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**Distribution, abundance and habitat use of the
mongoose lemur, *Eulemur mongoz*, on
Anjouan, Comoros.**

Lucy Jayne Ormsby

**A dissertation submitted to the University of Bristol in accordance with the requirements for award of
the degree of MSc (R) in the Faculty of Science, School of Biological Sciences, January 2019**

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Abstract

Eulemur mongoz is found in Madagascar and the Comoros. It is listed as Critically Endangered on the IUCN Red List, threatened by habitat destruction and hunting in Madagascar. The introduced population on the Comoros has not been included in IUCN red list assessments. It has been suggested that this population could serve as an important reservoir for the conservation of the species, however thorough surveys are needed to confirm this. In this thesis, I investigate the distribution, abundance and habitat use of the species on the Comoros island of Anjouan, to determine status and conservation needs.

I used species distribution modelling with a consensus approach to predict the distribution of *E. mongoz* on Anjouan using only presence data. I used hierarchical modelling to predict the effect of habitat on abundance of *E. mongoz*, using data collected on transect surveys and vegetation surveys. I used distance sampling to estimate population density on the island.

An area of 239 km² of suitable habitat was predicted on Anjouan, with 6 km² of highly suitable habitat. Density of *Syzygium aromaticum* and species richness were found to have a significant effect on lemur abundance. A density of 23 lemurs/km² was estimated, with a population estimate of 9919(95% CI 5541-17755) lemurs. My results suggest that *E. mongoz* has a large range on Anjouan, has a wide tolerance to environmental variables and is flexible in its use of habitat. My results also suggest that species rich agroforestry and degraded forest play an important role in the conservation of the species. My study confirms the importance of this population for the conservation of the species. I recommend that an action plan should include reforestation with native and exotic species to increase the area of species rich habitat, as well as ongoing monitoring on Anjouan and surveys of the Mohéli population.

Dedication

For my Grandma, Jane Beryl Kirk.

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Author's declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's *Regulations and Code of Practice for Research Degree Programmes* and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

SIGNED:

DATE: 08/01/2019

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List of abbreviations

AIC - Akaike Information Criterion values
AICc - Akaike Information Criterion values corrected
AOO - Area Of Occupancy
AUC - Area Under Curve
CEPF - Critical Ecosystem Partnership Fund
CI - Confidence Interval
CV - Coefficient Of Variation
DBH - Diameter at Breast Height
DEM - Digital Elevation Models
ECDD - Engagement Communautaire pour le Developpement Durable
FAO - Food And Agriculture
GAM - Generalised Additive Model
GBM - Generalised Boosted Models
GDP - Gross Domestic Product
GLMs - Generalised Linear Models
GPS - Global Positioning System
IUCN - International Union for Conservation Of Nature
MaxEnt - Maximum Entropy Modelling
n - number of elements
NGO - Non Governmental Organisation
ROC - Receiver Operating Characteristic
RF - Random Forest
SDMs - Species Distribution Models
SD - Standard Deviation
 \bar{x} - sample mean

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1. Introduction

1.1 Summary

The mongoose lemur, *Eulemur mongoz*, occurs in north western Madagascar and on the Comoros islands of Anjouan and Mohéli (Mittermeier et al. 2010). It is one of two species of lemur that is found in the wild outside of Madagascar, and is an introduced species to the Comoros (Tattersall 1976, Pastorini et al. 2003). The status of this species was upgraded in 2012 from Vulnerable to Critically Endangered by the IUCN Red List assessment, due to ongoing habitat loss, unsustainable levels of hunting and hybridisation with *Eulemur rufus* (Schwitzer et al. 2013; Andriaholinirina et al. 2014).

Information on the status of the *E. mongoz* population on the Comoros is lacking, and previous surveys have not produced a population estimate or distribution map. The conservation needs of the population have not been identified and the population has not been included in the IUCN Red List assessment or action plan for the species.

My thesis focuses on the *E. mongoz* population on the island of Anjouan in the Comoros, and aims to obtain information on its distribution and population size. This will contribute to an assessment of the conservation status of the Comoros population, and inform any required conservation management plans. This chapter will give a background on *E. mongoz* including results of previous surveys; a description of the study site; and the aims and structure of the thesis.

1.2 Lemurs

The Lemuriformes infraorder consists of 111 taxa and 107 species that are unique to Madagascar (C. Schwitzer, pers. comm.), with the result that globally, this country has the highest primate species endemism and the second highest primate species diversity (Schwitzer et al. 2013). Lemurs are important flagship species for the threatened biodiverse forest habitats of Madagascar and represent evolutionary lineages specific to the island (Schwitzer et al. 2013). In 2012, 94% of lemur species were classified as being threatened

with extinction by the IUCN Red List assessment (Schwitzer et al. 2013) due to anthropogenic pressures such as hunting and destruction of forest habitat, which have increased following recent political instability (Mittermeier et al. 2010, Schwitzer et al. 2013). As a result, conservation of lemurs is urgent (Schwitzer et al. 2013).

1.3 *Eulemur mongoz*

Eulemur mongoz (fig. 1.1, fig. 1.2) is one of twelve *Eulemur* species, and belongs to the family Lemuridae (Mittermeier et al. 2010). It occurs in north western Madagascar and in the Comoros on Anjouan and Mohéli (Mittermeier et al. 2010), (fig. 1.3). In Madagascar, it only occurs in the regions of Ambato-Boéni and Ankarafantsika in the northwest (Mittermeier et al. 2010). It is one of two species of lemur that is found in the wild outside of Madagascar and is likely to have been introduced by humans to the Comoros (Tattersall 1976, Pastorini et al. 2003). The first known record of *E. mongoz* in the Comoros was made on Anjouan in 1655 (Mittermeier et al. 2010) and genetic analysis suggests that the species was introduced not long before this (Pastorini et al. 2003).

The species usually occurs in small groups comprising an adult pair, in which the female is dominant, and one to four offspring (Tattersall 1976, Curtis and Zaramody 1999) but can also form larger groups (Tattersall 1976, Nadhurou et al. 2017). It is one of two socially monogamous *Eulemur* species (Curtis 2004, Tattersall and Sussman 2016). It has a cathemeral activity pattern (Tattersall 2006) and can shift proportion of diurnal and nocturnal activity according to season (Tattersall 1976, Rasmussen 1999, Curtis et al. 1999, Curtis and Rasmussen 2003). The species is found in dry deciduous forests and scrub in Madagascar and in humid forest and anthropogenic regrowth in the Comoros (Andriaholinirina et al. 2014).

The status of *E. mongoz* was upgraded in 2012 from Vulnerable to Critically Endangered by the IUCN Red List assessment, due to ongoing habitat loss, unsustainable levels of hunting and hybridisation with *E. rufus* on Madagascar (Schwitzer et al. 2013, Andriaholinirina et al. 2014).



