	Impiry tao anatin’ny 7 andro farany teo?	Vaninandro inona no tena fihinananao hena (Maintany/Orana/Izy roa)	Ahoana no ahazoana ny hena? (Mividy/Mihaza/Fanomezana)	Aiza no mividy?/no mihaza?/ Iza no manome?	Raha mividy, ohatrinona /kg na / biby?	Nahoana no mividy (mora, matsiro,..? Nahoana no mihaza? (Mora hita, tadiavina..? Miny manonome (misy antony manokana?	Ahoana ny fomba fihazana?

Q12. Efa nihaza sy nivarotra ve ianao?

Biby	Karazam-biby	Impiry teo amin’ny fiainanao?	Impiry tamin’ny taona lasa?	Vaninandro inona no tena famarotanao?	Ahoana no fomba hihazanao?	Impiry isan-kerinandro eo ianao no mihaza?	Amin’ny ankapobeny, biby firy no azonao isaky ny mandeha mihaza?	Aiza ianao no mihaza?	Aiza no hivarotanao azy avy eo?	Ohatrinona no hamarotanao azy /kg na /biby?	Inona no antony hohazanao sy hamarotanao?

Q13. Inona no biby dia efa nohazainao be indrindra eo amin'ny fiainanao?

_____

Q13a. Alaharo araka ny habetsahan'ny azonao (ny biby izay efa nohazainao ihany).

Varika: ___ Vorona: ___ Trandraka: ___ Bibilava: ___ Lambo: ___ Fosa: ___ Hazandrano: ___ Ramanavy: ___

Q13b. Inona no biby mora hazaina indrindra? _____ Nahoana? _____

_____

Q14. Misy fady mifandray amin'ny biby aty amin'ity toerana ity ve? ENY TSIA

Fady inona? _____

Fizarana 4. Fiarovana ny zavaboahary

Q1. Ahoana ny hevitrao momba ny fiarovana ny zavaboahary? _____

_____

Q2. Nahoana ny olona no miaro ny zavaboahary? _____

_____

Q3. Ho an'iza no iarovan'olona ny zavaboahary? Ahoana no mahatonga anao hieritreritra izany? ____

_____

Q4. Tianao ve ny fiarovana ny zavaboahary?

TENA TIANAO TIANAO TSISY AMBARA TSY TIANAO TENA TSY TIANO

Q4a. Inona no anton'izany? _____

_____

Q4b. Mahazo tombony amin'ny fiarovana ny zavaboahary ve ianao? ENY TSIA

Inona? _____

Q5. Fantatrao ve inona no atao hoe faritra voaaro ? ENY TSIA

Q5 Inona no dikan'izany? _____

_____

Q6 Inona araka ny hevitrao no antony niarovana na ny Ala? _____

_____

Q7Ahoana ny eritreritrao amin'ny fiarovana ity ala ho Parka Nasionaly ?

TENA TIANAO TIANAO TSY MAMPANINONA TSY TIANAO TENA TSY TIANO

Q7a. Inona no anton'izany? _____

_____

Q7b. Mahazo tombony amin'ity ala ity ve ianao? ENY TSIA Inona?_____

_____

Q8 Efa nisy niresaka taminao momba ny fiarovana ny tontolo iainana ve? ENY TSIA

Iza? _____ Miasa amin'iza/inona izy ireo? _____

Avy aiza izy ireo? _____

Inona no noteneniny anareo? _____

Nanova ny fihevitrao momba ny fiarovana ny zavaboahary ve izany? ENY TSIA

Nahoana? _____

Appendix Table S1. Details of the predictors used in models 1 and 2, including their function (Type: Dependent Variable 1 and 2 (DV1/2), Random Effect (RE), Blocking Factor (BF), Independent Variable (IV)).

Name	Type	Description	Levels
Protected sp. Consumed	DV1	Sum of C1 individual species consumed last year	1 - ∞
Unprotected sp. Consumed	DV2	Sum of pest, game, unlisted individual species consumed last year	1 - ∞
Fish/eel Consumed	DV3	Sum of fish/eel consumed last year	1 - ∞
Village	RE	The village the household resides within	Categorical Village Name
Region	BF	The geographical area the household resides within	Menabe, Marovoay, Moramanga, Vatovavy-Fitovinany
Forest Size	IV	Size of the nearest primary forest (km^2)	1 - ∞
Village Size	IV	Total number of households within the household's village	1 - ∞
Household Distance	IV	Household distance to forest edge (m)	1 - ∞
Education	IV	Interviewee's highest level of education	None, Preschool, Primary, High School, Tertiary
Poverty	IV	Household wealth metric (increasing poverty)	0 – 1
Conservation Benefit	IV	Does the interviewee receive any personal benefit from conservation	Yes/No

Appendix Table S2. The total frequencies of all species (Protection Category 1 Class 1 (C1C1), Category 2 Class 1 (C1C2), Category 2 (C2), Category 3 (C3), Not Listed (NL), Mixed (multiple species and protection)) consumed by households.

Animal	Species	Common name	Protection	Total consumed lifetime	Total consumed last year
Bat	*Pteropus rufus*	Madagascan flying fox	C3	3663	481
	Eidolon dupreanum	Straw-coloured fruit bat	C3	836	88
Bird	*Accipiter francesiae*	Frances's sparrowhawk	C3	1514	47
	Agapornis cana	Madagascar lovebird	C1C2	30	0
	Ardea ibis	Cattle egret	NL	101	0
	Asio madagascariensis	Madagascar owl	C1C2	30	4
	Cinnyris sp.	Sunbird sp.	Mixed	20	5
	Coracopsis sp.	Vasa Parrot sp.	C1C2	3104	616
	Coturnix coturnix	Common quail	C3	10	0
	Coua caerulea	Blue coua	C1C2	689	327
	Coua coquereli	Coquerel's coua	C1C1	55	2
	Coua cristata	Crested coua	C1C2	30	0
	Coua gigas	Giant coua	C1C1	325	51
	Eagle sp.	Eagle sp.	C1C1	5006	3
	Foudia madagascariensis	Madagascar red fody	C3	54	2
	Hypsipetes madagascariensis	Madagascar bulbul	C3	60	4
	Leptosoumus discolor	Cuckoo roller	C1C2	67	7
	Lophotibis cristata	Madagascar crested ibis	C1C1	2174	330
	Margaroperdix madagarensis	Madagascar partridge	C3	60	0
	Numida meleagris	Helmeted guinea-fowl	NL	17258	2464
	Pidgeon sp.	Unspecified	Mixed	20	2
	Sarkidiornis melanotos	Comb duck	C3	32	0
	Tachybaptus pelzelnii	Madagascar grebe	C1C1	1290	17
	Terpisphone mutata	Madagascar paradise fly-catcher	C3	80	15
	Treron australis	Madagascar green pigeon	C1C2	1101	66
	Unspecified	Waterfowl sp.	Mixed		0
Carnivore	*Mungotictis decemlineata*	Narrow-striped mongoose	C1C1	1702	163
	Cryptoprocta ferox	Fosa	C1C2	81	8
	Eupleres goudotii	Falanouc	C1C2	20	1
	Felis sp.	Wild cat	NL	87	11
	Fossa fossana	Malagasy striped civet	C1C1	281	14
	Galidia elegans	Ring-tailed mongoose	C1C1	116	17
	Galidia fasciata	Broad-striped mongoose	C1C1	4	0
	Viverricula indica	Small Indian civet	NL	289	72
Eel	*Anguila sp.*	Eel	NL	105979	4489
Fish	*Tilapia sp.*	Tilapia	NL	6169445	76675

	Carp sp.	Carp	NL	650	100
Frog	*Hoplobatrachus sp.*	Hoplobatrachus sp.	C1C2	33	0
	Mantidactylus grandidieri	Grandidier's Madagascar Frog	C3	747	44
	Mantidactylus guttulatus	Gray Madagascar Frog	C3	34	15
Lemur	*Hairy-eared dwarf lemur*	Allocebus trichotis	C1C1	72	2
	Eastern woolly lemur	Avahi laniger	C1C1	811	62
	Geoffroy's dwarf lemur	Cheirogaleus major	C1C1	50	0
	Fat-tailed dwarf lemur	Cheirogaleus medius	C1C1	420	21
	Aye aye	Daubentonia madagascariensis	C1C1	1	0
	Common brown lemur	Eulemur fulvus	C1C1	623	27
	Mongoose lemur	Eulemur mongoz	C1C1	503	79
	Red-bellied lemur	Eulemur rubriventer	C1C1	32	0
	Red-fronted lemur	Eulemur rufifrons	C1C1	221	31
	Bamboo lemur	Hapalemur griseus	C1C1	731	12
	Indri	Indri indri	C1C1	6	0
	Milne-Edward's sportive lemur	Lepilemur Edwardsi	C1C1	2	0
	Weasel sportive lemur	Lepilemur mustelinus	C1C1	54	8
	Red-tailed sportive lemur	Lepilemur ruficaudatus	C1C1	36	23
	Madame Berthe's mouse lemur	Microcebus berthae	C1C1	50	7
	Brown mouse lemur	Microcebus rufus	C1C1	551	205
	Coquerel's mouse lemur	Mirza coquereli	C1C1	113	3
	Pale fork-marked lemur	Phaner pallescens	C1C1	3	0
	Greater bamboo lemur	Prolemur simus	C1C1	29	2
	Coquerel's sifaka	Propithecus coquereli	C1C1	37	0
	Diademed sifaka	Propithecus diadema	C1C1	600	17
	Verreaux's sifaka	Propithecus verreauxi	C1C1	567	80
	Black and white ruffed lemur	Varecia variegata	C1C1	320	4
Reptile	*Tortoise*	Tortoise	Mixed	649	0
	Crocodylus niloticus	Nile crocodile	C1C2	11	0
	Pyxis planicauda	Flat-backed spider tortoise	C1C1	8	1
	Turtle sp.	Turtle	Mixed	1	0
Tenrec	*Echinops telfairi*	Lesser hedgehog tenrec		16985	856
	Hemicentetes semispinosus	Lowland streaked tenrec	C1C2	11497	2661
	Tenrec ecaudatus	Common tenrec	C3	35499	2293
Bush pig	*Potamochoerus larvatus*	Bushpig	C2	27003	1043

Appendix Table S3. The significant predictors (variables) for the binomial and Poisson models of protected species (C1) consumption. The posterior mean estimate (post.mean), Lower 95% Confidence Interval (l-95% CI), Upper 95% Confidence Interval (u-95% CI), the effective sample size adjusted for autocorrelation (eff.samp), and the Markov Chain Monte Carlo p-value (pMCMC).

Model	Variables	post.mean	l-95% CI	u-95% CI	eff.samp	pMCMC
Binary	(Intercept)	-0.38616	-1.45136	0.66743	3691	0.4706
	Moramanga	-0.19847	-1.30441	0.80062	4943	0.7012
	Vatovavy-Fitovinany	-2.89985	-4.42518	-1.36197	5079	< 0.001 ***
	Household Distance	0.71404	0.35938	1.07044	3100	< 0.001 ***
	Conservation Benefit	-0.59133	-1.26183	0.10137	2397	0.0953 .
	Household Education	0.23243	0.02365	0.43285	2524	0.0255 *
Poisson	(Intercept)	0.43315	0.06105	0.77719	5510	0.02487 *
	Moramanga	1.2356	0.71384	1.79521	6680	< 0.001 ***
	Vatovavy-Fitovinany	1.02157	0.35461	1.66014	5693	0.00385 **
	Poverty	0.1871	0.02416	0.35927	6182	0.02744 *
	Forest Size	0.28322	0.04149	0.5689	5347	0.02897 *

Appendix Table S4. The significant predictors (variables) for the binomial and poisson models of unprotected species (C4) consumption. The posterior mean estimate (post.mean), Lower 95% Confidence Interval (l-95% CI), Upper 95% Confidence Interval (u-95% CI), the effective sample size adjusted for autocorrelation (eff.samp), and the Markov Chain Monte Carlo p-value (pMCMC).

Model	Variables	post.mean	l-95% CI	u-95% CI	eff.samp	pMCMC
Binary	(Intercept)	1.8113	1.04608	2.62824	3675	< 0.001 ***
	Moramanga	-1.91681	-2.80029	-1.01711	5231	0.000204 ***
	Vatovavy-Fitovinany	-0.48493	-1.63856	0.79099	7009	0.421429
	Household Education	-0.21346	-0.40185	-0.02249	2810	0.026327 *
Poisson	(Intercept)	1.20734	1.0373	1.36046	4839	< 0.001 ***
	Poverty	-0.08544	-0.21304	0.03583	7053	0.18538
	Forest Size	0.23367	0.07181	0.4078	7800	0.00846 **

Appendix Table S5. The significant predictors (variables) for the binomial and poisson models of fish and eel consumption. The posterior mean estimate (post.mean), Lower 95% Confidence Interval (l-95% CI), Upper 95% Confidence Interval (u-95% CI), the effective sample size adjusted for autocorrelation (eff.samp), and the Markov Chain Monte Carlo p-value (pMCMC).

Model	Variables	post.mean	l-95% CI	u-95% CI	eff.samp	pMCMC
Binary	(Intercept)	1.25956	-0.5165	3.05955	3376	0.14918
	Moramanga	4.38441	1.67049	7.47529	471.3	0.00102 **
	Vatovavy-Fitovinany	5.39611	1.73096	9.4859	607.5	0.00490 **
	Poverty	-0.41628	-0.81497	0.02438	1110.8	0.05265 .
	Forest Size	1.75717	0.26271	3.2514	901.2	0.01490 *
	Household Distance	0.62075	0.05634	1.17666	872.2	0.02653 *
Poisson	(Intercept)	3.694611	3.270797	4.150614	7928	0.001 ***
	Moramanga	0.003238	-0.442468	0.469194	7325	0.982051
	Vatovavy-Fitovinany	0.826779	0.337205	1.363789	7800	0.001282 **
	Poverty	-0.140925	-0.254639	-0.020177	7800	0.014872 *
	Village Size	0.142521	-0.018976	0.296389	7800	0.074615 .
	Forest Size	0.419649	0.198481	0.632969	7800	0.000769 ***
	Conservation Benefit	-0.34961	-0.714818	0.011564	7800	0.061282 .