Figure 1.1 Female *E. mongoz* on Anjouan



Figure 1.2 Male *E. mongoz* on Anjouan

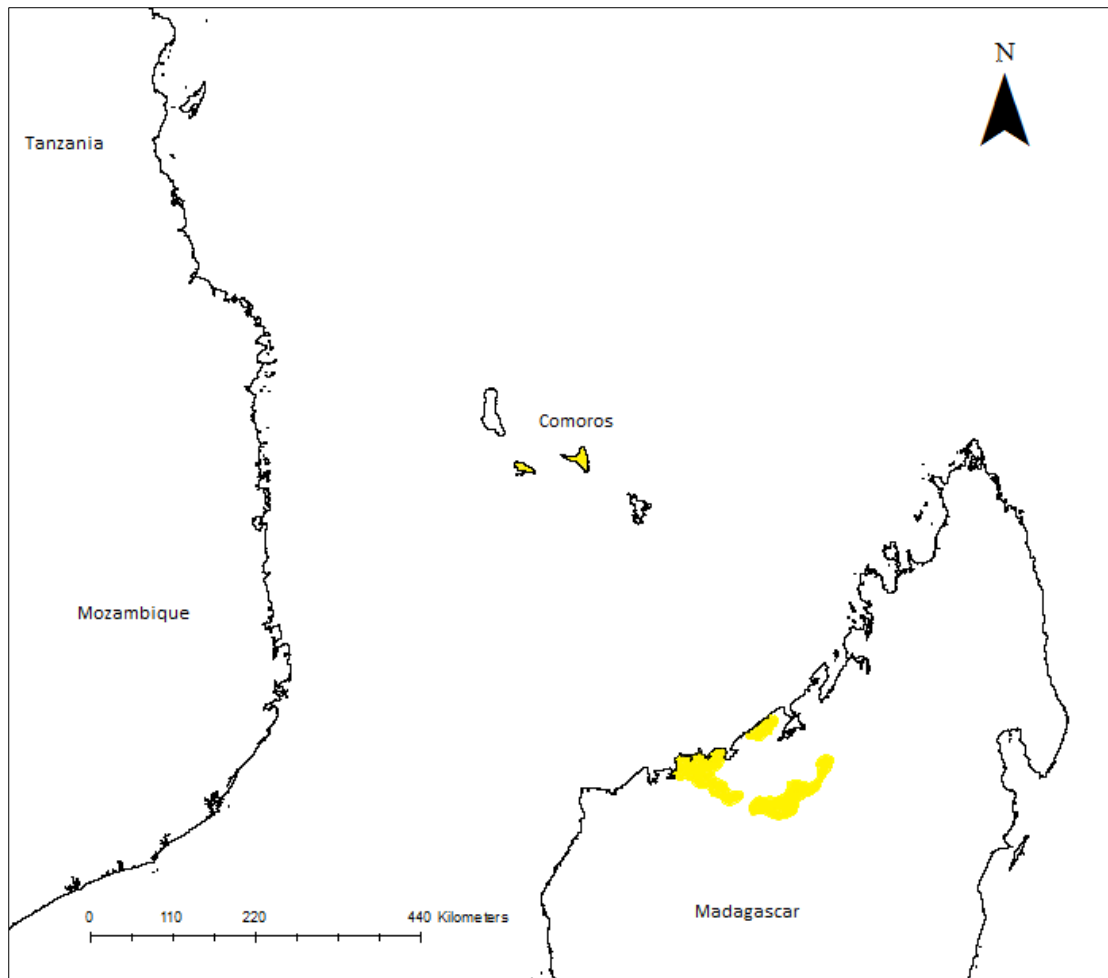


Figure 1.3 Geographic range of *E. mongoz* shown in yellow: the species is found on the Comoro islands of Anjouan and Mohéli, and in north western Madagascar

1.4 Previous surveys

The most recent survey of *E. mongoz* in Anjamena, north western Madagascar took place in 2008 (Andriaholinirina et al. 2014). Here, its habitat consists of semideciduous, seasonally dry anthropogenic regrowth forest, in which exotic species such as *Tamarindus indica* (tamarind) and *Ziziphus jujuba* (jujube) are abundant (Curtis and Zaramody 1998). This habitat has been highly fragmented, and fragment size and canopy cover were found to be correlated with *E. mongoz* density (Shrum 2008). Densities of 2.5 groups per km² and 10 individuals per km² were recorded; a significant decrease from the 16 groups and 45 individuals per km² recorded in the previous survey in 2000 (Müller et al. 2000, Shrum 2008, Andriaholinirina et al. 2014).

Surveys of the Comoros were first conducted in the 1970s. At this time, habitat on Anjouan was reported to consist of native forests in the highlands and anthropogenic regrowth, including agroforestry, in the lowlands containing a variety of exotic species such as *Mangifera indica* (mango), *Artocarpus heterophyllus* (jackfruit), *Artocarpus altilis* (breadfruit), *Albizia lebbek* and *Terminalia catappa* (Tattersall 1976, Tattersall pers. comm.). On Mohéli, most of the island's vegetation consisted of anthropogenic regrowth, including agroforestry dominated by *Cocos nucifera* (coconut palms) and including *Cananga odorata* (ylang-ylang), *Musa* spp. (banana), *Manihot esculenta* (cassava) and *Oryza* sp. (rice) (Tattersall 1976). The surveys identified a much higher abundance of lemurs in the native forest of Anjouan than in anthropogenic habitat, but a relatively high abundance of *E. mongoz* in similar anthropogenic habitat on Mohéli (Tattersall 1976). This suggested that the species was as successful in anthropogenic habitat as in primary forest (Tattersall 1976).

Accelerated deforestation was recorded on Anjouan between the 1983 and 1994 surveys (Tattersall 1998). In 1994, *E. mongoz* was abundant in native forest remnants, but these had become restricted to inaccessible slopes and numbers could not be determined (Tattersall 1998). Anthropogenic habitat in the coastal lowlands was considered to support a relatively healthy population of *E. mongoz*, but this had also reduced in area since 1983 and soil erosion had increased (Tattersall 1998). On Mohéli, an increasing human population had resulted in clearance of mature humid forest in most areas below the ridgeline at 450m (above sea level), to make way for cultivation even on very steep slopes (Tattersall 1998). Human impact had resulted in increased soil erosion and streams becoming intermittent (Tattersall 1998). Lemurs were still recorded in anthropogenic habitat, alongside larger streams, but at a much lower frequency than on previous surveys (Tattersall 1998).

In 1997, interview surveys were conducted on Anjouan to investigate local attitudes to *E. mongoz*; these identified that capture of lemurs for pets was common (Clark 1997). The population was not thoroughly surveyed but lemurs were reported to be present within and surrounding many villages (Clark 1997). The species was reported to occur at most interview locations, except in areas without tree cover in the South. It was therefore suggested to have a wide distribution on the island (Clark 1997).

Encounter surveys of *E. mongoz* on Anjouan and Mohéli in 2012 recorded 1.64 individuals per km and 0.48 groups per km over both islands (Nadhrou et al. 2017). This study found larger group sizes in degraded forest (native forest mixed with anthropogenic regrowth, see table 1.1 for full habitat definitions) than in native forest and suggested that degraded forests provide suitable habitat and higher resource availability (Nadhrou et al. 2017). They also found lemurs at higher elevations than had been recorded in 1998. As a result, they suggested that the population on the Comoros could be important for the survival of the species, as a potential genetic reservoir (Nadhrou et al. 2017).

1.5 Diet and ecological flexibility

Ecological flexibility has been reported in many species of the genus *Eulemur* (Volampeno et al. 2011a, Donati et al. 2011, Campera et al. 2014, Sato et al. 2016). Ecological flexibility is the ability of a species to adapt to environmental changes and exploit alternative resources by adjusting its diet or behaviour (Sato et al. 2016, Eppley et al. 2017). Dietary flexibility, also referred to as dietary switching, allows a species to adapt to changes in food availability by changing its diet (van Schaik et al. 1993, Chapman et al. 2002), whereas behavioural flexibility can include changes in activity patterns, ranging or group size to increase access to food, and is shown in species with limited dietary flexibility (Sato et al. 2016). Ecological flexibility can enable primates to adapt to habitat disturbance (Riley 2007, Donati et al. 2011, Sawyer et al. 2017). Within the *Eulemur* genus, dietary flexibility is reported to be relatively low, whereas behavioural flexibility is more common (Sato et al. 2016). For example, collared lemurs *Eulemur collaris* adapt to degraded habitat by decreasing group size, increasing feeding time and increasing range size (Donati et al. 2011, Campera et al. 2014).

Initial studies of *E. mongoz* at Ampijoroa in Madagascar indicated that this species was mainly nectarivorous, including exotic plant species in its food sources (Sussman and Tattersall 1976). The species was later suggested to switch from mainly nectar feeding in the dry season to a frugivorous/folivorous diet in the wet season (Andriatsarafara 1988). Studies in Ampijoroa identified flexibility in the diet of *E. mongoz* (Rasmussen 1999). Fruit made up 61.5% of the overall food budget from December to June (and the rest consisted of new leaves, mature leaves and nectaries), however the proportions of different food types consumed varied from month to month (Rasmussen 1999). New leaves were the dominant component of the diet in December, when frugivory was low, and during May and June

nectar made up more than 50% of the diet (Rasmussen 1999). More recent dietary analysis revealed that the Anjamena population has a predominantly frugivorous diet, which can also include leaves, flowers, nectar, seeds, ants, dead wood, soil, and even fledgling birds (Curtis 2004). This population was found to consume mature fruit during both seasons, with more nectar and seeds during the wet season, and more flowers and leaves during the dry season; maintaining a high-energy diet throughout the year (Curtis 2004). Therefore, there is evidence that dietary flexibility allows the species to cope with seasonal changes in food availability. *E. mongoz* on Anjouan is suggested to have an opportunistic feeding strategy that makes it more adaptable to different habitats (Nadhrou et al. 2017). Successful introduced species are more likely to be adaptable, behaviourally flexible or habitat generalists (Mooney and Cleland 2001, Duncan et al. 2003, Sol et al. 2008). Ecological flexibility may therefore have enabled *E. mongoz* to successfully colonise the Comoros and utilise anthropogenic habitat.