Chapter Five

Retaliatory killing and human perceptions of Madagascar's largest carnivore and livestock predator, the fosa (*Cryptoprocta ferox*)

Abstract

Fosas (*Cryptoprocta ferox*) are Madagascar's largest carnivores, occupying much of the forested landscape. This study provides the first evaluation of fosas' conflict with humans, a problem for many small and medium sized carnivores worldwide. We examined fosas' predation of poultry, its spatio-temporal occurrence, and subsequent retaliatory killing. Over 1750 households were interviewed across four regions, encompassing Madagascar's major forest types (deciduous/rainforest) and its major protected area classifications (national park, reserve and unprotected forest). Fosa predation was the third highest cause (15%) of poultry mortality, with coops ineffective in reducing predation. Predation of poultry was more prevalent in deciduous forests, and most common during the evenings of the dry season. Over half of all interviewees disliked fosas, with loss of poultry the most commonly stated reason. Respondents' that had suffered poultry depredation and those with lower educational attainment were more likely to dislike fosas. Interviewees that disliked fosas and those that were wealthier were most prone to have killed a fosa. A minimum of thirty fosas was killed in retaliation during the interview's previous year. Given fosas' population is in decline, and most of Madagascar's forests are too small to support sustainable populations, these killings are likely to be detrimental to vulnerable sub-populations. These results shed insight into the cultural perceptions and predation patterns of a medium sized carnivore, with relevance to worldwide human-wildlife conflict of often overlooked smaller carnivores. We suggest that educational programs, watchdogs and robust coop construction may be effective tools in improving attitudes and reducing retaliatory killing.

Keywords: Eupleridae, Livestock depredation, Human wildlife-conflict, Carnivores, Conservation.

This chapter forms the basis of a paper to be submitted to Biodiversity and Conservation of which I am the lead author. My co-authors are Luke J Dollar, Paul Johnson and David W Macdonald.

Introduction

Carnivore populations are in global decline, with human conflict and retaliatory killing a leading cause (Woodroffe 2000; Sillero-Zubiri and Laurenson 2001; Treves and Karanth 2003; Cardillo et al. 2004; Lichtenfeld et al. 2015). While larger carnivores may be particularly at risk, owing to larger home ranges, low population densities, and low fecundity (Woodroffe and Ginsberg 1998; Cardillo et al. 2004), conflict with carnivore populations is not limited to larger species. Across the globe many small to medium carnivores are also persecuted, most often for their predation upon domestic poultry (Macdonald et al. 2000; Macdonald and Feber 2015; Macdonald et al. in press).

Madagascar's carnivores, the Eupleridae, have been described as one of the most understudied and threatened group of carnivores worldwide (Brooke et al. 2014). The Eupleridae's largest carnivore, the fosa (*Cryptoprocta ferox*) weigh on average 6 - 7 kg (Hawkins 1998; Dollar 2006) and are found across Madagascar's forested landscape. They are thought to be a keystone species due to their predation of lemurs and other species (Dollar et al. 2007; Hawkins and Racey 2008a). Fosas occupy home ranges of up to 50 km^2 (Lührs and Kappeler 2013) at population densities of 0.17 – 0.22 individual/km^2 in rainforests and deciduous forests (Hawkins and Racey 2005; Gerber et al. 2010). It is this extensive ranging and predation on larger prey that leads them to encounter humans and their poultry. Knowledge of this relationship however, has hitherto been largely anecdotal.

Fosas have reportedly been killed for straying into villages where they may be perceived to be a threat to poultry (Albignac 1973; Hawkins 1998; Jones et al. 2008) and other small livestock such as lambs (Gardner and Davies 2014). Recent research in the southeast rainforest of Ranomafana National Park (Kotschwar Logan et al.

2014) suggests fosas are not believed to affect many poultry keepers: 21% of interviewees who kept poultry reported predation within the previous year, with less than 1% of these losses attributed to fosas. However, individual attacks can be serious, with local farmers reporting incidents where fosas have killed all of their poultry once they had gained entry into the coop (Albignac 1973), so called 'surplus killing' which is likely to promote negative attitudes towards a predator, as has been observed of the red fox in the UK (Kruuk 1972).

Negative attitudes towards fosas are not caused solely by poultry predation (Kotschwar Logan et al. 2014). There are cultural taboos (known as *fady*) surrounding them, the most commonly cited of which is the belief that they consume the remains of villagers' ancestor's (Ruud, 1960; Jones et al. 2008). Their resemblance to dogs is also a negative influence (Gardner and Davies 2014), perhaps partially explained by a recent study purporting dogs to be overwhelmingly disliked in villages in Ranomafana National Park (Valenta et al. 2016). There are currently no published studies verifying these anecdotal accounts of human persecution of fosas. Given fosas' life history characteristics, potential persecution raises questions as to their long-term persistence in a landscape shared with humans. In conserving fosas it is critical that we understand this conflict.

This study examines fosas' impact across four regions, encompassing a sample of Madagascar's protected and unprotected areas. Our objectives were to: 1) Identify respondents' livestock ownership and protective practices; 2) Examine the frequency and cost of fosa predation relative to other causes of poultry mortality; 3) Identify fosas' primary temporal and seasonal periods of predation; 4) Estimate the annual numbers of fosas killed and examine variation among the four regions; 5) Identify the circumstances where predation of domestic poultry and therefore

retaliatory killing of fosas is most likely, and 5) explore interviewee attitudes towards fosas. This information is fundamental for evaluating the retaliatory killing of fosas and medium size predators in general, and understanding its socio-economic and cultural drivers.

Methods

Study Area

Surveys were conducted across four sites in Madagascar. Sites were chosen (in align with Chapter 4) to encompass a representative sample of two of the fosas' most extensive habitat types (deciduous and rainforest). Madagascar has a hierarchy of protected areas ranging from; Category I, Strict Natural Reserve, forbidding visitor entry; Category II, National Park, managed to allow public entry; and Category III, Special Reserve which are preserved purely for conservation, with a minimal tourist focus (MNP 2014). Our four sites incorporated two National Parks, one Special Reserve, one Private Reserve, and two unprotected areas (Table 1).

Located in the Marovoay region, Ankarafantsika National Park (ANP)(16°14' S latitude, 46°55' E longitude) is Madagascar's largest (1350 km^2) tract of dry deciduous forest. ANP is surrounded by a population of over 37,000 inhabitants in 133 villages and hamlets (MNP 2016). A road intersects the park's southwest border and is flanked by six rural villages. These villages, in addition to two villages to their southwest (not located nearby any roads) are the only villages located inside the forest.

The central western region of Menabe encompasses the largest fragments of deciduous forest. Three forests are situated along a south-north axis in Menabe's north. Andranomena Special Reserve (ASR)(20°17' S latitude, 44°50' E longitude)

contains 64.20 km^2 of forest with two large villages flanking its perimeter. North of Andranomena is the privately managed Kirindy reserve (20°04’ S latitude, 44°66’ E longitude), a former forestry concession and now a centre of research. Lastly Ambadira, unprotected and our most northerly forest, is bordered by the large village of Lambokely and has experienced significant deforestation and agricultural conversion during recent years (Zinner et al. 2013).

Covering over 155 km^2, Andasibe-Mantadia National Park (AMNP)(18°23’ S latitude, 48°28’ E longitude) is located in the Moramanga region, and is one of the largest and most visited of Madagascar’s protected areas. The commune of Andasibe lies at its centre, and is surrounded by several villages to the north, whilst the closest southerly villages are located along the Route Nationale 2.

Situated in the Southeast region of Vatovavy-Fitovinany, the commune of Kianjavato (21°38’ S latitude, 47°87’ E longitude) is surrounded by several unprotected, and fragmented primary forests of Sangasanga, Tsiazonamboa, Ambatovaky, Tsitola and Vatovavy. These few remaining forests are characteristically low elevation humid evergreens surrounded by grassland, agricultural and secondary forests (Manjaribe et al. 2013).

Table 1. Summary of our study regions, including the results of our three models: percentage of households (HH) to experience fosa poultry predation; percentage of households to kill a fosa; and the average household attitude score.

Forest Type	Region	Protection Status	Forest Size (km^2)	Total Villages	Households Interviewed	Fosa Predation (HH%)	Fosas Killed (HH%)	Mean HH Attitude Score
Deciduous	Marovoay	Ankarafantsika National Park	1,350	8	363	22%	5%	2.83
	Menabe	Andranomena Special Reserve	64	2	190	16%	4.11%	3.03
	Menabe	Kirindy Private Reserve	710	2	266	41%	1.79%	2.74
	Menabe	Unprotected	710	1	206	37%	1.94%	2.65
Rainforest	Moramanga	Andasibe-Mantadia National Park	155	6	362	11%	5.96%	2.43
	Vatovavy-Fitovinany	Unprotected	Various < 10	5	359	7%	0.42%	2.56

Sampling strategy and interview protocol

Field staff were trained to interview independently within each village. Prior to household interviews our research objectives were explained to the village president who gave permission for survey commencement.

Villages were categorised as ‘small’ or ‘large’, roughly corresponding to villages less than or greater than 100 households, During surveys all households in small villages were visited, whilst only a sample of households within large villages were interviewed.

Once a house was selected, its head was requested for interview and verbal consent acquired. If the individual was absent a further two appointments were scheduled.

Within larger villages, the area was divided into districts and sampled using the zig-zag transect method (East et al. 2005). This method allows households not located on streets to be visited and ensures a representative sample may be extrapolated from populous villages. Each interviewer was instructed to walk a zig-zag transect, sampling every second household. If the head of the household wasn’t present or was unwilling to be interviewed the next household was surveyed. The potential bias introduced by unwilling respondents was negligible as fewer than 2.5% declined to participate.

Questionnaire design

A pilot questionnaire was devised and trialled in ANP during 2013. The results of the pilot questionnaire were not used in this analysis, however the results and feedback proved useful in the shaping its ultimate design.

The questionnaire (with background theories and additional methodology detailed in Chapter 4) was divided into four sections addressing respondents': i) demographic and socioeconomic information; ii) livestock ownership history; iii) dietary patterns; and iv) conservation perceptions and experiences. To promote trust, participants remained anonymous (Singer et al. 1995), however they were asked to reveal baseline demographic and socioeconomic information, such as employment, education, ethnicity, household family structure, and livelihood indicators such as asset ownership. Questionnaire section two aimed to record participants' details of livestock ownership, specifically: i) breed and quantity; ii) use of protective measures such as coop or snares; iii) what they perceived to be the causes of poultry mortality, both for the previous year and for their lifetime, and the season the causes were most prevalent in; iv) their perceptions of the significance of fosas as a cause of poultry mortality; and v) attitudes towards fosa. Participants were also asked sensitive questions regarding the details of any fosa-conflict encounters, including: the number killed; seasonal and temporal occurrence; reason for killing, and their use of any fosa killed. Given the sensitivity of the question and interviewee's potential reluctance to answer truthfully, interviewees were also asked to report of known inhabitants of their local village to have killed a fosa. This questioning-method was included to best account for unreported mortalities, and to produce a more accurate enumeration of fosas' killed. Despite the potential for misinformation when incorporating third-party estimates, claims were validated through the crosschecking of spatial-temporal information. Given the killing of fosas within villages was a rarity, interviewees were able to accurately recall these events, and interviewers were able to deduce the year and location of each attack. These events were collated together as a team to ensue pseudo-replication was mitigated.

Analysis

Data were analysed using the statistical package R (R Core Team 2016). Fisher Exact Tests and Chi-Squared tests of Independence were used in the analysis of seasonality, diel period, forest type, and interviewee coop usage's relationship with fosa poultry predation.

Three sets of generalised linear mixed effect models (GLMM) were used to examine the association of our explanatory variables with three response variables, i) fosas' predation of poultry; ii) interviewees' attitude towards fosas and, iii) retaliatory killing of fosas (Appendix S1).

Last Year Predation was measured as a binary 'yes/no' response to a question asking if the respondent had experienced fosa poultry depredation during the previous year. Nine a priori variables thought to potentially impact a household's susceptibility to fosa predation included; Forest Size, Village Size, River Barrier, Household Distance, Flock Size, Flock Coop, Flock Snare and Region (Appendix S1).

Region was included as a fixed blocking factor accounting for geographic variation. This was included in all statistical models as an aspect of study design. Given the nesting of households within villages the identities of individual villages were included as levels of a random effect. Pearson's Chi-squared tests of Independence and Pearson Correlation Coefficients were used to identify collinearity among predictors. Forest type and Protection were not included as predictors in the GLMMs as they were highly confounded with Region.

A GLMM model with a binomial family and a logit link function (package lmer 1.1 - 12) was used to model the binary response variable, Last Year Predation. Akaike's information criterion (AIC) was used to rank models according to the most parsimonious set of predictors (Burnham and Anderson 2002). Model averaging was

not used for the reasons given in (Cade 2015), principally that with any non-trivial level of collinearity among predictors, inevitable with most observational studies, model averaged parameter estimates are unreliable. Instead, where no single model was clearly dominant, we scrutinised the pattern of parameter estimates in the models with highest weights.

Attitude towards fosas, measured on a 5-point likert scale was used as an ordinal response variable and modelled with the fixed-effect predictors, Poverty, Education, Protection, Poultry Owned, Lifetime predation, Conservation Benefit, Conservation Experience, and Conservation Attitude (and Village identity as a random effect). A cumulative logit function was fit using the R package 'ordinal' (version 2015.6-28). Model selection was as previously described.

The final series of models exploring the potential predictors influencing the retaliatory killing of fosas followed the same set of methods prescribed in model one. The binary response variable (did interviewee's report having killed at least one fosa during their lifetime) was thought to be potentially influenced by Poverty, Conservation Experience, Conservation Benefit, Conservation Attitude, Attitude, and Region (Appendix S1). The household's relative poverty level was estimated using several of the indicators contained within the Multidimensional Poverty Index (MPI)(Alkire et al. 2015). This metric uses three dimensions (education, health and living standard) to measure poverty, with weighted indicators within each dimension combining to create a more representative estimate of poverty. Unfortunately given the structure of our questionnaire our estimate contained only indicators from the MPI's living standard dimension. Our poverty estimate equally weighted six indicators to create a relative estimate of household poverty measuring poverty in an increasing scale from 0 to 1 (maximum poverty score 1.0). Our indicators included

assets ownership (i.e. mobile phone, radio, bicycle), roof material, wall material, floor material, access to electricity and access to safe drinking water. Unfortunately, the poverty metric was unavailable for one of the regions (Marovoay) due to changes in the content of the questionnaire between the initial surveying of Marovoay in 2014 and the interviewing of the remaining regions in 2015. Consequently two series of models were used for this response, with Poverty not included where all regions were used and with Poverty included (excluding observations from Marovoay).

Results

In total 1746 households were interviewed (1325 male, 410 female, mean age 42.4 ± 13.3 and 38.8 ±13.9) over six months from April – June 2014, and May – August 2015 (Table 1). 725 households were interviewed within and surrounding national parks, with 456 and 565 conducted within reserves and unprotected forests. Respondents were overwhelmingly farmers (77.5%). Most respondents' highest level of educational attainment was either primary school (43.6%), or junior secondary (24.6%). A substantial minority reported having no education (22.5%). Senior secondary or tertiary education was not commonly reported (8.7% and 0.7% respectively).

Livestock ownership and practices

Approximately 80% (n = 1391) of respondents owned livestock. Of these respondents, chickens (45.6%), zebu (25.1%) and ducks (15.6%) were most commonly owned. Chickens were also bred in the greatest numbers, with a mean of 15.4 (15.63 SD) owned per respondent.

87% of respondents who reared poultry used a protective structure. The majority, n = 595 (63%) stored their poultry in coops, inside their home (22%), or inside a cattle-pen (8.8%). 85% of poultry owners housed their poultry during the afternoon and evening, with the overwhelming majority doing so throughout the entire year (91%). Poultry were most commonly protected due to general security concerns and fear of predators (45.3% and 44.6% of respondents).

Poultry Mortality

86.7% of poultry owners (n=1136) reported experiencing poultry mortality to any cause during the last year. Mortality resulting from disease (40.4%) was most commonly reported. Mortality to predation was most often attributed to birds (17.0%) with fosa depredation recorded by 276 respondents (15.3%).

Predation by fosas was significantly more prevalent in western deciduous forests than the eastern rainforests (Figure S1).

Fosa depredation was significantly more likely to be reported as occurring during the evening in the dry season than any other season (Chi-squared test of independence, $X^2 = 138.12$, df = 4, $p < 0.001$). There was no evidence that the use of a coop was associated with the frequency of poultry depredation (Appendix S2). In response to fosa depredation the majority of respondents did nothing (37.68%), improved their coop (36.52%), bred dogs (8.12%), created traps (4.35%), scared the predator away (4.35%), or attacked the fosa (2.03%).

The most parsimonious model evaluating a household's susceptibility to previous year poultry depredation included the predictor's Region and Snare (Appendix S3). These significant predictors were included in a final model with Region and Snare the only significant predictors (at $p < 0.01$ and $p < 0.05$)(Appendix

S3). Odds ratios indicated that households in Moramanga were 3.45 times and Vatovavy-Fitovinany were 7.14 times less likely to report predation compared with those in Marovoay (the arbitrary reference level)(Figure 1). The percentages reporting fosa predation were 22% in Marovoay, 30% in Menabe, 10% in Moramanga and 6% in Vatovavy (Table 1). Poultry keepers who used snares were 2.30 times more likely to have sustained poultry predation than those who did not (Figure 1).

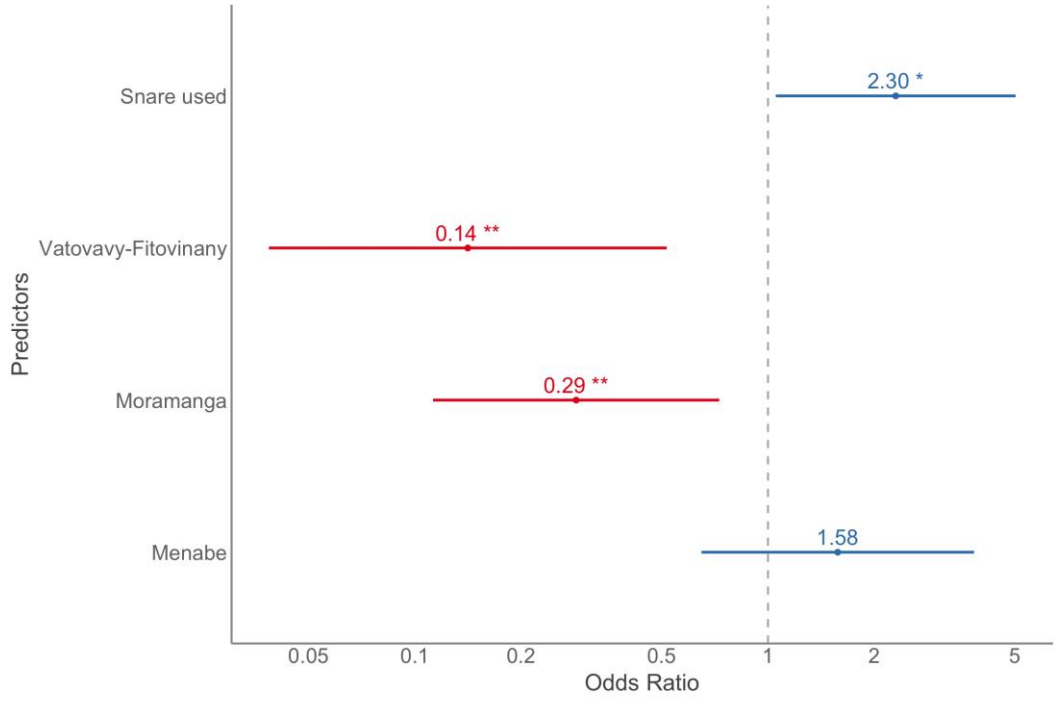

Figure 1. The significant predictors of fosas' reported predation of poultry (with 95% confidence intervals). The x-axis displays the odds of households sustaining poultry predation that were located in a region or used a snare, against Marovoay the reference region. The level of significance is denominated by * $p < 0.05$, and ** $0 < 0.01$.

Attitudes

Over half of all respondents disliked fosas (responding either ‘Strongly Dislike’ or ‘Dislike’ to the question, 55.7% n= 967)(Figure 2). The most commonly stated reasons were fosas’ depredation of poultry, their perception as their enemy and fosas’ reputedly fierce nature. Conversely, of the 22.4% of respondents that liked fosas (responding ‘Like’ or ‘Strongly Like’, the principal reason was their status as a native species, with interviewees also liking fosas as they believed them to be an impressive animal. Other respondents reported mixed emotions because of their dislike of fosas’ poultry depredation but appreciation for their beneficial role in consuming pest species such as rats.

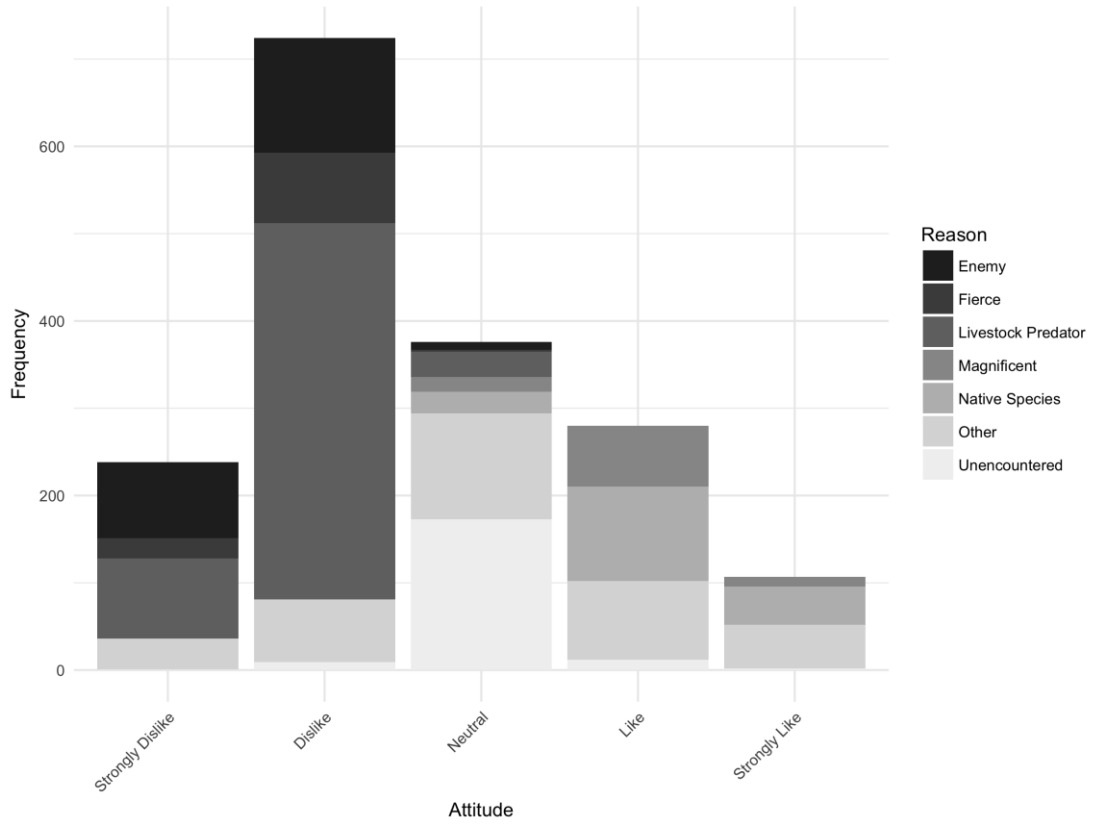

Figure 2. The interviewees’ attitudes towards fosas and their prescribed reason.

74.4% (n = 1203) of respondents believed fosas were of no personal benefit, mostly citing poultry depredation (44.8%)(Appendix S4). In contrast, the remaining respondents (n = 414) saw fosas as beneficial for their role as a rat predator (23.9%), source of tourism revenue (21.2%) and ecosystem component (16.5%). When asked if respondents were fearful for their poultry, the majority of respondents who kept poultry (52.6%, n = 713) weren't concerned about fosas. The most popular reason stated was the presence of geographical barriers surrounding their village (i.e. a river)(33%)(Appendix S4). Conversely, respondents who were concerned for their poultry most commonly cited fosas' persistence whilst hunting (28%). The majority (73%, n = 970) of respondents did not believe that fosa populations should be controlled, principally due to their beliefs that fosas are one of god's creations (33.3%), that control isn't a feasible solution (16.5%) or that fosas have a right to survive (12.6%). The remaining interviewees believed that fosa overpopulation increased poultry depredation (44.6%).

The models examining interviewee attitude towards fosas revealed the strongest associations with Education, Lifetime Predation, and Region (Appendix S5). Interviewees who have experienced fosa predation during their lifetime were significantly more likely to have a negative attitude (Appendix S5)(Figure 3). Likewise, interviewees' with lower levels of educational attainment were also more prone to exhibit negative attitudes (Figure 5). Interviewees from Moramanga and Vatovavy-Fitovinany were more likely to hold a negative view of fosas compared with those from Menabe (Appendix S5).

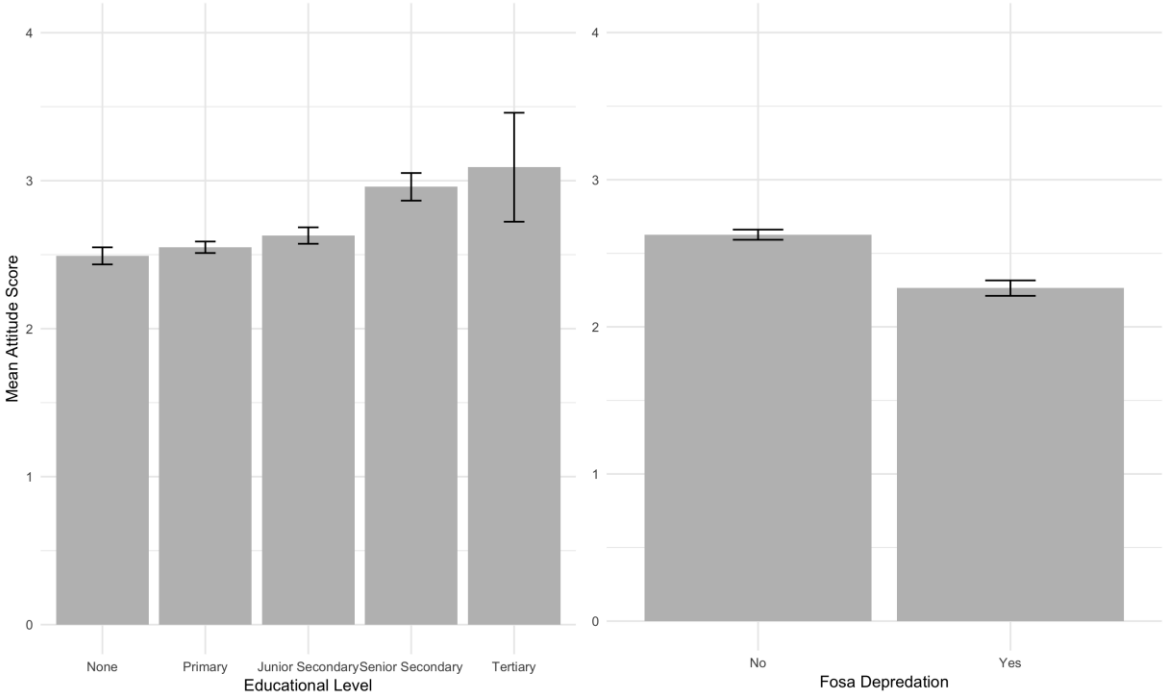

Figure 3. The significant predictors of interviewees' attitude towards fosas, including the standard error of the mean.

Retaliatory killing

Only 41 respondents (2.3%) claimed to have attempted to kill a fosa during their lifetime, with 32% (n=13) of these successful. A total of nine fosas were reportedly killed by an interviewee during the previous year (with nine more killed during their lifetime). The vast majority (85%) of these 18 total mortalities occurred in deciduous forests (Chi-sq $x^2 = 8$, df = 1, $p < 0.05$). 52.5% of respondents used snares, or batons and blowpipes (12.5% respectively) to attack fosas. 85% of interviewees claimed poultry depredation as the reason for attacking fosas. Approximately half of respondents either ate or discarded the fosa, with the remaining interviewees selling or giving away the carcass as a gift.

85 (4.86%) respondents knew of someone who had attacked a fosa during their lifetime, with 63.5% of these reported by the respondents to have killed a fosa.

21 fosas were purportedly killed in the previous year, with approximately 50 killed during their lifetime. Combining reported killed by interviewees and those known to have been killed locally, 30 were killed during the previous year. A further 25 fosas were known to have been killed during the five preceding years, with 34 killed during the remainder of their lifetime (Figure 4).

AMNP (Moramanga region) had the highest number of fosas killed during the last year (13 individuals) and last five years (14 individuals)(Figure 4). Ankarafantsika (Marovoay region) had the second highest number of individuals killed (8) during the last year. Across the regions, 4% of households killed fosas in Marovoay, 2% in Menabe, 4% in Moramanga, and 0% in Vatovavy-Fitovinany. No patterns were discernible between forests of different ecoregion or protection level.