1.6 Threats

In general, lemurs in Madagascar are facing a range of threats from human activities including illegal logging both within and outside of protected areas, slash-and-burn agriculture (tavy), collection of wood, charcoal production, seasonal burning of dry forests for cattle pasture, live capture of lemurs to be kept as pets, and hunting of lemurs for food (Mittermeier et al. 2010, Schwitzer et al. 2013). An absence of effective law enforcement due to political instability following the coup in 2009 has exacerbated these problems and made conservation of lemur habitat incredibly challenging (Mittermeier et al. 2010, Schwitzer et al. 2013).

The population of *E. mongoz* in Madagascar is threatened by significant fragmentation of its native forest habitat by tavy, conversion to pasture for cattle farming and charcoal production (Shrum 2008). The species is also hunted for food (Mittermeier et al. 2010, Andriaholinirina et al. 2014), and the hunting of lemurs is known to take place in Ankarafantsika National Park, in which *E. mongoz* is present (García and Goodman 2003, Pastorini et al. 2009). Hybridisation with *E. rufus* in a small area in western Betsiboka has also been confirmed (Zaramody and Pastorini 2001, Pastorini et al. 2009). Although this can help a population adapt to a new environment and has played a role in species radiation (Arnold 2002, Seehausen 2004) it can also increase the threat of extinction by diluting the

gene pool of the parent population if the hybrid species is successful (Arnold and Meyer 2006).

The population on the Comoros faces different pressures. There has been very little environmental protection on the Comoros (Tattersall 1998) and levels of deforestation are high. However, the native forest habitat has been largely converted to agroforestry and crop plantations rather than pasture. *E. mongoz* is not subject to hunting (Clark 1997, Tattersall 1998), but is instead captured to be kept as a pet, usually resulting in death (Clark 1997). The lemurs may also be affected by recreational use of slingshots by children (Tattersall 1998). They are perceived as crop-raiding pests (Clark 1997, Tattersall 1998, Nadhurou et al. 2017) and use of poison by farmers to deter crop damage has been reported (Tattersall 1998). A recent study of human impact on lemurs on Anjouan and Mohéli revealed that 80% of farmers admitted to throwing stones at lemurs, and that more than 80% of farmers perceived them as a threat to crops (Nadhurou et al. 2017). The species may therefore be less threatened on the Comoros than in Madagascar but could still be significantly impacted by these factors.

1.7 Lemur conservation

A conservation action plan has been created for most species of lemur, including for *E. mongoz* on Madagascar (Schwitzer et al. 2013). The action plan consists of four key elements: involvement of local communities in lemur conservation, development of lemur ecotourism, developing long-term research projects at important sites, and establishing captive insurance colonies of endangered lemurs (Schwitzer et al. 2013). For *E. mongoz*, the conservation plan encompasses the five sites in Madagascar at which it occurs but does not include the Comoros because the population here has been considered as introduced rather than naturalised. Varied criteria for considering an introduced species as naturalised have been suggested (Hettinger 2001). Hettinger (2001) recommends that an exotic species is considered as naturalised when it 'persists in its new habitat and significantly adapts with the resident species and to the local abiotia'. The level of adaptation required may be lower where the exotic species can occupy an unfilled niche (Hettinger et al 2001). The length of time required to naturalise can vary and will be faster in species with shorter reproduction times (Hettinger et al 2001). *E. mongoz* could potentially be considered as naturalised on the Comoros, having been introduced several hundred years ago, with a fast rate of

reproduction and few natural competitors. This population could therefore arguably be included in the IUCN Red List assessment and species action plan.

There are no lemur conservation projects in place in the Comoros. Based on previous studies, conservation education has been recommended as a necessary measure for reducing human-lemur conflict on the Comoros (Clark 1997, Nadhurou et al. 2017). A local NGO, Dahari, is working on biodiversity research, rural development and natural resource management on Anjouan. As part of Dahari's research to identify biodiversity conservation priorities on Anjouan, my study will identify conservation needs of *E. mongoz* on Anjouan, and recommend conservation measures that could be included in an action plan to protect the species on the Comoros.

1.8 Study site: Anjouan, the Comoros

Anjouan, the location of my study, is one of four islands that make up the archipelago of the Comoros, along with Mayotte, Grand Comore and Mohéli. The Comoros is located in the Mozambique Channel and has a total land area of 2236 km² (International Monetary Fund 2010). The islands are of volcanic origin with steep slopes (Doulton et al. 2015). Globally, it is one of the poorest countries (UNDP 2014). Anjouan has an area of 425 km² and maximum elevation of 1595m. The island is formed of three ridges which converge in the central region (Tattersall 1976). These are surrounded by many steep valleys and terrain is mountainous (Green et al. 2015). The climate is tropical and the wet season is between November and April (Green et al. 2015).

Agriculture generates approximately 49% of GDP in the Comoros. The sector consists of subsistence crops: *Musa* spp., *Colocasia esculenta* (taro), *M. esculenta*, and *C. nucifera*; commercial vegetable crops: *Solanum lycopersicum* (tomato), *Lactuca sativa* (lettuce), *Solanum tuberosum* (potato), and *Allium cepa* (onion); export crops: *Vanilla planifolia* (vanilla), *Syzygium aromaticum* (clove), *C. odorata*, *Coffea* spp. (coffee) and *Capsicum* spp. (pepper); orchard production: *Citrus* spp. (citrus fruit), *Persea Americana* (avocado), *M. indica*, *A. heterophyllum*, and *Psidium* spp. (guava); and forestry (International Monetary Fund 2010).

The Comoros has incurred high levels of deforestation in recent years, with the country listed as having the highest annual net loss of forest in the world from 2000-2010 (FAO 2010). Heavy dependence on wood fuel has contributed to the significant rate of deforestation, estimated at 500ha per year (International Monetary Fund 2010). On Anjouan, the majority of the population depends on agriculture (FAO 2010). Erosion and ecological degradation are significant and most permanent rivers are now intermittent (Doulton et al. 2015).

Land use maps for the Comoros were produced by the ECDD (Engagement Communautaire pour le Développement Durable) project (<https://ecddcomoros.org>) in 2013 (fig. 1.4) (Green 2013). Habitat on Anjouan was classified according to four main categories (table 1.1), which were determined based on plant species and human disturbance (Green et al. 2015). Natural forest occupied 29 km², degraded forest 59 km², agroforestry 138 km² and non-forest 173 km² (Green 2013). Natural and degraded forests were restricted to high altitude zones (Green et al. 2015).

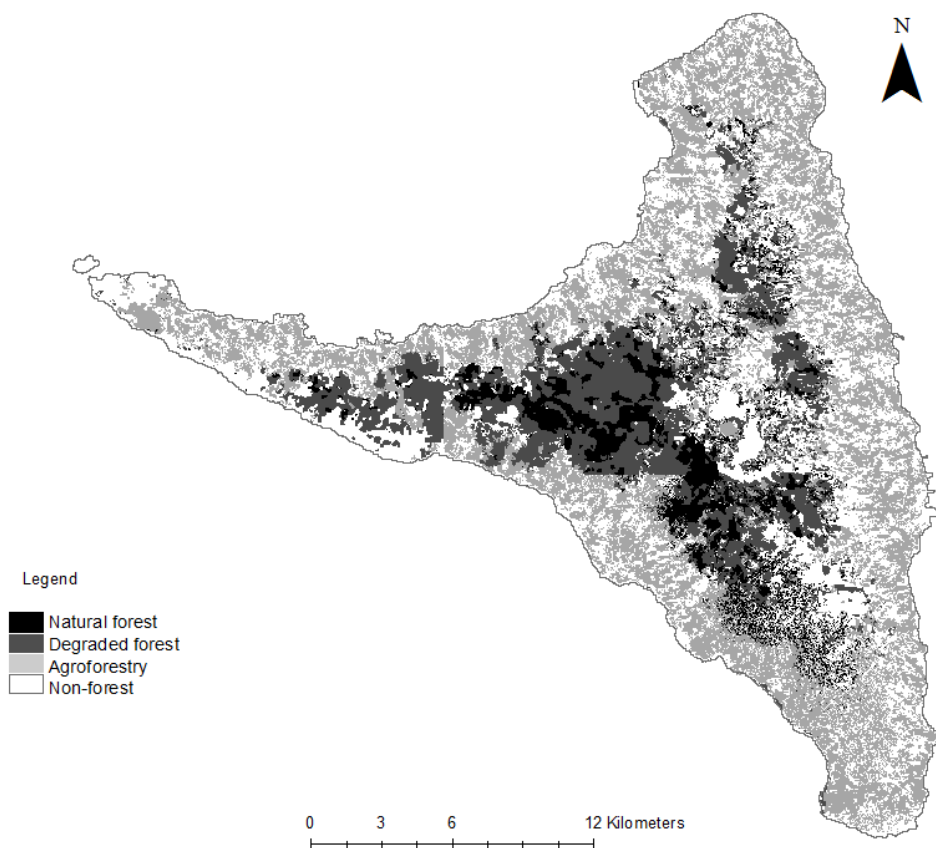


Figure 1. 4 Map of land cover on Anjouan (Green 2013). The map shows the four main habitat types that were identified by the ECDD project.