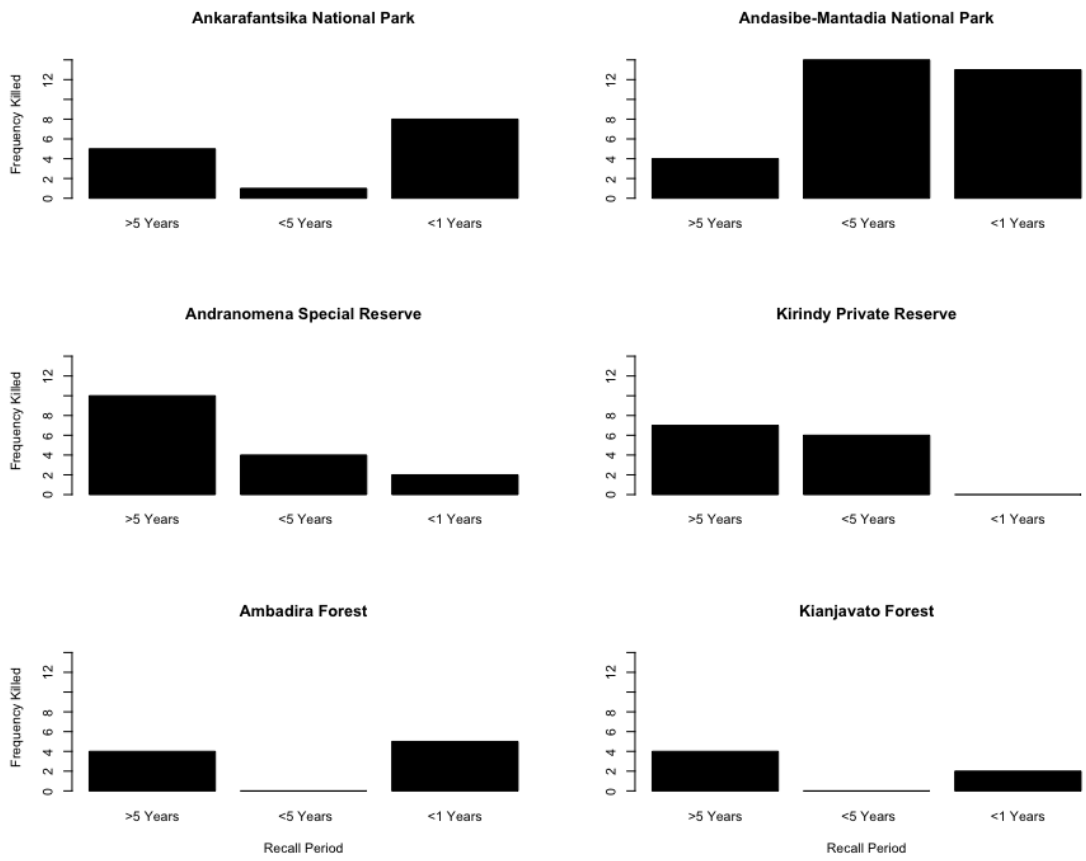

Figure 4. Interviewee recounts of the total fosas to have been killed during livestock predation events over the past year, five years and lifetime across the six forests (each row displays national parks, reserves and unprotected forests).

The final set of models investigated a household's potential for retaliatory killing of fosas. The highest weighted model contained attitude and region, with interviewees' more likely to retaliate when holding a negative attitude. The analysis was repeated, this time including Poverty and excluding ANP households. Model selection revealed similar results with Attitude and Region, including the new Poverty predictor to be contained in the most parsimonious model (Appendix S6).

The final model including the significant predictors (Attitude, Region and Poverty) revealed that interviewees' from Vatovavy-Fitovinany were less likely to

engage in retaliatory killing, whilst those that held negative attitudes towards fosas, and/or wealthier respondents were significantly more likely to engage in retaliatory killing (Appendix S6)(Figure 5). Odds ratios showed poorer interviewees' were 3.13 times less likely to kill a fosa (an increment of 1.0 on the 'Poverty' scale, i.e. the difference between the poorest and wealthiest individuals, had this effect on the response), and interviewees' who held favourable views towards fosas were 2.56 times less likely to have attempted killing them (an increment of one ordinal unit had on average this effect on the response, Figure 5).

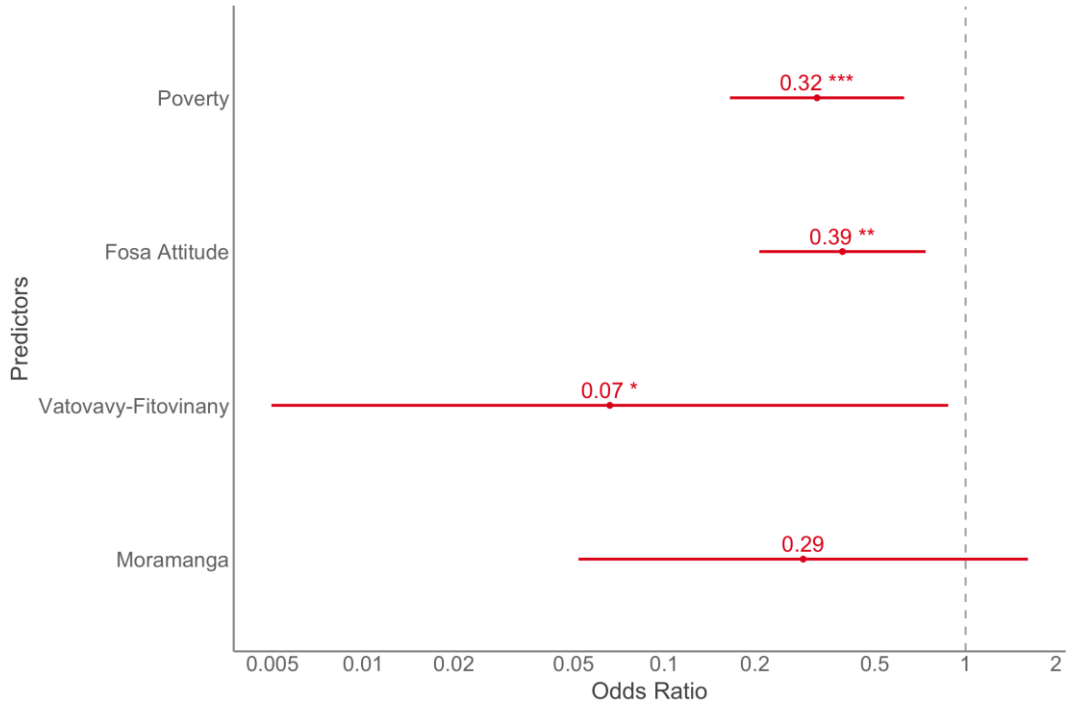

Figure 5. Forest plot of the three significant predictors of retaliatory killing, Attitude, Poverty and Region (reference level is Menabe) (with 95% confidence intervals). The level of significance is denoted by *** $p < 0.01$, ** $p < 0.05$ and *** $p < 0.10$.

Discussion

Fosa predation was perceived by the interviewees to be one of the greatest causes of poultry mortality. Its occurrence was principally concentrated in Madagascar's western forests, and most often recorded during the dry season in the evening. There was no evidence that poultry coops were effective in reducing fosa predation, likely owing to their poor construction. Most interviewees' disliked fosas, with poultry predation the most commonly stated reason. Fosas were commonly liked due to their endemicity, their impressiveness and their role as a rat predator. Interviewees that had suffered poultry depredation and those with less education were most likely to dislike fosas. Interviewees that disliked fosas and those that were wealthy were most likely to have killed a fosa. We estimated that a minimum of thirty fosas was killed in retaliation across our study regions during the year before interviews. Our results suggest that a strategy to reduce retaliatory killing should focus upon educating communities of fosas' importance, whilst promoting the construction of sustainably built, robust poultry coops, in align with the use of watchdogs.

Poultry depredation

Recent estimates from Ranomafana suggested that < 1% of households' poultry mortality was attributable to fosas (Kotschwar Logan et al. 2014), supporting historical reports of anecdotally infrequent attacks (Albignac 1973; Hawkins 1998). By contrast, approximately one in six interviewees' in our study reported fosa depredation. Together, these observations indicate that perceived predation by fosas is not rare, but that it is not the most economically damaging agent. Disease killed nearly 40% of interviewees' poultry, with Newcastle disease the likely virus. Newcastle disease has been previously reported as particularly virulent, and the

principal cause of rural poultry mortality in other areas of Madagascar (Maminiaina et al. 2007). Poultry mortality from birds of prey was the second most common cause, although its impact is less detrimental due to their predation of chicks (costing around 400 Ariary). Conversely fosas more commonly consume adult chickens, typically valued at around 12,000 Ar (3,600 Ar = 1 USD). Fosas' tendency to kill all chickens when it has entered a coop, a previously acknowledged predation characteristic, can result in a substantial cost to affected households (Albignac 1973; Merson personal observation). With some 70% of Malagasy households currently living below the poverty line (< 1 USD/day), the individual cost of fosas' predation upon respondents' livelihoods may be significant. In the absence effective coops, retaliatory killing of nuisance fosas is the likely response.

Fosas' predation of poultry was significantly more frequent in deciduous forested regions. This may be attributable to higher fosa densities in deciduous forests (Hawkins and Racey 2005; Gerber et al. 2010). Anecdotal reports also support these estimates: trapping studies yield far greater trapping success in deciduous regions (Luke Dollar unpublished, Merson personal observation). Higher fosa predation rates may also be due to lower prey availability in accord with greater hibernation of deciduous forest living species during dry seasons.

Throughout both forest types, poultry depredation was significantly more likely to occur during the dry season (May to November). This pattern aligns with the aestivation and torpor of many of Madagascar's mammals, a common adaptation to survive periods of low rainfall and reduced food availability during the austral winter (Schmid 2000; Dausmann et al. 2009; Kobbe and Dausmann 2009; Lyman 2013). Hawkins and Racey's (2008b) dietary analysis found seasonal differences in the relative frequency of prey species in the fosas' diet. The analysis however didn't refer

to differences in absolute numbers of prey species consumed between seasons. It might then be possible that higher winter poultry predation is a preferred strategy to combat reductions in species common during the summer months, such as tenrec (Lovegrove and Génin 2008). Furthermore, most respondents claimed fosa poultry predation occurred most frequently during the months of October – November. These months not only represent the end of the dry season, a period in which fosas would have felt the brunt of winter and its associated reductions in prey, but also coincide with fosas' mating season. A recent study of fosa sociobiology in western Madagascar estimated increases in male home range during the breeding season from 40 to 50 km^2 (Lührs 2012). These changes in male home range may increase the propensity for overlap between fosas and human settlements. This promotes a scenario whereby increased ranging behaviour, poor body condition and increased metabolic demands create a higher propensity for settlement interaction in search of prey.

Lastly, fosa predation of poultry was significantly more prevalent during the evening. Despite fosas' cathemeral activity patterns, peaking during the crepuscular hours (Dollar 1999; Gerber et al. 2012b), fosas are highly active during the evenings (Farris et al. 2015a). Recent research revealed fosas to occupy distinct temporal niches from humans and dogs (Gerber et al. 2012b; Farris et al. 2015a), a likely an example of temporal exclusion, with fosas avoiding larger animals and humans. It may then be expected, similar to other instances of carnivore livestock predation (Patterson et al. 2004), that fosas would choose to hunt poultry when human activity is presumably at its lowest during the evenings (when people are assumed to be mostly asleep).

Households that used snares and those living in Menabe were significantly more likely to experience fosa predation. The positive association with snare use is

likely explained by the proximate reason that households using snares have experienced higher historic levels of fosa predation and are therefore more likely to use snares in the future. Likewise, Menabe is a deciduous forest and contains Kirindy Reserve, one of the few forests in Madagascar with a highly habituated fosa population. Fosas in this sub-population may be less deterred by human presence, and more willing to venture into villages. In addition, this region has historically and is today experiencing severe rates of annual deforestation (Zinner et al. 2013), with many of the remaining forests too small to sustain long-term fosa populations (Hawkins and Racey 2005). Given fosas' large home ranges, individuals in this region may be more inclined to leave the forest, promoting interaction with nearby villages.

Attitudes

Fosa poultry predation was strongly linked to respondent attitudes, with twice as many interviewees who reported losses disliking fosas. The most commonly cited reason for disliking fosas was their predation of poultry, whilst peoples' perception of fosas as an enemy, and their similarity to dogs also stated. Alternatively, another possible reason for the interviewee's purported dislike for fosas could be the influence of the questionnaire's order. Interviewees were asked to state their attitude towards fosas after describing any historical killings of fosas. As discussed in Chapter 4, this could result in interviewees reporting their dislike for fosa as a result of negative emotions generated from previous questioning.

Despite seemingly pragmatic reasons for Malagasy dislike of fosas, underlying *fady* (taboos) may also have shaped modern perceptions. Fosas similarity to dogs was mentioned. Dogs are frequently disliked in this culture due to their perceptions as being dirty, and their occasional theft of food. Another underlying *fady* regularly cited

was their dislike of fosas as a result of their consumption of their ancestor's remains. Given some burial sites (for example tombs within mountainside caves) could be easily accessed by foraging fosas, the claim may have some validity and has been reported elsewhere (Ruud, 1960; Jones et al. 2008). Anecdotes have also been retold across regions from Menabe to Andasibe, with stories occasionally heard of fosas having eaten missing people, packs of fosas attacking and consuming zebu, and fosa attacks upon lone individuals – often resulting in death. The validity of these stories is unknown, however, given our understanding of fosas' behaviour they are unlikely to be true. These stories do however reinforce a fundamentally negative perception of fosas. Our observation that attitudes were related to education suggests this is at least partly reversible, perhaps by educational programs.

Fosas were commonly liked as a predator of rats, and as a native species and interestingly appreciated for their aesthetic appeal. Educational programs highlighting fosas' benefit as a rat predator were initiated by co-author L. Dollar in ANP wherein almost half of the total respondents that cited this reason were located. Such educational programs show potential to change attitudes and ultimately reduce retaliatory killing.

Interviewees' who had experienced fosa predation, and those with lower education were more likely to negatively perceive fosas. This could be expected as students progressing through higher education are more likely to be exposed to the concepts of conservation and its benefits. This conservation awareness therefore influences interviewees' attitudes, so that fosas are not purely perceived as a livelihood damaging species, but also as a key component of Madagascar's ecosystem. Interestingly, interviewees' from Moramanga were most likely to negatively perceive fosas. This region encompassed AMNP, Madagascar's most

visited national park. Despite its monetary benefits (employment, tourist revenue, park fees), many of the households interviewed were within the poorest villages. These villagers are still reliant upon traditional livelihoods and are typically not receiving the benefits associated with the park. It is also probably relevant that this region also recorded the greatest number of fosas killed during the previous year, and five years. This highlights the relationship between attitude and retaliatory killing.