Table 1.1 Definitions of land cover classes identified on Anjouan, as defined by the ECDD project (reproduced from Green 2013: table 1)

Land cover class	Land cover sub-class	Definitions
Natural Forest		Little trace of human impact and a closed canopy. Heavy growth of moss on tree trunks and tree ferns present.
Degraded Forest		Closed canopy consisting of native species but some signs of human pressure such as selective logging and/or clearing of understory vegetation for firewood and fodder. Some presence of non-native trees or crops.
Agroforestry	Dense Agroforestry	Dense canopy dominated by agroforestry species. Natural or non-natural
	Open Agroforestry	More open canopy consisting of agroforestry species. Natural or non-natural understory.
Non-Forest	Plantation	Few native and/or non-native trees present but dominated by crops.
	Pasture	Largely grassland used for grazing livestock. Some native and/or non-native trees may be present.
	Scrub	Low vegetation cover, natural or non-natural. Some agriculture and/or trees.
	Padza	Very degraded land with little nutrients, very little low vegetation cover.

1.9 Thesis aims and objectives

Eulemur mongoz is Critically Endangered in Madagascar and faces extinction in the coming decades. Previous surveys on the Comoros have indicated continued habitat loss and decline in the population (Tattersall 1998) but have also highlighted the use of anthropogenic habitat and areas surrounding human settlements by the species (Clark 1997, Tattersall 1998, Nadhurou et al. 2017). The potential for *E. mongoz* on the Comoros to form a genetic pool or reservoir sub-population for future translocations to Madagascar has been suggested (Clark 1997, Nadhurou et al. 2017) but reliable abundance estimates are required to support this. Thorough, up-to-date surveys are needed to determine the current status on

the Comoros, and to inform the next Red List re-assessment of the species as well as any necessary conservation action.

My thesis focuses on the *E. mongoz* population on Anjouan. The aim of the thesis is to map distribution and obtain a population estimate on Anjouan, as well as to investigate habitat requirements of the species. This will contribute to an assessment of the status of *E. mongoz* on the Comoros, and identify its conservation needs on Anjouan. My project was conducted with the NGO Dahari, as part of research to identify terrestrial conservation priorities on Anjouan and influence conservation policy and practise in the Comoros (funded by Critical Ecosystem Partnership Fund, CEPF).

In chapter 2, I use species distribution mapping to predict habitat suitability across the island, based on environmental variables and presence records obtained from a combination of survey methods. This will produce a predictive distribution map of *E. mongoz* on Anjouan, and identify macrohabitat requirements and important areas for the species on the island. In chapter 3, I use hierarchical modelling to investigate the effect of habitat on abundance of *E. mongoz*, and distance sampling to estimate density of the species on Anjouan. This will identify microhabitat requirements and give a population estimate that can be used as a baseline for ongoing monitoring, and to give an indication of the current status of the population. In Chapter 4, I discuss the results and conservation implications of the thesis.

2. Chapter two. Using Species Distribution Modelling to predict the distribution of the mongoose lemur, *E. mongoz*, on Anjouan, Comoros.

Species distribution modelling can be used to predict occurrence of a species based on its environmental niche. This can be used to identify areas of suitable habitat for a species, and to inform management decisions. The distribution and conservation needs of *E. mongoz* on Anjouan are not currently known. In this chapter, I use species distribution modelling to predict the distribution, and to identify important areas of suitable habitat, for *E. mongoz* on Anjouan. I conducted species distribution modelling with a consensus approach, using presence data collected from transect, interview and camera trap surveys and opportunistic sampling. An area of 239 km² of suitable habitat was predicted, with 6 km² of highly suitable habitat. My results suggest that *E. mongoz* has a large range on Anjouan, with a wide tolerance to environmental variables and is flexible in its use of habitat. Reforestation to create corridors between patches of suitable habitat would improve habitat suitability on the island.

2.1 Introduction

Correlative species distribution models (SDMs), alternatively known by a variety of terms including habitat suitability models and ecological niche models, (Elith and Leathwick 2009), are empirical models relating species data to environmental conditions at known locations (Guisan and Zimmermann 2000, Guisan et al. 2017). SDMs use presence, presence-absence or abundance species data to identify known locations of species occurrence (Guisan and Thuiller 2005). Environmental conditions at these locations are defined by environmental predictor variables, usually obtained from digital maps; e.g., bioclimatic maps and digital elevation models (DEM) (Guisan and Zimmermann 2000). Environmental predictor variables can be classified along ecological gradients based on their impact on the species: direct (e.g., temperature), indirect (e.g., elevation) and resource (e.g., food) gradients (Austin 2002). These models provide information on potential species distribution, ecological niche limits and predicted occurrence or spatial habitat suitability for specific locations and across a landscape (Guisan and Zimmermann 2000, Elith and Leathwick 2009, Aguirre-Gutiérrez et al. 2013, Domisch et al. 2013, Franklin 2013).

The fundamental environmental niche of a species is defined by the environmental variables that allow the species to sustain viable populations (Hutchinson 1957). The area actually occupied by a species is termed the “realised niche”, which is the fundamental niche restricted by biotic factors (Hutchinson 1957, Pulliam 2000). The realised niche may be of a larger area than the fundamental niche, if part of this consists of sink habitat (Pulliam 1988, 2000). Sink habitat is habitat in which a population can occur but in which birth rate does not exceed death rate, so the population can only be maintained by immigration from nearby source habitat (Pulliam 1988). Correlative SDMs fit the realised niche of a species by modelling the distribution of suitable habitat, and this method is applied to studies using presence observations collected in the field (Guisan and Zimmermann 2000, Kearney and Porter 2009). Mechanistic SDMs are an alternative method that aims to fit the fundamental niche, instead linking data on physiological, morphological or behavioural traits to spatial habitat data and thus incorporating fitness components into the model (Kearney and Porter 2009).

Species distribution modelling is useful in conservation decision making and ecological management (Guisan and Thuiller 2005, Addison et al. 2013, Guisan et al. 2013). SDMs can be used to identify problems (Guisan et al. 2013), for example informing conservation status assessments to identify population decline (Rushton et al. 2004, Späth et al. 2018), predicting species invasions (Lozier and Mills 2011, Poulos et al. 2012, Barbet-Massin et al. 2018) and predicting the impact of climate change on species distributions (Beaumont et al. 2008, Barbet-Massin et al. 2009, Kearney et al. 2010). They may also inform solutions (Guisan et al. 2013); identification of critical habitat can improve monitoring (Fuller et al. 2018) and inform selection of suitable areas for species reintroduction (Ardestani et al. 2015, Chucholl 2017, Malone et al. 2018), protected areas (Fajardo et al. 2014, Pereira et al. 2018, Spiers et al. 2018), and wildlife corridors (Liu et al. 2013).