Retaliatory killing

A total of nine fosas were reportedly killed across the four regions during the previous year, with this estimate increasing to thirty including third-party accounts. It is clear that this should be interpreted as a minimum given the question's sensitivity and the interviewee's probable reluctance to answer questions truthfully for fear of persecution. Interpreting the impact of these mortalities is difficult, with current island-wide population estimates likely to be inaccurate, and varying between 2,635 – 8,626 adults (Gerber et al. 2012a). However, when considering the current population, it must be acknowledged that most of these sub-populations now persist in extremely fragmented forests that are almost certainly too small for sustainable populations (Hawkins and Racey 2005). Hence it is expected that the fosa population is decreasing (Hawkins 2016). For some of these isolated populations, these additional mortalities to human persecution can only accelerate the decline. It's therefore foreseeable that these annual rates of mortality are unsustainable, particularly within smaller forests where negative anthropogenic influence and sub-population decline is at its greatest.

In absolute numbers AMNP and ANP, the two largest forests and national parks, had the highest number of fosas killed during the previous year (including total recorded). Despite offering the highest legal protection and greatest tourist visitors,

these forest's protected status did not apparently reduce retaliatory killing compared to forests of less protection. It would also be assumed that underreporting in these regions would be at its highest, as increased forest protection, NGO, and tourism presence, would likely result in greater sensitivity to report illegal or socially undesirable behaviours (Razafimanahaka et al. 2012).

These results were congruent with our model, with the Vatovavy-Fitovinany region the only significant region-level predictor of retaliatory killing. This region contained the smallest forests, with households significantly less likely to have reportedly killed a fosa. This may suggest that larger forests, with large fosa populations such as ANP and AMNP offer greater conflict potential.

Respondents' with negative attitudes towards fosas were most likely to kill them for poultry predation. This result seems intuitive but must be considered in the context of sociological theories discussed in Chapter 4, in that, general attitudes alone aren't always a determinant of a predicted behaviour (St John *et al*. 2010). Also, contrary to our expectation, wealthier households were most likely to have killed fosas. It was thought that poorer households with lower food security would be less tolerant of fosa predation and most likely to retaliate. We speculate that perhaps these households may have political or social power in association with greater wealth, and feel at greater liberty to kill fosas than poorer households with presumed less social/political power. Future research into community political and social structure may reveal the truth of such speculation.

When asked what interviewees' did with a killed fosas' remains, approximately half of respondents said they consumed the animal. Despite previous studies indicating the existence of *fady* forbidding consumption in different regions (Ruud, 1960; Gardner and Jones, 2014; Jones et al. 2008), this result further supports

the consumption of fosa across Madagascar (García and Goodman 2003; Golden 2009; Farris et al. 2015b; Reuter et al. 2016). This trend likely a reflect's growing poverty and food insecurity across Madagascar.

Fosas were principally killed in retaliation for their consumption of poultry. This stems from a widespread and rational human's inclination to protect livelihoods. It is also likely to be exacerbated by the unclear and conflicting legislation defining fosa protection (Rakotoarivelo *et al*. 2011). Despite protection under national law, this legislation is confounded by separate legislation allowing the killing of nuisance species that damage an individual's property (Category 1, Class 2 Protected Species). Under this interpretation of the law most villagers feel justified in killing fosas. Such conflicting legislation is unhelpful and damaging to efforts to not only protect fosas, but to also establish a common culture to conserve Madagascar's native species.

Conclusion

Our results suggest that efforts to promote knowledge of the fosa could encourage tolerance, even in the presence of some livelihood impact. Fosa predation was reported by a minority of poultry keepers, where it was likely not as economically important compared with the major poultry source of mortality, disease. In reducing retaliatory killing, educational material has the potential to promote positive attitudes based on fosas' status as an iconic endemic species, tourist attraction and predator of other pests, including rats. Furthermore, the design and creation of robust poultry coops, in align with the use of watchdogs, an observed spatio-temporal deterrent of fosas (Gerber et al. 2012a; Gerber et al. 2012b; Farris et al. 2015a; Farris et al. 2015b) could reduce retaliatory killing. Co-author L. Dollar is currently developing such coops, and their efficacy will soon be measured in the field. Given the island-wide

intrusion of humans into forested habitat, retaliatory killing reduction strategies must be trialed and deployed to ensure the persistence of one of Madagascar's most important species.

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Appendices

Appendix Figure S1.

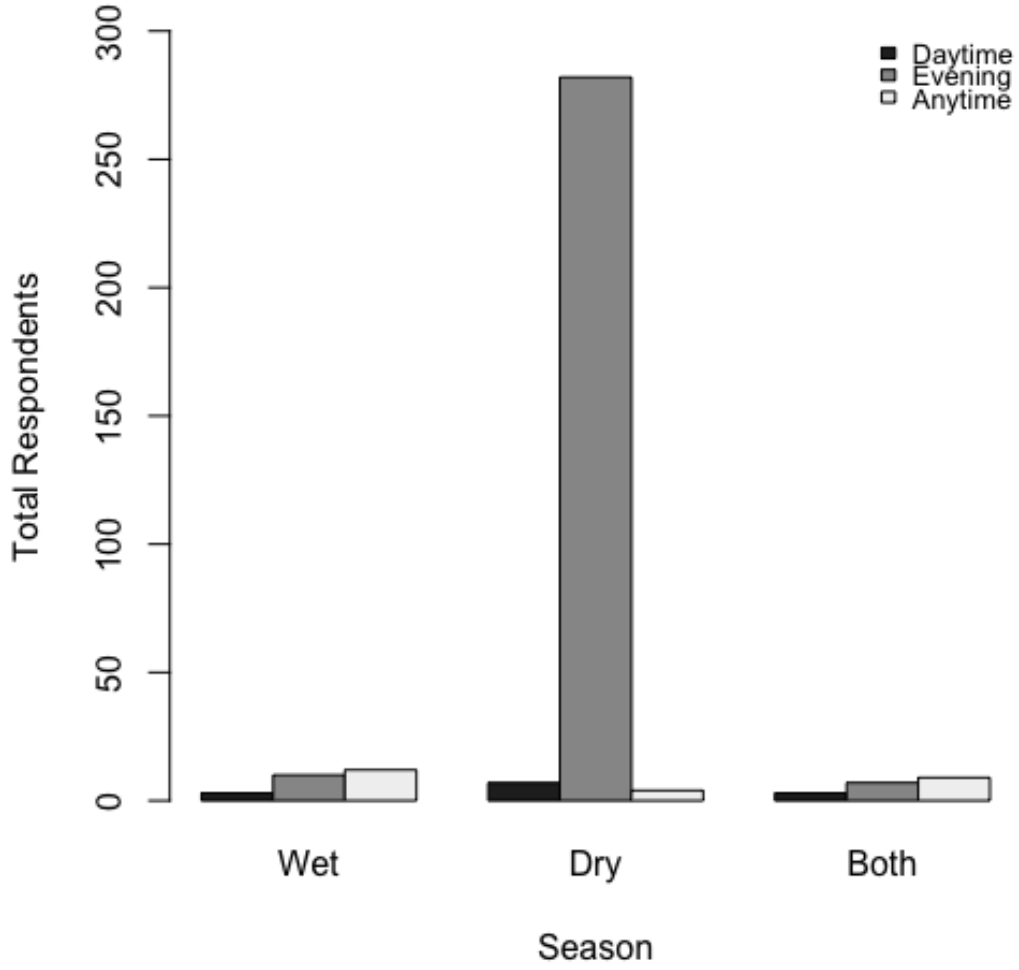

Figure S1. Poultry predation season versus diel period. (Chi-squared test of independence, $X^2 = 138.12$, df = 4, $p < 0.001$).

Appendix Table S1: Description of the response variables and predictors used within each of the three sets of GLMMs. The model variables included: Dependent Variable 1/2/3 (DV1, DV2, DV3); independent variable model 1/2/3 (IV1, IV2, IV3); Fixed Blocking Factor model 1/2/3 (BF1, BF2, BF3), and random effect model 1/2/3 (RE1, RE2, RE3).

Variable	Description	Levels	Model
Last Year Predation	Fosa predation of poultry previous year	Yes/No	DV1
Fosa Attitude	Interviewee's attitude towards fosa	Strongly Dislike, Dislike, Neutral, Like, Strongly Like	DV2, IV3
Retaliation	Retaliatory killing of fosa during interviewee's lifetime	Yes/No	DV3
Village	The village where the household is located	Categorical Village Name	RE1, RE2, RE3
Region	The geographical area the household is located	Marovoay, Menabe, Moramanga, Vatovavy-Fitovinany,	BF1, BF2, BF3
Forest Size	Size of the nearest primary forest (km^2)	1 - ∞	IV1
Village Size	Total number of households within the household's village	1 - ∞	IV1
River Barrier	Presence of river between village and nearest forest	Yes/No	IV1
Household Distance	Household distance to forest edge (m)	1 - ∞	IV1
Flock Size	Total number of poultry owned by interviewee	1 - ∞	IV1
Flock Coop	Coop used to protect poultry	Yes/No	IV1
Snare	Snare used surrounding coop	Yes/No	IV1
Poverty	Household wealth metric	0 - 1	IV2, IV3
Education	Interviewee's highest level of education	None, Primary, Junior secondary, Senior secondary, Tertiary	IV2
Poultry Owned	Poultry owned by household	1 - ∞	IV2
Lifetime Predation	Fosa predation of poultry life time	Yes/No	IV2
Conservation Experience	Has the interviewee been educated on the benefits of localised conservation	Yes/No	IV2, IV3
Conservation Attitude	Interviewee's attitude towards conservation	Strongly Dislike, Dislike, Neutral, Like, Strongly Like	IV2, IV3
Conservation Benefit	Does the interviewee receive any personal benefit from conservation	Yes/No	IV3

Appendix Table S2. A) The total number of households that own poultry in deciduous and rainforests to have experienced fosa depredation (percentage of households in brackets) (Chi-squared test of independence, $X^2 = 121.67$, df = 1, $p < 0.01$). B) The total number of households that own poultry to have experienced fosa depredation that house their poultry in a coop and not in a coop (percentage of households in brackets) (Chi-sq $X^2 = 0.69786$, df = 1, p = 0.4035).

A)

	Predation	**No Predation**
Deciduous	297 (42.1%)	408 (57.9%)
Rainforest	50 (11.3%)	394 (88.7%)

B)

	Predation	**No Predation**
Coop	299 (32.5%)	620 (67.5%)
No Coop	48 (36.6%)	83 (63.4%)

Appendix Table S3. a) Model selection output for the highest weighed models of the predictors of a households' likelihood to sustain fosa poultry predation. Degrees of freedom (df), log likelihood (logLik), Akaike's Information Criterion (AIC_c), relative change in Akaike's Information Criterion from top model (ΔAICc), and Akaike's Information Criterion weight (AIC_cwt). b) The modelled output for the most parsimonious predictors, Snare and Region. P-value (Pr (>|z|)) at significance level ($p < 0.001$***, $p < 0.01$ **, $p < 0.05$ *).

a)

Model	Df	logLik	AICc	Δ AICc	AIC_cwt
Region + Snare + Forest Size	7	-519.38	1052.85	0	0.15
Region + Snare + Village Size	7	-519.75	1053.6	0.75	0.11
Region + Snare	6	-520.96	1053.99	1.14	0.09
Region + River + Snare	7	-519.95	1054	1.15	0.09
Region + Forest Size + Village Size	7	-520.24	1054.58	1.73	0.06
Region + Forest Size	6	-521.54	1055.16	2.31	0.05
Region + Village Size	6	-521.61	1055.29	2.44	0.05

b)

Variables	Estimate	Std. Error	z value	Pr (>|z|)
(Intercept)	-1.3786	0.3172	-4.347	1.38e-05 ***
Menabe Region	0.4549	0.4535	1.003	0.3158
Moramanga Region	-1.2513	0.4762	-2.628	0.0086 **
Vatovavy-Fitovinany Region	-1.958	0.6621	-2.958	0.0031 **
Snare (Yes)	0.8333	0.3993	2.087	0.0369 *

Appendix Table S4. Interviewees' stated response and reason to various attitudinal questions.

Question	Yes: Reason	Total Respondents	%	No: Reason	Total Respondents	%
Do fosa provide any benefit?	Rat predator	100	23.9	Poultry Predator	540	44.85
	Tourists & Revenue	88	21.2	No Benefit	369	30.65
	Ecosystem Component	70	15	Don't know	128	10.6
	Prevents human forest entry	46	11	Other	167	13.9
	Other	121	28.9			
Are you scared of fosa for your poultry?	Fosa are persistent	210	28	Village geographically protected	212	33.1
	Fosa are carnivorous	144	19.2	Don't own poultry	178	27.7
	Fosa scare poultry	80	10.7	Own dog	61	9.5
	Chickens are easily killed	67	8.9	Coop is secure	57	8.9
	Other	249	33.2	Other	133	20.8
Should fosas' population be controlled?	Overpopulation means greater depredation	169	46.6	God's creation	309	31.3
	Fosa kill poultry	69	19	Control isn't feasible	163	16.5
	Other	125	34.4	Fosa should be allowed to survive	124	12.6
				Other	390	39.6

Appendix Table S5: a) Model selection output for the highest weighed models containing the predictors of a households' attitude towards fosas. Degrees of freedom (df), log likelihood (logLik), Akaike's Information Criterion (AIC_c), relative change in Akaike's Information Criterion from top model (ΔAICc), and Akaike's Information Criterion weight (AIC_cwt). b) The modelled output for the most parsimonious predictors, Education, Lifetime Predation and Region. P-value (Pr (>|z|)) at significance level ($p < 0.001$***, $p < 0.01$ **, $p < 0.05$ *).

a)

Model	**Df**	**logLik**	**AICc**	ΔAICc	AIC_cwt
Conservation Benefit + Education + Lifetime Predation + Region	10	-1346.39	2713.01	0	0.18
Conservation Benefit + Education + Lifetime Predation + Poultry Owned + Region	11	-1345.82	2713.91	0.9	0.12
Education + Lifetime Predation + Region	9	-1347.93	2714.04	1.03	0.11
Conservation Benefit + Education + Conservation Experience + Lifetime Predation + Region	11	-1346.23	2714.73	1.72	0.08
Education + Lifetime Predation + Poultry Owned + Region	10	-1347.27	2714.77	1.76	0.08
Conservation Benefit + Education + Lifetime Predation + Region + Poverty	11	-1346.29	2714.85	1.84	0.07
Conservation Benefit + Conservation Attitude + Education + Lifetime Predation + Region	11	-1346.38	2715.03	2.01	0.07
Education + Conservation Experience + Lifetime Predation + Region	10	-1347.67	2715.57	2.55	0.05
Education + Lifetime Predation + Region + Poverty	10	-1347.83	2715.88	2.87	0.04
Conservation Attitude + Education + Lifetime Predation + Region	10	-1347.9	2716.02	3.01	0.04
Education + Conservation Experience + Lifetime Predation + Poultry Owned + Region	11	-1346.95	2716.18	3.16	0.04
Education + Lifetime Predation + Poultry Owned + Region + Poverty	11	-1347.12	2716.51	3.5	0.03
Conservation Attitude + Education + Lifetime Predation + Poultry Owned + Region	11	-1347.26	2716.78	3.77	0.03
Education + Conservation Experience + Lifetime Predation + Region + Poverty	11	-1347.57	2717.41	4.4	0.02
Conservation Attitude + Education + Conservation Experience + Lifetime Predation + Region	11	-1347.64	2717.54	4.53	0.02
Conservation Attitude + Education + Lifetime Predation + Region + Poverty	11	-1347.77	2717.8	4.79	0.02

b)

Variables	Estimate	Std. Error	z value	Pr(>|z|)
Lifetime Predation	-0.90432	0.15114	-5.983	p < 0.001 ***
Moramanga Region	-0.92748	0.17582	-5.275	p < 0.001 ***
Vatovavy-Fitovinany Region	-0.38755	0.18304	-2.117	0.034237 *
Education	0.25712	0.07191	3.576	0.000349 ***

Appendix Table S6: a) Model selection output for the highest weighed models containing the predictors of a households' retaliatory killing of a fosa. Degrees of freedom (df), log likelihood (logLik), Akaike's Information Criterion (AIC_c), relative change in Akaike's Information Criterion from top model (ΔAICc), and Akaike's Information Criterion weight (AIC_cwt). b) The modelled output for the most parsimonious predictors, Fosa Attitude, Poverty and Region. P-value (Pr (>|z|)) at significance level ($p < 0.001$***, $p < 0.01$ **, $p < 0.05$ *).

a)

Model	df	logLik	AICc	Δ	Weight
Fosa Attitude + Region + Poverty	6	-85.02	182.12	0	0.43
Fosa Attitude + Conservation Benefit + Region + Poverty	7	-84.69	183.48	1.36	0.22
Fosa Attitude + Conservation Education + Region + Poverty	7	-84.93	183.96	1.84	0.17
Fosa Attitude + Conservation Attitude + Region + Poverty	7	-84.98	184.05	1.93	0.16
Region + Poverty	5	-90.28	190.61	8.49	0.01

b)

Variables	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-1.9295	0.8198	-2.354	0.018593 *
Moramanga Region	-1.2416	0.8765	-1.417	0.156593
Vatovavy-Fitovinany Region	-2.7201	1.3198	-2.061	0.039299 *
Fosa Attitude	-0.9413	0.3244	-2.902	0.003706 **
Poverty	-1.1361	0.3397	-3.345	0.000824 ***

Chapter Six

Thesis Discussion

Threatened fosas, threatened Madagascar

Do the threats facing fosas represent those common to Madagascar's fauna? In principle yes, many of the fosas' threats presented in this thesis are intrinsically intertwined with those facing its ecosystem. Madagascar, as with much of the third and developing world, is realising the loss of its flora and fauna largely as a result of institutional[1] and organisational failure (Didia 1997; Barrett et al. 2001; Smith et al. 2003; Adams et al. 2004; Acheson 2006). However, this does not disqualify the importance of understanding threats specific to individual species. In investigating fosas' most pertinent conservation threats, this thesis has examined the impact of deforestation and habitat degradation (Chapter Two), exotic species (Chapter Two and Three), bushmeat consumption (Chapter Four) and retaliatory killing (Chapter Five).

Deforestation and habitat degradation

Madagascar's forests have been radically reduced from its former levels (Harper et al. 2007; Mayaux et al. 2013; Vieilledent et al. 2017), with high rates of annual deforestation threatening much of its remaining area (Allnutt et al. 2013; Grinand et al. 2013; Zinner et al. 2013). As a result, very little primary forest remains, with edge effects a pervasive problem for its flora and fauna (Lehtinen et al. 2003; Lehman et al. 2006; Harper et al. 2007; Vieilledent et al. 2017).

Against predictions, Chapter Two did not uncover a negative association between habitat degradation and fosa occupancy. Two of the occupancy model's most important predictors (forest cover and total core area) were habitat degradation

[1] Institutions in this context are being defined by North North, D.C., 1990. Institutions, institutional change and economic performance. Cambridge university press. *"as any constraint humans devise to shape their interactions."*

metrics, however neither displayed a clear trend with fosa occupancy. Similar results were recorded in contiguous rainforests on Madagascar's eastern coasts with no significant habitat predictors of fosa occupancy (Gerber et al. 2012b; Farris et al. 2015b). Our results, in agreement with previous research, suggest fosas are capable of traversing degraded and non-forested habitat (Hawkins 1998; Irwin and Raharison 2009). Evidently, fosas do appear more resilient than some of their Euplerid relatives in persisting in anthropogenically disturbed contiguous forests (Gerber et al. 2012b; Farris et al. 2015b; Farris et al. 2016). This facet of fosa behaviour likely confounded the occupancy results presented in Chapter Two, and in previous studies (Gerber et al. 2012b; Farris et al. 2015b), making the examination of fine-scale habitat degradation difficult in contiguously forested landscapes.

Despite fosas relative 'resilience' to small-scale forest degradation, previous forest fragment and village surveys have shown fosas are unlikely to persist far from continuous forest (Gerber et al. 2012b; Kotschwar Logan et al. 2014). It is therefore likely, that fosas' long-term landscape distribution is limited by a forest's size, with fosas' large spatial requirements typically confining them to larger forests. In contrast several smaller Euplerids (requiring less space) are capable of persisting in smaller fragments (Gerber et al. 2012b). In this regard, fosas' large spatial requirements (Lührs 2012b) hinder their island-wide persistence, insomuch that large portions of Madagascar's fragmented forests are likely of insufficient size to support viable long-term populations (Hawkins and Racey 2005).

Exotic species

Islands comprise some of the most ecologically damaged ecosystems, and are particularly vulnerable to invasive species (Vitousek et al. 1997). However, the

impact of invasive species upon Madagascar's endemics has until recently received less attention than other islands worldwide (Kull et al. 2014).

Chapters Two and Three highlighted the threat of invasive carnivores. Cats and dogs, arguably two of the world's most successful invasive mammalian predators (Vanak and Gompper 2009; Medina et al. 2011; Hughes and Macdonald 2013) pose a direct threat to fosas and Madagascar's fauna. In Chapter Two a strong negative association was reported between feral cat trap success and fosa occupancy. This pattern was posited as a potential result of fosas and cats high temporal overlap in activity (Chapter Three), underpinned by exploitation competition in the consumption of similar species (Brockman et al. 2008), and/or interference competition between adult cats and juvenile/sub-adult fosas.

Evidence was also presented as to the competitive threat posed by dogs. This was reported in Chapter Three whereby fosas exhibited greater nocturnality in ANP than ASR in association with higher dog (and human) presence. Fosas' higher nocturnal activity in association with dog presence, contrasts with greater cathemeral activity in a dog and mostly human absent portion of ANP (Rahajanirina 2003). These patterns of fosa behavioural change in response to dog presence have also been observed at two different rainforest sites (Gerber et al. 2012c; Farris et al. 2015a). Given dog's larger size, sociality and high spatial-temporal overlap with humans (Chapter Two and Three) dogs present considerable threats in both the exhaustion of shared ground-dwelling prey species, and the exclusion of fosas from shared habitat.

Chapter Two presented the direct and indirect transmission of disease between exotic and endemic species as a potential 'silent killer'. Recent research unveiled the widespread prevalence of *Toxoplasmosis gondii* in wild fosas (Pomerantz et al. 2016) and is of considerable concern given its history of fatal transmission in captive lemurs

and fosas (Spencer et al. 2004; Juan-Sallés et al. 2011; Corpa et al. 2013; Siskos et al. 2015). It may then be postulated that cats and dogs' high landscape occupancy (Chapter Two) is of greater impact than their pure competition for resources, with disease transmission a potentially significant threat to fosas' long-term health.

In this thesis, feral cats, dogs and civets have been considered as competitors to fosas, but their broader impact upon Madagascar's fauna is equally, if not more damaging. Their negative relationship with Madagascar's Euplerids has been documented in rainforests (Gerber et al. 2012b; Farris et al. 2015a; Farris et al. 2015b; Farris et al. 2015c; Farris et al. 2016). Feral cats' negative association with birds, likely underpinned by predation, was recorded in Chapter Two and previously observed in Masoala-Makira (Farris et al. 2015b). This negative association is unsurprising, with exotic species prominent role in the extinction risk of birds, most prominently on island dwelling species well documented (Clavero et al. 2009). Not only are Madagascar's small, most vulnerable species susceptible to predation, but cats, dogs and civets' have also been recorded to prey upon the island's larger vertebrates. This has been highlighted in their consumption of adult and infant lemurs (Sauther 1989; Goodman et al. 1993; Gould 1996; Brockman et al. 2008). Furthermore, Irwin et al.'s (2010) literature review of patterns of species change to anthropogenic disturbance, revealed surprisingly little empirical research documenting the impact of exotic species. In considering our results, and the acknowledged paucity of exotic species research, future empirical insight into their impact, and strategies for their removal are required.

Bushmeat consumption

Chapter Four examined the drivers, variance and impact of bushmeat consumption on Madagascar's wild species, including fish and eel that are both caught wild and aquaculture reared. Domestic animals were the most highly preferred meat whilst, whilst fish and eel were preferred over bushpig and tenrec, the other most highly preferred wild (and legally huntable) species. Malagasy species protection laws offer legal protection (Rakotoarivelo et al. 2011), with species classified as: strictly protected species (Category 1 Class 1); protected species with hunting permitted under authorisation (Category 1 Class 2); pest species allowing unrestricted hunting (Category 2); and game species which are permissibly hunted under licence (Category 3). Most Category 1 Class 1 protected and endangered species, such as lemurs and Euplerids were the least favoured meat. Consumption of wild species was principally driven by wealth, with poorer households more likely to consume greater quantities of protected species, whilst wealthier households were more likely to consume fish and eel. These collective results suggest that there is little desire to consume most wild species, with poorer households unable to afford domestic or highly preferred game (tenrecs) and unprotected species (fish, eel, bushpig). The lack of preference for wild species has been reported previously (Randrianandrianina et al. 2010; Jenkins et al. 2011) with poverty considered a major driver of protected species consumption (Jenkins et al. 2011; Borgerson et al. 2016; Reuter et al. 2016).

In considering our results within Madagascar's socio-economic and political context, much of its most vulnerable fauna is facing an extremely threatened future. The country's rapidly growing population, one of the highest in Africa, is also one of the poorest. Food security is of significant concern, with Madagascar exhibiting the fourth highest rates chronic malnutrition, with half of its children suffering from

malnutrition or stunting (World Food Program 2016). In fact, the plight of many Malagasy livelihoods was highlighted last year with predicted famine in Southern Madagascar threatening nearly 850,000 people (FAO 2016). Many of these, Madagascar's poorest and most marginalized demographic, are their rural subsistence farmers (IFAD 2016), those often living within and surrounding Madagascar's forests. Without short-term intervention and the long-term improvement of livelihoods, the unsustainable consumption of protected and endangered species will continue to the detriment of Malagasy and their national biodiversity.

Retaliatory killing

Retaliatory killing of large carnivores has played a prominent role in their global decline. *C. ferox*'s extinct relative *Cryptoprocta spelea* was of more comparable size to today's extant large carnivores, however *C. spelea* and Madagascar's other megafauna are now extinct (Goodman et al. 2004). Fosas now fulfill their niche as Madagascar's apex predator, and the most susceptible endemic carnivore to retaliatory killing. Few other Malagasy carnivores are at risk with most Euplerids, small, insectivorous, and/or strongly avoid human settlements. However, *Galidia elegans* (Albignac 1973; Kotschwar Logan et al. 2014), *Galidictis fasciata* (Borgerson 2015), feral cats and civets (Kotschwar Logan et al. 2014) have been reportedly killed for poultry predation. Their threat as Madagascar's greatest livestock predator is limited due to their geographical confinement to regional forests. Conversely, fosas' island-wide forest distribution (Hawkins 2016) makes them particularly susceptible to widespread persecution and mortality across Madagascar.

Chapter Five provided the most comprehensive, empirical insight into fosas' predation of poultry. It was reported as the third largest cause of interviewees' annual

poultry mortality, significantly higher than previous estimations (Kotschwar Logan et al. 2014). Poultry predation was significantly more common in western deciduous forests, during the dry season and in the evening. Furthermore, chicken coops (in their current form) were found to be ineffective in reducing fosa poultry predation. The majority of respondents disliked fosas, with predation of poultry the most quoted reason. GLMMs revealed interviewees' that had experienced fosa predation and those with less education were more prone to dislike fosas. Furthermore, retaliatory killing of fosas was significantly more likely by households' that disliked fosas and those that were wealthy. As a result, thirty fosas were purportedly killed in retaliation across our survey regions during the previous year.

A total of 38 fosas (this includes 8 fosas consumed as bushmeat in Chapter Four) were reportedly killed last year. The vast majority of fosas, and other carnivores killed and consumed is typically opportunistic, and a result of their killing for poultry predation. This has been confirmed in other sociological surveys documenting the consumption of civets, feral cats, *G. elegans*, and *G. fasciata* (Kotschwar Logan et al. 2014; Borgerson 2015; Reuter et al. 2016). The literature empirically enumerating fosas killed widely varies in its estimates, likely underpinned by variations in survey method and region. Perhaps the first evidence was García and Goodman (2003), who noted the consumption of two fosas in a transient raffia worker's camp. In Masoala-Makira where sociological and carnivora research is rich, 31 fosas were purportedly consumed in the previous year (Farris et al. 2015b), with previous research estimating it to be occurring unsustainably in that region (Golden 2009). Conversely Reuter et al. (2016) reported annual household consumption rates of < 1%, with this low estimate undoubtedly reflective of their surveying of few communities living alongside forest. Lastly, Kotschwar Logan et al. (2014) reported only 0.6% of interviewees to have

experienced fosa poultry in the previous year, but 32.3% of interviewees claimed to have hunted fosas during the previous five years. These reports give credence to the widespread killing of fosas across Madagascar, undoubtedly of significant detriment to the population's long-term viability.

Research limitations

In summarising the results of this thesis, there are several limitations that must be considered when reflecting upon their interpretation and applicability. Considering the financial and time constraints of a fieldwork focused PhD, several methodological approaches were employed to best mitigate these constraints. These methodological limitations, and their potential influence upon the interpretation of this thesis' results will be discussed in this section.

In Chapter Two the methodological limitations of our camera-trap grid design were discussed. Firstly, the spacing of cameras within the grid was posited to have implications for the accuracy and applicability of fosa occupancy estimates. Due to the lack of available trails across our two study sites, we were required to establish grids with stations spaced approximately 500 m apart, over 40 km^2. Given the home range of female and male fosas is relatively large (20 – 40 km^2), these camera-trap grids are likely of insufficient size to encapsulate many individual home ranges. Furthermore, the relatively small distance between stations means that individual fosas could theoretically traverse several stations in one day, potentially over-estimating fosa occupancy, and risking spatial-autocorrelation (Mackenzie 2006; O'Connell et al. 2010). These facets of our camera-trap design, and the potential for over-estimation of our site occupancy were considered when interpreting our results.