Information on species distribution and conservation status is required in order to make effective conservation management decisions (Guisan et al. 2013), particularly for endangered species (Hirzel et al. 2001, Rushton et al. 2004). The IUCN red list assessment criteria include measures of decline in population size, and restriction in the extent of occurrence (IUCN Standards and Petitions Subcommittee 2017). Species distribution modelling has become a key tool in species status assessments (Chefaoui et al. 2005, Ferraz et al. 2012) and is recommended by the IUCN Red List guidelines as a method of mapping

distributions with increased accuracy, to reduce uncertainty in status assessments (IUCN Standards and Petitions Subcommittee 2017). Increased accuracy is required to correctly identify sites of high habitat suitability (Guisan et al. 2006). Alternative methods such as use of survey data may offer incomplete or spatially-biased information on distribution (Wilson et al. 2005). Species distribution modelling is also a cost-efficient method as it enables prediction of occurrence in unsampled areas (Wilson et al. 2005, Guisan and Thuiller 2005, Elith et al. 2006).

Inclusion of SDMs in conservation programs increases their success, as they can identify environmental factors that limit distribution and affect survival (Corsi et al. 1999, Razgour et al. 2011, Guisan et al. 2013, Ibouroi et al. 2018). Identification of areas of best habitat suitability (Santos et al. 2006) and areas in which a species is more vulnerable (Márcia Barbosa et al. 2003) are key to effective conservation planning, as demonstrated by a multitude of case studies (e.g. Thorn et al. 2009, Marini et al. 2010, Wilting et al. 2010).

Eulemur mongoz is listed as Critically Endangered on the IUCN Red List due to hunting and habitat loss in Madagascar (Andriaholinirina et al. 2014). It occurs on Madagascar and in the Comoros, however as it was introduced by humans the Comoros population has not been included in the status assessment. It has been suggested that the Comoros population may act as a reservoir population and could be important for the conservation of the species (Clark 1997, Nadhurou et al. 2017), but the current status is not known. Up to date information on the status of the species on the Comoros is required, to identify conservation needs, and to inform conservation management of the species. In this study I aim to use species distribution modelling to predict the distribution of *E. mongoz* on Anjouan, based on predicted habitat suitability across the island. This will provide information on the status of the population, which may inform future status re-assessments for the species; will enable identification of suitable habitat for *E. mongoz*; and help to determine conservation priorities on Anjouan.

I aim to answer the following questions:

- 1) What is the current predicted distribution of *E. mongoz* on Anjouan?
- 2) Which environmental factors are important in determining their distribution?
- 3) Which areas on the island have the best habitat suitability for the species?

Although previous surveys have reported a decline in the population (Tattersall 1998), *E. mongoz* has been reported to have a wide distribution on Anjouan (Clark 1997). It is reported to use different habitat types (Tattersall 1976, 1998, Nadhurou et al. 2017), with larger group sizes in degraded forest (Nadhurou et al. 2017). As an ecologically flexible and successful introduced species, it is likely to be adaptable to a range of environmental conditions. I therefore predict that *E. mongoz* will have a wide tolerance to environmental variables and a large range on the island.

2.2 Methods

2.2.1 Data collection

We recorded presence data for *E. mongoz* across Anjouan (see Chapter 1 for a full description of the study site, including habitats found on Anjouan) from October 2015 to June 2016 using a combination of different survey methods. These were transect sampling, interviews with farmers, systematic camera trap sampling and opportunistic survey methods; which are described below.

Transects

Twenty-three transects of between 500m-1000m were established across the island using a random systematic sampling design created with QGIS 2.8.2 (QGIS Development Team 2015) (fig.2.1). Transects were 1000m in length where terrain permitted. Transects were positioned in a North-South direction, except for one which was positioned North East-South West due to inaccessible terrain. Three systematically determined points were found to be inaccessible, therefore these transects were relocated to randomly selected points within accessible forest. Transects were set up by walking from the starting point in a fixed direction using a compass and GPS to maintain accuracy. Trees were marked with paint to allow identification of the route on repeat surveys, and vegetation was not cut. Transects were walked between November 2015 and May 2016. Transects were surveyed using a distance sampling protocol, so that the transect data could also be used for distance analysis. Distance sampling entailed walking the transects at a slow and constant speed (less than 1km per hour). GPS points were collected for observations of lemurs along the transect where possible. For each observation, presence of a group, number of individuals in the group, and perpendicular distance (m) from the transect to the centre of the group at their

location when first detected were recorded. A total of 79 transect surveys were conducted including repeat surveys, with a range of 2-8 surveys per transect ($\bar{x} = 3.43, SD = 1.50$). This was because some sites were difficult to access frequently, and extra surveys could be conducted at some of the shorter transects. Transects were walked at different times of day, mostly during early morning (6:00-10:00) ($n=45$) and late afternoon (15:00-18:00) ($n=26$) when lemurs were observed to be more active. Four surveys were conducted at midday. Only four surveys were conducted after dark when lemurs were observed to be more active than during the day, as walking the transects at night proved to be difficult due to the nature of the terrain. Transects were surveyed by 1-6 observers ($\bar{x} = 2.75, SD = 1.42$). As the number of surveys at different time periods varied across transects, presence data could be biased towards transects with more early or late surveys. Combining transect data with opportunistic, camera trap and interview methods along transects aimed to increase the likelihood of obtaining true presence data across the survey area.

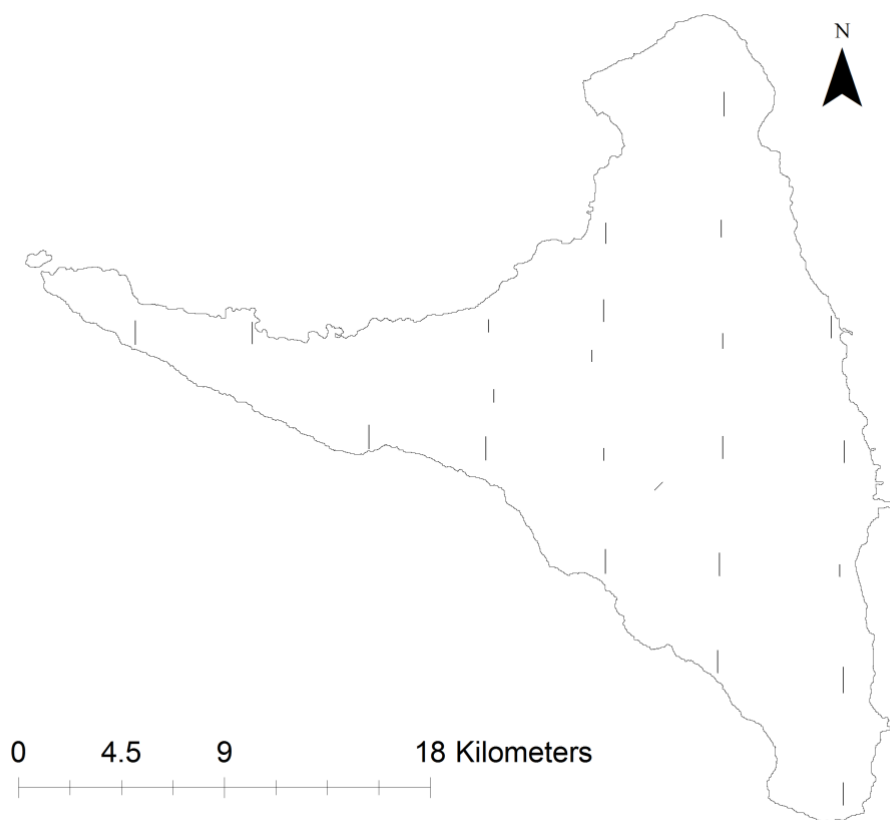


Figure 2. 1 Location of transects on Anjouan.

Interviews

Interviews were carried out opportunistically with farmers who were encountered during transect surveys or other field work during the study period. Farmers were asked if they had seen lemurs in the area; if they had, they were asked for specific information on the location, date and regularity of the sightings. GPS points were obtained for observations which were considered to be reliable (i.e., the interviewee could give clear details about the location and timings of the observation).

Camera traps

Bushnell 12MP Trophy Cam HD Essential Low Glow Trail cameras (model BN119736) were placed on all transects for between 2-4 days, between March-May 2016. One camera was placed close to the 500m point on each transect, in an accessible tree. If there were no accessible trees at this location, the camera was placed in the first accessible tree encountered on the transect. Cameras were placed inside a waterproof container which was secured to the trunk or a stable branch, at canopy level. Cameras were baited with bananas and set up to take photos at one-second intervals upon detection of movement. GPS points for locations in which cameras detected presence of lemurs were recorded.

Opportunistic sampling

GPS coordinates were recorded for opportunistic sightings of lemurs across the island throughout the study period.

2.2.3 Environmental layers

Nineteen bioclimatic variables from *WorldClim* (<http://www.worldclim.org>) were used. These consisted of average monthly climate data for minimum, mean and maximum temperature and precipitation between 1970-2000 (Fick and Hijmans 2017). These variables were downloaded and the data for Anjouan were extracted using *ArcGIS Spatial Analyst* (ESRI, Redlands, California, USA) and saved in image format as raster layers for analysis. Additional environmental layers that were created by the ECDD project were used, these were aspect, elevation, slope, distance from forest (comprising natural and degraded forest), distance from roads and urban areas, distance from rivers and habitat type (Green et al. 2015). Aspect is the compass direction the surface faces, in this case East to West (measured in degrees). Slope is the gradient of the surface (degrees or percent). Distance from forest is

the distance from core areas of natural and degraded forest, elevation is obtained from a 30m resolution digital elevation model (DEM) (Green et al. 2015). The habitat variable consisted of the four habitat types defined by the ECDD project: natural forest degraded forest, agroforestry and non-forest (Green et al. 2015) (table 1.1). These variables were chosen because they represent vegetation type, human impact, and environmental or climatic conditions that may affect habitat quality for *E. mongoz* on Anjouan. The bioclimatic variables were rescaled from 1km² to 5m² resolution by slicing without interpolation, using *ArcGIS spatial analyst*, to match the resolution of the ECDD layers. Spatial extent of all layers was also matched.

2.2.4 Statistical analysis

A range of algorithms can be used to fit SDMs (Aguirre-Gutiérrez et al. 2013), either in individual models or an ensemble of models (Guisan et al. 2017). Ensemble forecasting is a method of species distribution modelling that combines the results of several models fitted with different algorithms, using different techniques (Araujo and New 2007). As there can be significant variability between alternative model projections, and different algorithms may have different levels of accuracy, this method can result in a more robust forecast than an individual model (Elith et al. 2006, Araujo and New 2007). Consensus forecasting is a method of examining results of an ensemble model by calculating the mean or median of the ensemble of forecasts (Araujo and New 2007). This allows the main trend to be extracted from the range of model projections in the ensemble, and therefore the error of the consensus forecast should be lower than that of an individual forecast (Araujo and New 2007). Ensemble modelling with consensus forecasting was applied to this dataset.

Species distribution models require the following assumptions to be met: that the environmental variables represent all the important predictors for the niche; that the species observations are appropriate for the model; that appropriate statistical methods are used; that the environmental variables are accurately measured; that the species data are unbiased and species observations are independent (Guisan et al. 2017). A minimum of 30 presence observations are needed to produce accurate results, with more than 50 presence points being the recommended sample size (Guisan et al. 2017), The selected variables are thought to represent environmental conditions on the island, and are all considered to be of ecological importance to the lemurs. The species observations are not based on measures of

fitness therefore it is not possible to exclude sink populations if present, however the dataset is appropriate for a correlative SDM. The selected model is appropriate for presence data. It is difficult to ensure that all important predictors for the niche are represented by the environmental variables, however the selected variable layers contain the most accurate environmental data available for the modelled cells. Systematic sampling was conducted to collect unbiased data and any spatially biased points were removed from the dataset.

2.2.4.1 Model fitting and evaluation

Ensemble modelling was carried out using *R* 3.4.1 (R Development Core Team 2017) *BIOMOD2* package (Thuiller et al. 2009). The following five algorithms were selected to construct the ensemble models (Aguirre-Gutiérrez et al. 2013): Maximum Entropy Modelling *maxent* (MaxEnt) (Phillips et al. 2006), Generalised Boosted Model *gbm* (GBM) (Ridgeway 1999), Random Forest *randomForest* (RF) (Breiman 2001), Generalised Linear Models *glm* (GLMs) (McCullagh and Nelder 1989) and Generalised Additive Model *gam* (GAM) (Hastie and Tibshirani 1999). GAM models were run with a spline function, with three degrees of smoothing. As the selected algorithms require the use of background data, pseudo-absence data were randomly generated across the study area, excluding locations of presence points (Zaniewski et al. 2002, Barbet-Massin et al. 2012). The number of pseudo-absences generated was ten times the number of presence points in the model, with one replicate set of pseudo-absences and 10 repeat model runs to reduce bias (Barbet-Massin et al. 2012). This method was selected because model accuracy has been found to increase as number of pseudo-absences approaches 10000 (Barbet-Massin et al. 2012).

A repeated split sample cross-validation procedure was used to evaluate models, whereby 80% of the original dataset was used for model calibration (training set) and was evaluated against the remaining 20% (validation set), with area under the curve (AUC) of the receiver operating characteristic (ROC) (Swets 1988). This was repeated ten times, with training and evaluation data randomly selected for each run. An AUC < 0.70 indicates poor model fit and an AUC > 0.90 indicates excellent model fit (Swets 1988). The influence of important variables on the probability of species presence was analysed using the evaluation strip procedure (Elith et al. 2005). Committee averaging methods were implemented in the consensus forecast, whereby the unweighted median forecast was selected to obtain the average forecast from the ensemble of models (Araujo and New 2007). This gave equal

weighting to all models in the ensemble, and ensured that accuracy of the ensemble forecast was higher than at least half of the individual models (Araujo and New 2007). Relative contribution of environmental variables to the model was assessed using a permutation test (Thuiller et al. 2016).

2.3 Results

A total of 159 presence points were collected across the island. The largest number of points was obtained from opportunistic sampling, followed by interviews (table 2.1; Fig. 2.2). As more points were obtained from opportunistic sampling than any other method, duplicated and clustered presence points that were recorded at frequently visited locations (n=69), were removed prior to analysis to reduce sampling bias. This ensured that there was no more than one point per grid cell in the final dataset. Ninety presence records were kept for the model. Pearson’s correlation test was used to test the environmental variables for multicollinearity. Variables with a correlation value of > 0.60 were rejected from the model (table 2.2); these were elevation, annual mean temperature, isothermality, max temperature of warmest month, min temperature of coldest month, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, mean temperature of coldest quarter, precipitation of wettest month, precipitation of driest month, precipitation seasonality, precipitation of wettest quarter, precipitation of driest quarter and precipitation of coldest quarter. Of 15 variables, 11 were retained (table 2.2): aspect, distance from roads and urban areas, distance from forest, distance from rivers, slope, habitat, mean diurnal range, temperature seasonality, temperature annual range, annual precipitation and precipitation of warmest quarter.

Table 2.1 Number of presence records obtained using each method

Method	Number of presence records
Transects	11
Opportunistic sampling	94
Camera traps	10
Interview	44

Table 2.2 Environmental variables that were included or excluded from the species distribution model.

Excluded environmental variables	Included environmental variables
Elevation	Aspect
Annual mean temperature	Distance from roads and urban areas
Isothermality	Distance from forest
Max. temperature of warmest month	Distance from rivers
Min. temperature of coldest month	Slope
Mean temperature of wettest quarter	Habitat
Mean temperature of driest quarter	Mean diurnal range
Mean temp warmest quarter	Temperature seasonality
Mean temp coldest quarter	Temperature annual range
Precipitation of wettest month	Annual precipitation
Precipitation of driest month	Precipitation of warmest quarter
Precipitation seasonality	
Precipitation of wettest quarter	
Precipitation of driest quarter	
Precipitation of coldest quarter	