A second limitation of our camera-trap design was the use of single-season occupancy models. Single season occupancy models provide only a snapshot of the driver's of an individual's predicted occupancy at a single point in time, and do not consider long-term processes. Consequently, multi-year surveys are more robust in examining long-term processes, increasing our ability to understand the true impacts of habitat degradation and exotic species on Madagascar's native carnivores.

Chapter's Four and Five focused upon the data derived from household interviews examining certain illegal and/or sensitive topics. Consequently, our direct questioning of an individual household's participation in these activities (i.e. consuming protected species, or killing a fosa in retaliation for poultry depredation) is likely affected by non-response and social desirability biases (Fisher 1993; Groves and Peytcheva 2008; John et al. 2010; Nuno and John 2015). In Madagascar Razafimanahaka *et al*. (2012) illustrated the potential impact of direct questioning on the underreporting of bushmeat consumption in areas of greater conservation enforcement and awareness (i.e. protected areas) versus areas of less sensitivity. The potential limitation of the direct questioning technique is a particular concern in our study, where the identity of the household is required to model its characteristics in examining the variance of bushmeat consumption across protected and unprotected areas. Consequently, the risk of superficially lower levels of reported bushmeat consumption in protected versus unprotected areas could potentially obscure any true underlying pattern in consumption. As a result of this inherent methodological limitation, certain techniques (i.e. anonymity, questionnaire structure, local guide) were implemented to improve interviewee responsiveness. Despite this potential limitation, Andasibe-Mantadia National Park, arguably the region in which the sensitive questions would be most sensitive and subject to non-response, reported the

highest rates of illegal behaviours (bushmeat consumption). This doesn't discount the potential effects of direct questioning, however it at least provides some consolidation in our interview process and the validity of our results.

The final major limitation of our study was the selection of our study regions. These regions were selected to allow the simultaneous implementation of several of simultaneous studies. However, this strategy is admittedly, a limitation, as if unbound by these time and fiscal constraints, alternative and additional study sites could have been chosen to represent a greater sample of Madagascar's protected area system.

Threat mitigation, what must be done?

In mitigating the risk of fosa extinction, a multi-faceted strategy must be implemented. This strategy should address the core results of this thesis and seek to: reduce poultry predation; improve Malagasy attitudes towards fosas; improve Malagasy husbandry and agricultural practices; and reduce exotic species abundance.

Reducing retaliatory killing

The construction of robust poultry coops, the use of watchdogs and the improvement of Malagasy attitudes towards fosas are complimentary strategies to reduce retaliatory killing. The construction of fortified enclosures to reduce carnivore livestock predation is well documented (Treves and Karanth 2003). Its success usually varies depending on a variety of factors, including: the carnivore species' behavior; livestock breed; enclosure building and maintenance costs; herd-size; husbandry practices; and the surrounding landscape (Ogada et al. 2003; Distefano 2005; Inskip and Zimmermann 2009). Given the immense spectrum of carnivore-conflict geographically, there is typically no universal method of best practice. Successful

approaches should consider multi-faceted strategies, firmly entrenched in empirical local knowledge and in complicit partnership with focal communities.

In considering poultry predation in Madagascar, current coops are structurally ineffectual in reducing predation. Furthermore, despite interviewees reporting the housing of poultry in the evenings, husbandry techniques in reality are more likely unregulated, with poultry typically seen roaming villages freely. Previous attempts to build poultry coops have been attempted by Durrell Wildlife Conservation Trust, with little success due to the high cost of building coops for individual households. Communities were also unwilling to house poultry within communal coops for fear of theft and mismanagement. However, at present, supervisor L. Dollar is attempting the construction of cost-effective, structurally robust coops for households. Ensuring these coops are sustainably constructed, cost-effective and involve individual household buy-ins will be key for their success.

The adoption of watchdogs is another strategy that has been successfully implemented to deter livestock predators globally (Inskip and Zimmermann 2009; Rigg et al. 2011). Our results, and previous research (Gerber et al. 2012a; Farris et al. 2015c) has shown dogs' ability to spatio-temporally deter fosas. It might then be inferred that a community's dogs, tethered in the evening near poultry coops or nearby households closest to the forest edge could be a successful deterrence technique. Furthermore, ensuring dogs are tethered and not freely roaming through the forest in the evenings would have the added benefit of reducing their nighttime predation of endemic fauna.

A key driver of the retaliatory killing of fosas was negative human attitudes. L. Dollar has previously initiated education programs informing communities of fosas' benefits through their consumption of rats, an agricultural pest and transmitter

of disease. This program did have notable success with most households in our surveys reporting these positive attitudes towards fosas located within these educated communities. The adoption of a multi-faceted strategy involving the construction of poultry coops, implementation of watchdogs and education of fosas' benefits for the community and ecosystem is therefore an empirically supported strategy to reduce poultry predation and improve community attitudes.

Reducing bushmeat consumption

Reducing food insecurity through improved husbandry and agricultural practices is the logical response to reducing the consumption of Madagascar's protected species. However, caution must be taken when considering alternative livelihood approaches, as their monitoring is often infrequent, and their subsequent success has been varied and typically difficult to interpret (Roe et al. 2015; Wicander and Coad 2015). Furthermore many of these alternative livelihood projects are based upon flawed assumptions in terms of the appropriateness of the substitute, the applicability of the substitute to every household and community, and the scalability of this intervention to induce population-level reductions (Wright et al. 2016). In providing domesticated sources of meat as an alternative source of protein, their availability, price and cultural preferences must be considered (Van Vliet 2000).

Madagascar's rural poor heavily rely upon bushmeat for nutrition (Jenkins and Racey 2008; Randrianandrianina et al. 2010; Golden et al. 2011; Borgerson 2015; Hunter et al. 2015), but do not prefer it to domestic meat. Chicken was our interviewees' most preferred meat, and a preference reported across Madagascar. Unfortunately, rural poultry husbandry techniques are archaic, mired by disease and wildlife predation. Across our sites over 40% of interviewees poultry died annually

to disease (likely Newcastle Disease). Reducing poultry mortality, through the implementation of a vaccination program, the development of robust coops and the trial of watchdogs is one potential solution (with the combined objective of reducing retaliatory killing of fosas). Newcastle disease vaccination programs (in align with overall husbandry improvements) are currently being trialled and implemented in Makira-Masoala National Park in efforts to reduce bushmeat consumption, and improve Malagasy health (Guest 2013). Successful poultry vaccination programs (including poultry health, management, and biosecurity) have been implemented in Tanzania (Msoffe et al. 2010). However, other Tanzanian poultry production projects have reported improved human health was not necessarily associated with reduced bushmeat if basic food security wasn't met (Knueppel et al. 2009). This suggests that the concept has utility, but that the successful implementation of these programs must be carefully considered. In implementing these alternative livelihood programs, the context of local bushmeat consumption must be considered (Van Vliet 2000; Golden et al. 2011; Cundill et al. 2012). The program should be long-term, and it should include conditionalities and sanctions (to avoid bushmeat hunting as additional activity), whilst establishing monitoring protocols to evaluate the program's success (Roe et al. 2015; Wicander and Coad 2015), and refinement if needed.

Reducing exotic species abundance

Exotic species removal programs should be considered in reducing the abundance of cats, dogs and civets in their competition with fosas, and predation of Madagascar's endemic species. Feral cat eradication programs have been widely implemented on islands, with varying levels of success, typically associated with the island's size and eradication methods (Campbell et al. 2011; Nogales et al. 2013). Madagascar's large

size almost certainly prohibits complete eradication of exotic species due to the high cost, environmental and biological feasibility of such programs (Myers et al. 2000). However, localised programs targeting protected areas, through the species specific trapping of wild exotic carnivores, and the neutering of domestic dogs and cats in local villages is an initial step. Such cage trapping programs have been used with varied success (Campbell et al. 2011), however a dog euthanisation program in Ankarafantsika by L. Dollar did result in a substantial increase in fosa trapping rates in align with reduced dog trapping rates (Barcala 2009). Sterilisation programs, implemented by L. Dollar in ANP and another such program in Ranomafana, the Mad Dog Initiative are currently being implemented to reduce feral dogs/cats in Madagascar's forests. Insight from these programs should be used to investigate the creation of an island-wide MNP led exotic-species reduction strategy, combining both euthanisation and sterilisation strategies.

Deforestation and reduction in overall fosa habitat is clearly a significant threat to their long-term persistence. However, the political and socio-economic causes of its manifestation are beyond the scope of this discussion. It must be said that reducing forest loss in Madagascar is the most important and challenging goal for conservationists and the Malagasy government in protecting its biodiversity.

The fosa as a conservation tool

Conservationists' have long used species as surrogates for the greater preservation of ecosystems (Caro 2010). Species are often employed for their role as an indicator, keystone, umbrella and/or flagship species (Wilcox 1984; Noss 1990; Caro and O'Doherty 1999; Caro et al. 2004). When considering the difficulties of conservation in Madagascar (Ganzhorn et al. 2001), the utilisation of such a species, may prove

useful in the conservation of forests, fundraising and luring of tourism to impoverished regions. In considering the characteristics of keystone, umbrella and flagship species, I propose fosa *Cryptoprocta ferox* as an ideal surrogate for the conservation of Madagascar's biodiversity.

The landmark proposal of the keystone species concept (Paine 1966; 1969) has proved a useful tool for biologists in the conservation of biodiversity (Bond 1994; Power and Mills 1995). Keystone species are those that are thought to have a disproportionate effect upon the ecosystem in maintaining community integrity. They range from large carnivores, such as North American wolves (McLaren and Peterson 1994), whose top down predation ensures a healthy population ceiling of herbivores. To vastly different species like krill (Smith et al. 2007), whose trophic level is relatively low, but whose extreme abundance support a large variety of species from fish to filter feeders as large as basking sharks. Despite no experimental or observational evidence to date, fosa are likely a keystone species within Madagascar's ecosystem (Dollar 2006). Fosas' role as Madagascar's apex predator, and their large geographical distribution means their influence across Madagascar's landscape is pervasive. Fosas' have been recorded to be prolific predators, predominately consuming Madagascar's largest terrestrial mammals, lemurs (Dollar et al. 2007; Hawkins and Racey 2008b). However, they are also opportunists, capable of varying their diet regionally (Goodman et al. 1997), whilst overall consuming a variety of prey, including tenrecs, birds, rats, snakes, lizards, insects and crustaceans (Dollar et al. 2007; Hawkins and Racey 2008a). The effect upon these species' abundance is significant, with fosa predation estimated to remove up to 19% of its prey population per year (Hawkins and Racey 2008b). It is this large effect upon island-wide species

abundance and ecosystem composition that gives credence to fosa's role as a keystone species.

The umbrella species concept emphasizes the conservation of one species, whose metaphorical umbrella protects co-occurring species. This concept is not without controversy (Simberloff 1998; Andelman and Fagan 2000; Seddon and Leech 2008), however proponents argue for its simplicity and practicality for conservationists in land-use planning (Fleishman et al. 2001; Caro 2003; Roberge and Angelstam 2004; Caro 2010). Seddon and Leach (2008) reviewed the published literature for criteria in selecting umbrella species. They proposed seven criteria: "*well-known biology; large home range size; high probability of population persistence; co-occurrence of species of conservation interest; management needs that are beneficial to co-occurring species; sensitivity to human disturbance; and ease of monitoring*." From our current knowledge, and notwithstanding some ignorance, fosas do largely qualify as an umbrella species. As it stands, fosa's:

1. Biology and behaviour is well-known (Hawkins 1998; Dollar 2006; Lührs 2012a).
2. Home-range is the largest of all Madagascar's terrestrial species (Lührs and Kappeler 2013).
3. Island-wide distribution (Hawkins 2016) provides relative insurance, underwriting their population's persistence.
4. Forest distribution and large territories (Lührs and Kappeler 2013) encapsulate the spatial requirements of valuable co-occurring species.

5. Require the conservation of large contiguous forests, and their susceptibility to exotic species promotes the preservation of primary forest.
6. Sensitivity to human disturbance is varied, but evident. The impact of exotic species, invariably associated with human disturbance is clear (Gerber et al. 2012b; Farris et al. 2015b). Fosas' are equally susceptibility to direct killing when human-settlements adjoin forests.
7. Low population density and large home range can make monitoring difficult. However, camera trapping of trail systems is a successful monitoring tool. Baiting has also proven effective in identifying individuals for more robust surveying analyses (Gerber et al. 2010).

In considering fosas' attributes, and in entertaining other Malagasy species, fosas suitability as an umbrella species is convincing. No extant species in Madagascar occupy remotely comparable areas of forest, nor are distributed as widely, perhaps crowning Madagascar's apex predator its umbrella species.

Humans have long held an affinity with certain 'charismatic' species. Conservationists have leveraged upon this relationship within the adoption of single-species conservation programs in the broader preservation of ecosystems (Mittermeier 1988; Caro and O'Doherty 1999; Leader-Williams and Dublin 2000; Caro et al. 2004; Smith and Sutton 2008). Such charismatic species have been coined 'flagships' and have been redefined as " *a species used as the focus of broader conservation marketing campaign based on its possession of one or more traits that appeal to the target audience*" (Verissimo et al. 2011). Given the widespread use of charismatic

species in conservation, academics have attempted to demystify their qualities, with non-human charisma defined on the basis of its ecological (detectability to humans i.e. size, temporal activity), aesthetic (appearance, behaviour) and corporeal qualities (personal, often historical attachment) (Lorimer 2007). Recent research has also sought to determine the likely charisma of a species, aiding flagship species selection. Body size, IUCN status, but also baldness extent, threat to humans, and eye location (forward or side facing) were deemed important attributes (Macdonald et al. 2015). It's unsurprising then, that megavertebrates have been most used as flagship species by international institutions in conveying conservation issues to the public (Mittermeier 1988; Leader-Williams and Dublin 2000).

Madagascar's most emblematic species is undoubtedly the lemur, the world's most threatened group of vertebrates (Schwitzer et al. 2014). However, given fosas potential as a keystone and umbrella species, their suitability as a flagship species is likely much greater. This fact is mirrored by WWF's global species program (2016) which defines a flagship species as one that is selected as an ambassador of a habitat, typically large and charismatic and whose conservation promotes the preservation of other species. This highlights the typical selection of flagship species by conservation institutions who are not only charismatic but also appropriate as an umbrella species (Caro et al. 2004). In light of these conditions, and in considering fosa's biological characteristics, it is apparent that fosas exemplify a flagship species. Fosas' represent Madagascar's largest terrestrial mammal, display enigmatic behavior, and possess an attractive felid-like appearance - an important predictor of flagship suitability (Macdonald et al. 2015). Fosas however, have not been fully utilised as a flagship species, and are still largely unknown within western popular culture. When considering the immediate threats to Madagascar's forests, and the need to raise

awareness and boost rural economies, perhaps a threatened ambassador is what's needed.