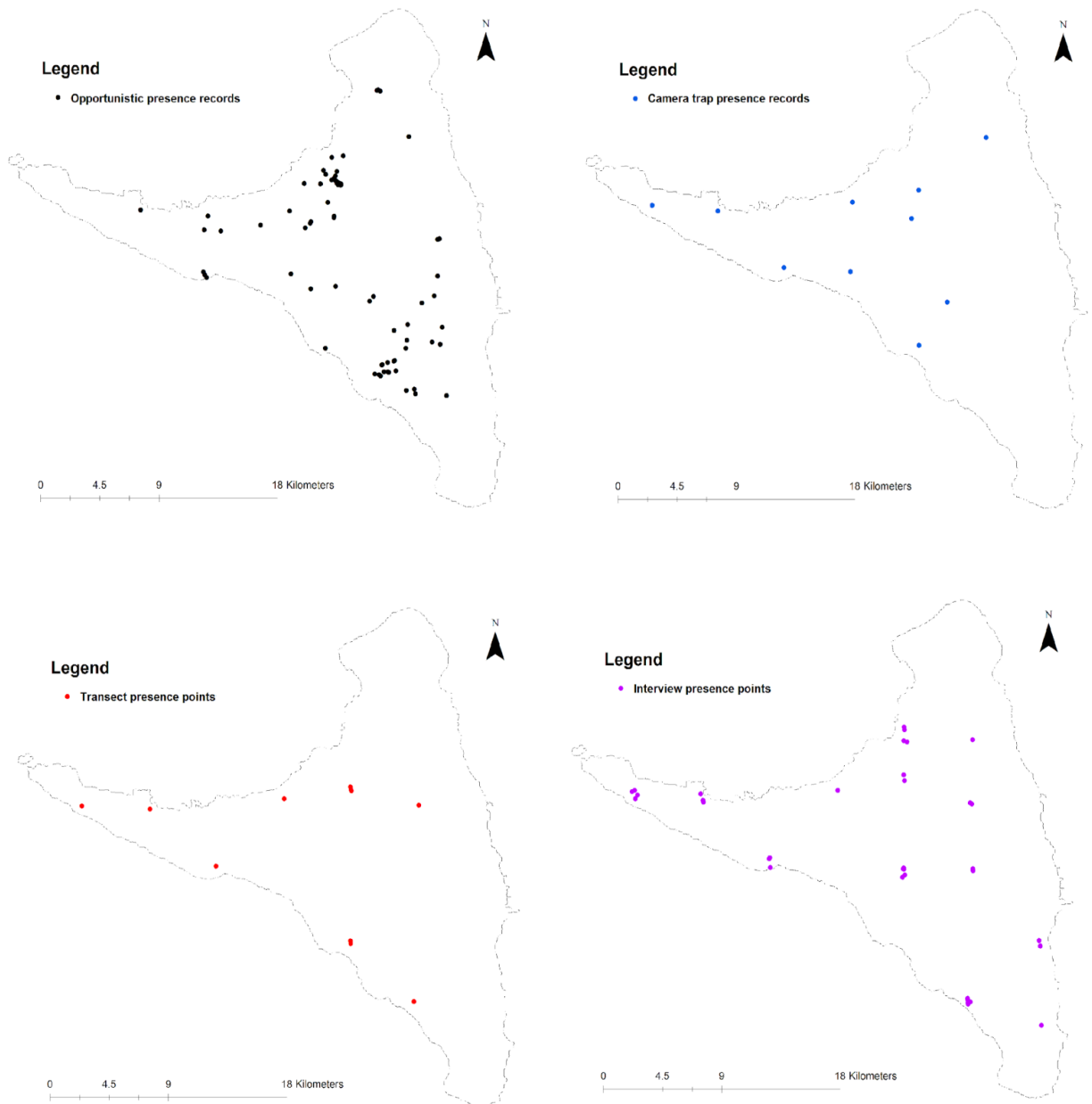
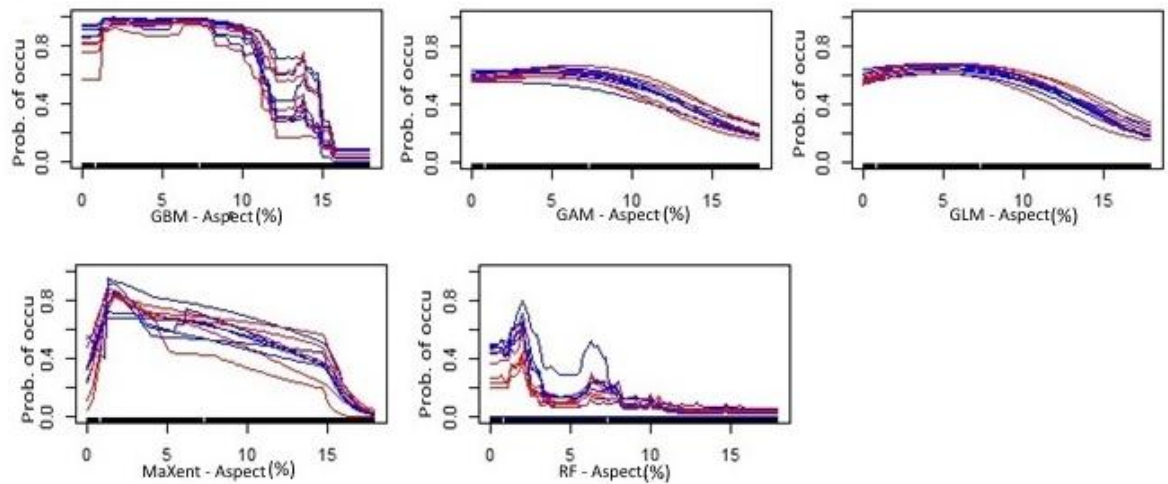


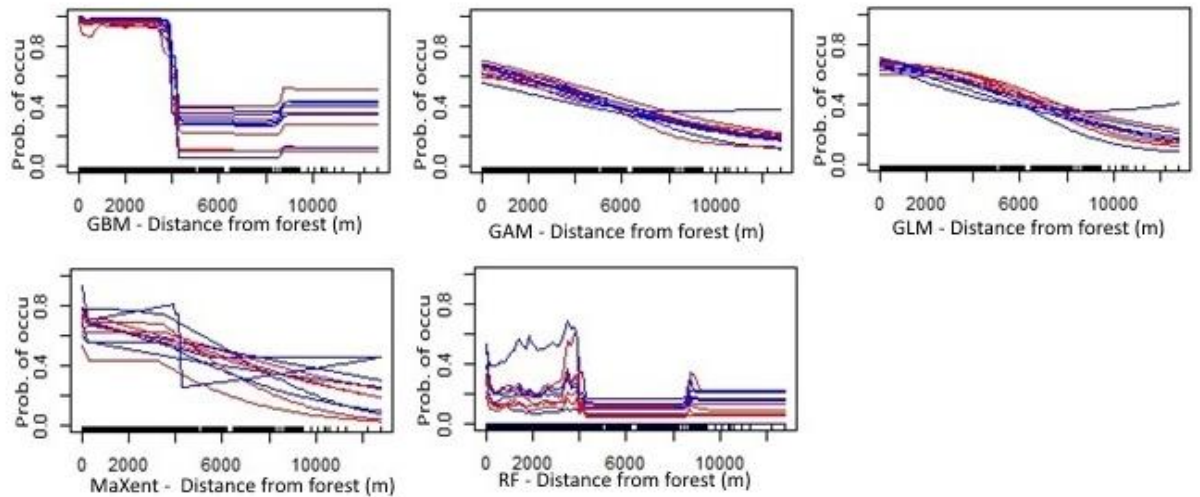
Figure 2.2 Distribution of presence records obtained using each sampling method: opportunistic sampling (top left), camera trap (top right), transect (bottom left), interview (bottom right).

Prior to running the consensus forecast, a total of 50 models were produced for the ensemble model. Variable response curves for these models show the relationships between the environmental variables and probability of occurrence that are predicted by the individual algorithms (fig.2.3). Probability of occurrence is predicted to decrease as aspect moves from west to east (fig.2.3a). Overall, probability of occurrence is predicted to decline as distance from forest increases (fig. 2.3b). Probability of occurrence is predicted to be