The intention of this section is to propose fosas' suitability as a keystone, umbrella and flagship species, not to argue the merits of each concepts' utility as a conservation tool. All concepts have received praise for their conceptual and practical utility in conservation (Caro 2010), but have also received criticism for ambiguity, the requirement of detailed knowledge in selecting species, and lacking in empirical evidence of their success (Mills et al. 1993; Seddon and Leech 2008). Alternatively, the selection of multiple surrogate species of keystone, umbrella, and/or flagship value has been proposed. This multi-species landscape approach selects different species to encapsulate various landscape parameters and thus the requirements of more species (Lambeck 1997). Regardless of the approach, fosas should be included within any single/multi-species conservation program, with their biological utility surpassing Madagascar's other species. Looking to the future, *Cryptoprocta ferox* could represent Madagascar's conservation icon in leading the conservation of its unique and important biodiversity.

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Appendices: Appendix A

Novel photographic and morphometric records of the Western Falanouc *Eupleres major* in Ankarafantsika National Park, Madagascar.

Abstract

Long-term research on Fosa *Cryptoprocta ferox* has been conducted in Ankarafantsika National Park since 1999, with rare sightings of the forest's second elusive carnivore, the Western Falanouc *Eupleres major*. During annual carnivore live-trapping from 1999-Present, a single Falanouc was captured on the 30th of March 2002. Since this capture, two photographs have been taken of the Falanouc. In June 2011 a project volunteer photographed a Falanouc during the day whilst conducting trap-checks. Recently, a second photograph was recorded during the largest systematic camera-trapping study of Madagascar's western carnivores. From April – July 2014 eighty paired camera-traps operated on average for 79 days, recording a sole image of the Western Falanouc at 01h18 on the 19 April 2014. Herein we discuss the morphometrics and photographic records of the Western Falanouc from Ankarafantsika National Park.

Malagasy Title

Fitantarana ara-tsary sy refy samihafa voaangona mikasika ny Fanaloka Andrefana *Eupleres major* ao amin'ny Valanjavaboahary Ankarafantsika, Madagasikara

Malagasy Abstract

Notanterahana nanomboka ny taona 1999 tao amin'ny Valanjavaboahary Ankarafantsika ny fikarohana lavitrezaka mikasika ny Fosa *Cryptoprocta ferox*. Tamin'izany no nahitana tsindraindray karazambiby mpihinankena iray hafa izay tsy mbola fahita, dia ny Fanaloka Andrefana *Eupleres major*. Nandritra ny fisamborana velona ireo karazam-biby mpihinankena izay fanao isan-taona nanomboka ny taona 1999 ka hatramin'izao dia indray mandeha ihany no nahazoana Fanaloka Andrefana,

ny 30 Marsa 2002. Nanomboka teo dia sarina Fanaloka Andrefana roa no azo. Tamin'ny Jona 2011 dia nisy mpikaroka mpilatsaka antsitrapo iray nahazo sarina Fanaloka Andrefana anankiray nandritra ny andro mazava tamin'ny fisafoana ireo fandrika napetrany. Vao tsy ela akory, nisy sary faharoa azo tamin'ny fakantsary fandrika nandritra ilay fikaroahana lehibe indrindra mikasika ny biby mpihinankena miaina amin'ny ilany andrefan'i Madagasikara. Ny volana Aprily ka hatramin'ny Jolay 2014 dia fakantsary fandrika miisa 80 no napetraka tao anaty ala nandritra ny 79 andro ka sary tokan'ny Fanaloka Andrefana no azo ny 19 April 2014 tamin'ny 01 ora sy 18mn maraina. Eto isika dia hiady hevitra mikasika ny refy samihafa sy ny sarin'ny Fanaloka Andrefana araka ny tahirinkevitra vao nangonina tao amin'ny Valanjavaboaharin'Ankarafantsika.

Keywords: Ankarafantsika, camera-trapping, *Eupleres*, Eupleridae, Falanouc.

This chapter forms the basis of a paper accepted to Small Carnivore Conservation: Merson S**,** Dollar L. & Macdonald D. (2017). Novel camera-trap record of the Western Falanouc *Eupleres goudotti major* in Ankarafantsika National Park. Small Carnivore Conservation 56.

Introduction

A paucity of information currently exists on the two proposed sub-species of the Genus *Eupleres*: *Eupleres goudotii* and *Eupleres major (*Albignac 1972). Each sub-species is typically confined to the geographically distinct landscapes of the eastern rainforests and western deciduous forests respectively (Hawkins 2008), despite proposed distributional overlap in the northerly rainforest of Montagne d'Ambre (Goodman and Helgen 2010). Much of our knowledge of the Falanouc has been derived from museum specimens or personal communications with rural Malagasy and hallmark studies (Goodman and Helgen 2010). Across its geographic range, sightings and trappings of the Falanouc have been rare, which may be due to its specialised diet of earthworms and nocturnal habits (Hawkins 2008). Recent technological advances in remote camera sensing now afford greater opportunities to document this enigmatic species.

The first camera-trap image of a Falanouc was recorded in Ranomafana National Park (RNP) in 1997 (Dollar 1999). Over a decade later in the same forest Gerber et al. (2012a) conducted the first systematic survey of Madagascar's carnivores using camera-traps, again documenting the eastern *E. goudotii*. This study was followed by Farris et al. (2014)'s documentation of the Eastern Falanouc during their extensive carnivore camera-trapping studies in the Masoala-Makira protected complex in northeastern Madagascar. Conversely, Madagascar's western dry deciduous forests have received considerably less attention with only one recent camera-trapping study of the Mariarano forest, located approximately 80km northwest of Ankarafantsika National Park (ANP) (. During this survey, the first camera-trap image of *E. major* was recorded from Madagascar's west coast.

Ankarafantsika National Park (16°12’ S, 47°09’ E) has been the focus of long-term Fosa capture surveys since 1999. The rarity in sightings of Ankarafantsika’s second elusive carnivore, the Falanouc, has been described by Dollar (Division of Arts & Sciences, Pfeiffer University, USA, verbally 2014), whose team have rarely encountered Falanouc, with only a few confirmed sightings, one physical capture and one volunteer photograph. From May to July 2014 we undertook the largest systematic camera-trap study in West Madagascar to document the effects of anthropogenic habitat disturbance upon Fosa occupancy. This study forms part of a wider investigation documenting the major anthropogenic threats to the conservation of the Fosa (Samuel Merson, Department of Zoology, The University of Oxford, UK, written 2015).

Methods

Study Area

ANP is located approximately 105 km from the port hub of Mahajanga. At 1350 km^2 ANP is the largest remaining tract of dry deciduous forest. The region is characterised by an average temperature of 26°C, with a dry season from May to November, and a wet season from December to April. The Route Nationale 4 (RN4) bisects the south-western portion of the forest and is flanked by six rural villages. These villages have a significant influence upon the surrounding forest, with large tracts of primary forest converted to savannah through slash and burn agriculture, rice fields and raffia plantations. Ampijroroa, the former name of the Special Reserve adjacent (and now incoprotated within) Ankarafantsika, is also the home to the local Madagascar National Park’s headquarters, which operates tourism throughout the surrounding area.

Volunteer photograph

Since 1999, typically during the dry season, trapping surveys for Fosa within a transect grid surrounding the Ampijiroa research station are conducted on an annual basis as part of a long-term monitoring program. With the aid of volunteers, traps are baited and checked during the early morning and late afternoon. In June 2011, the first known photograph of a Western Falanouc was taken by an Earthwatch volunteer in ANP (Figure 1). Despite the Falanouc's proposed highly nocturnal-crepuscular activity pattern (Goodman and Helgen 2010; Gerber et al. 2012b) this individual was photographed during the day. Such diurnal sightings are particularly rare.

Figure 1. Photograph of the Western Falanouc, taken by an Earthwatch volunteer in June 2011.

Camera-trap record

From May to July, eighty pairs of camera-traps (Cuddeback Ambush IR 1187) were placed along trails encompassing an area of approximately 40 km^2. Trail systems were chosen intentionally mindful of the target species (Fosa *Cryptoprocta ferox*)

frequent use of trails whilst traversing forest, as demonstrated by previous capture studies (Dollar 2006) and the frequent presence of faeces along trails. Camera trap stations were spaced approximately 750m apart, allowing an equal trapping effort across the sampling area. Site placement along trails was chosen to maintain equal distance from the nearest station but also to maximise chances of detecting passing animals and humans. At each camera-trap station, a pair of Cuddeback Ambush IR 1187 were placed flanking the trail, approximately 20-30 cm above the ground. This method allowed captured individuals to be photographed on both sides, improving species identification (Gerber et al. 2012a), whilst additionally accounting for individual camera failure.

At 01h18 on the 19 April 2014 a singular photograph captured an individual Western Falanouc (Figure 2). The camera-trap station (16°15′S, 46°49′E) was located in riverine degraded forest, nearby to a dry seasonal riverbed, and approximately 2.25 km from the nearest village, Ampombalava. The camera-trap station was in operation for 82 nights (night being defined as one 24 hour period in which one of the two cameras was in operation) from the 14 April – 4 July 2014, collecting a total of 1594 images. Within these images, 188 humans, 5 Dogs *Canis lupus familiaris*, 33 Zebu *Bos taurus*, and 9 Fosa were most notably observed.

Figure 2. Camera-trap image of the Western Falanouc *Eupleres major* taken on the 01h18 on the 19 August 2014. Note: the photograph is inverted.

Physical Capture

Trapping was conducted during the wet season from February - April 2002. A total of 38 “Havahart”, “Tomahawk” and/or “National” traps were placed evenly along trails at two sites surrounding Ampijiroa, bisected by the Route National 4. These sites were chosen as to encompass the two major local microhabitats, a riparian forest and a drier deciduous forest. Traps were baited with earthworms, sardines, corned beef, dry fish and chicken. When an individual Falanouc was captured, it was darted using a Pneu-Dart containing the anesthetising agent Telazol and moved to the campsite for the recording of morphometric measurements.

During approximately three and a half months of trapping, a single adult male Falanouc was captured on the 30 March (Table 1). Weighing approximately 2.4 kg, the male was on the lower scale of their proposed weight range from 2 – 4 kg (Albignac 1974). In alignment with museum specimens, the pelage was brownish

(Goodman and Helgen 2010), whilst the under fur was dense and covered by long guard hairs. Local villagers reported that females of this subspecies are greyish in color.

Table 1. Morphometric measurements of the captured male adult Western Falanouc.

Measurements	Value (mm)
Total length	790
Head and body length	550
Neck circumference	155
Chest circumference	330
Tail length	245
Tail circumference (base)	175
Tail circumference (mid)	100
Tail circumference (tip)	30
Ear length	39.17
Forelimb length	165
Hind limb length	212.5
Biceps circumference	97.5
Thigh circumference	150
Forefoot length	40
Forefoot width	32
Hind foot length	57
Hind foot width	37
Right testicle length	14.38
Right testicle width	14.43
Left testicle length	22.14
Left testicle width	13
Prepuce length	12.46

The hindlimbs were more developed than the forelimbs, whilst the forefoot consisted of two carpal pads that were notably separated, with the hindfoot featuring a bare metatarsal zone with short hair in the centre.

The cranium was 70 mm long (Table 2). There were two canines on the upper jaw and one on the lower jaw. The teeth were extremely specialized and very small/fragile; the carnassials were not very well developed which is likely explained by their diet of earthworms, insects and small invertebrates.

Table 2. Cranium and dental measurements of the captured male adult Western Falanouc.

Measurements	Value (mm)
Cranium length	70
Cranium width	41.33
Snout length	55
Snout width	36.5
Inter orbital distance	21.06
Mandible length	70
Mandible height	15.12
Upper canine n°1 length	3.13
Upper canine n°1 width	1.3
Upper inter canine distance (n°1)	3.53
Upper inter canine distance (n°2)	5.29
Lower canine length	3.23
Lower canine width	1.67
Lower inter canine distance	5.4

Discussion

This is the first photographic and morphometric documentation of the Western Falanouc in Ankarafantsika. The rarity of physical sightings has also been confirmed for the eastern sub-species. An observational recording of opportunistic Malagasy carnivore sightings in Analamazaotra forest in Andasibe from 1992 – 2010, documented only one Eastern Falanouc (Dolch 2011). In addition to these anecdotal recordings, Goodman and Helgen (2010) provided an exhaustive literature review to describe the species' geographic distribution through published records, unpublished records, and museum specimens. This review served to highlight the lack of data currently available on this little known species.

Given the obvious inefficacies of traditional methods for observing and/or physically capturing Falanouc, camera-trapping provides a more suitable non-invasive alternative. Gerber et al. (2012a) established a camera-trapping grid of approximately 27 paired cameras for a minimum of 5,565 nights across four sites of increasing habitat degradation. Within the primary and selectively-logged sites, a total of 2 and 16 *E. goudotii* were photographed, respectively. In the other major camera-trapping

study of East Madagascar's carnivores Farris et al. (2015) amassed a total of 202 images of *E. goudotii* in Masoala-Makira. This large number of photographs was in part due to an increased sampling effort of 15,253 nights across seven sites from August 2008 – 2013. Within the western forests of Madagascar the sole camera-trapping study of Malagasy carnivores captured six *E. major* across 24 sites during 227 nights in June – August 2012 (Evans et al. 2013). In contrast our total camera-trapping grid was in collective operation for a total of 6,269 nights, capturing a single image of *E. major* from April – July. Insofar as this low success rate is indicative of very low population density, this raises at least the possibility that anthropogenic pressures in Ankarafantsika could be responsible.

E. major and *E. goudotii* are currently listed as Endangered by the IUCN. Much of Madagascar's large fauna currently face significant pressures, predominately deforestation and hunting, two threats that are under current investigation in our study in Ankarafantsika. Within our study site, much of the landscape has been altered to savannah, agricultural fields, or experiences severe human and invasive species encroachment. Our camera-trapping grid encompassed a balanced mixture of these different habitats, with 34 camera-trap stations located in primary forest, 20 in degraded forest, and 25 found in savannah. Given much of this landscape has experienced significant habitat alteration, in alignment with human and invasive species presence, it could be expected that these factors collectively act as a strong Falanouc deterrent. This baseline information should be helpful in ongoing estimations of their population, distribution and ultimately in informing their conservation.

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