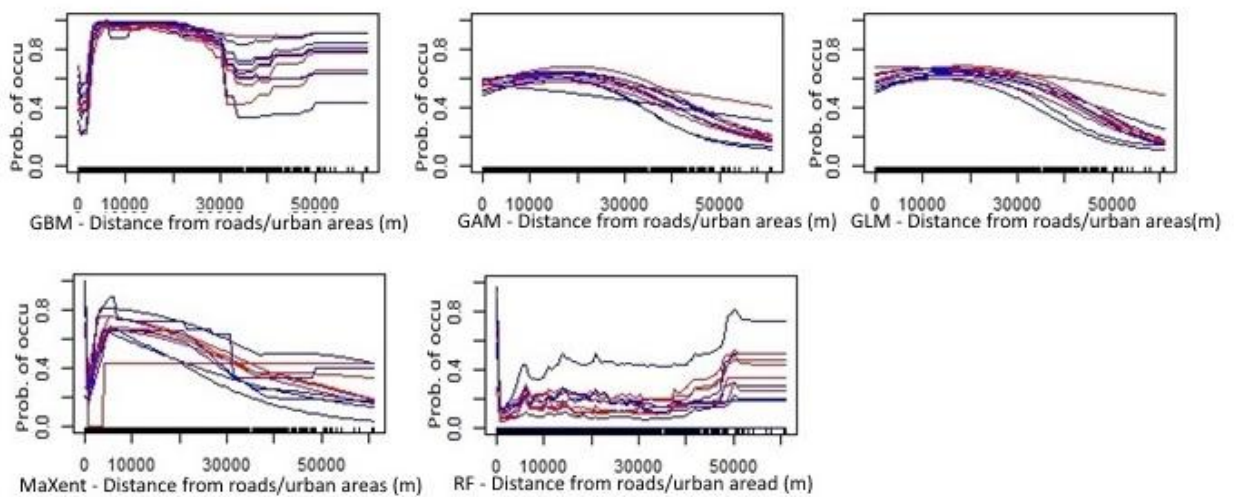
higher in relative close proximity to roads and urban areas but the relationship varies according to the algorithm used; overall, higher probability of occurrence is predicted at short-to-intermediate distances from roads (fig. 2.3c). The response curves indicate a negative correlation between probability of occurrence and slope (fig. 2.3d). Four out of five algorithms suggest a slight increase in probability of occurrence at the furthest distance from rivers but this relationship is weak (fig. 2.3e). There is no strong relationship between temperature seasonality and probability of occurrence (fig. 2.3f). There is slight variation in the relationship between probability of occurrence and habitat type between algorithms; GAM and GLM indicate an increase in probability of occurrence as habitat type approaches natural forest, whereas MaxEnt and RF show a peak in probability of occurrence in degraded forest (fig. 2.3g). There is variation between algorithms in the relationship between probability of occurrence and precipitation in warmest quarter, with MaxEnt and RF indicating a slight dip at the lower end of the scale (fig. 2.3h); overall there is no strong relationship. Response curves indicate a dip in probability of occurrence at higher levels of annual precipitation (fig. 2.3i). There is a weak relationship between probability of occurrence and temperature annual range (fig. 2.3j). There is no strong relationship predicted between probability of occurrence and mean diurnal range (fig. 2.3k).



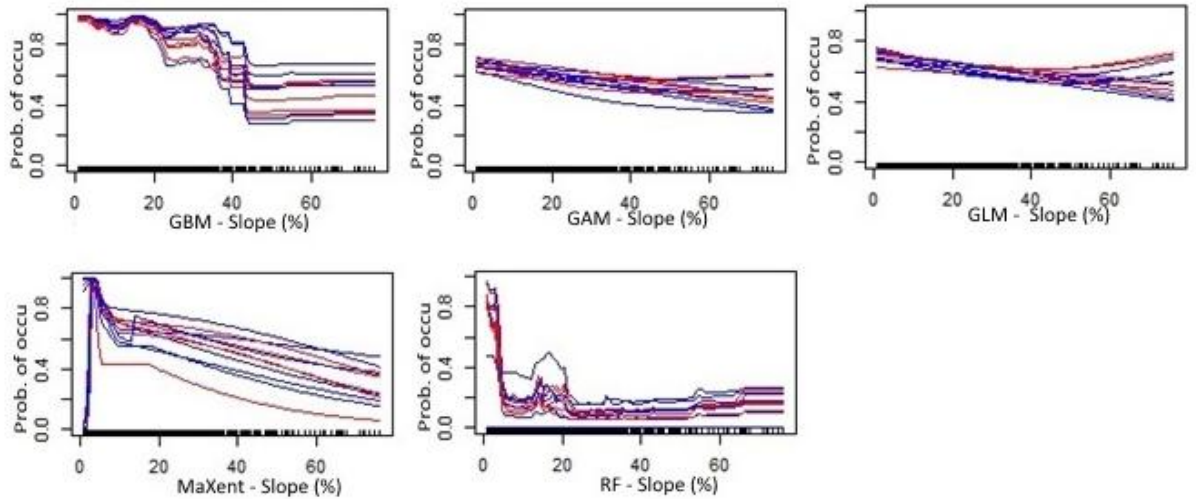
a. Response curve of variable 'Aspect' with 10 runs for each algorithm (x axis represents 'Aspect' and y axis represents 'probability of occurrence').



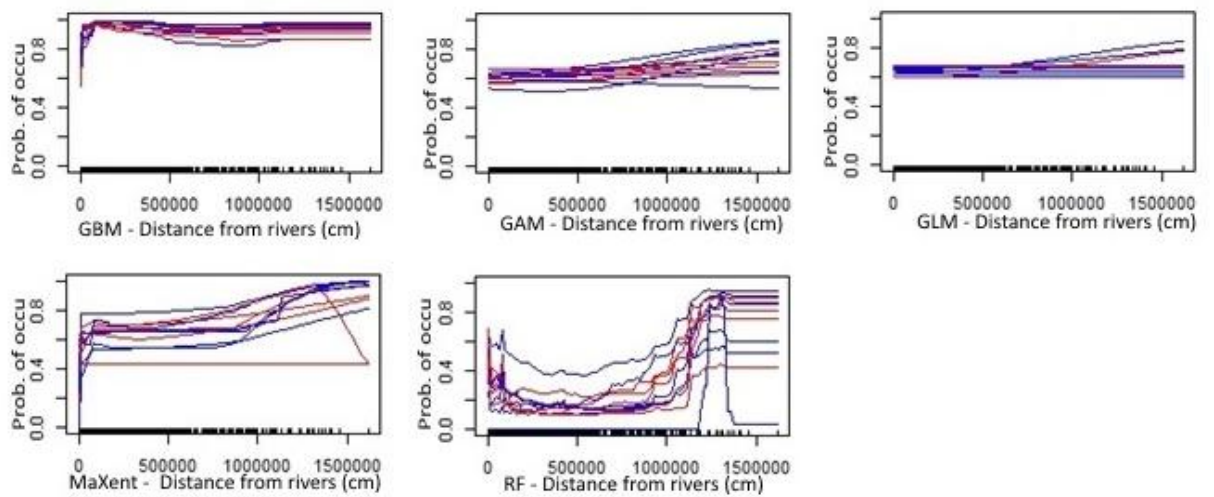
b. Response curve of variable 'Distance from forest' with 10 runs for each algorithm (x axis represents 'Distance from Forest' and y axis represents 'probability of occurrence').



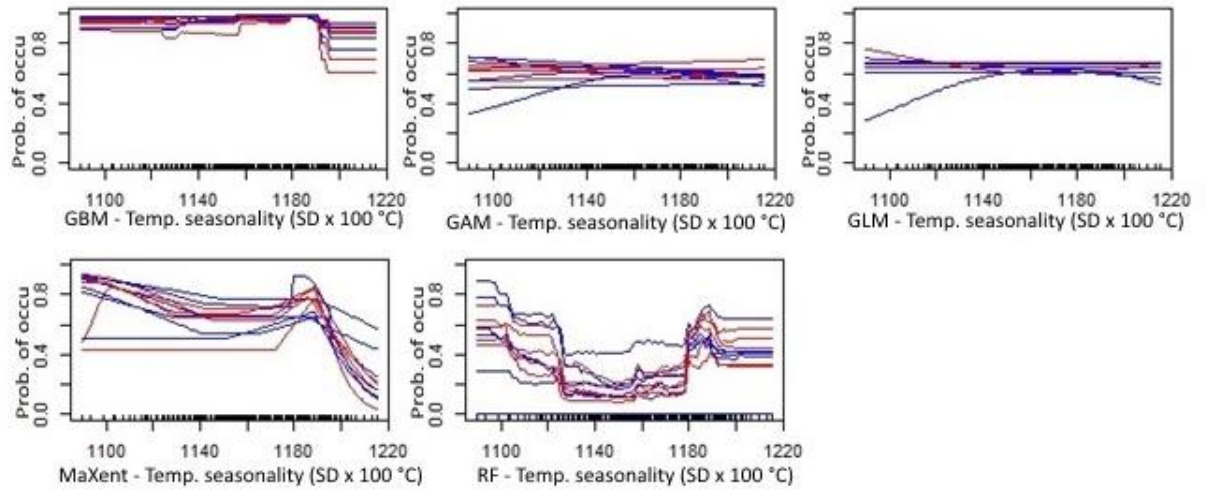
c. Response curve of variable 'Distance from Roads and Urban Areas' with 10 runs for each algorithm (x axis represents 'Distance from Roads and Urban Areas' and y axis represents 'probability of occurrence').



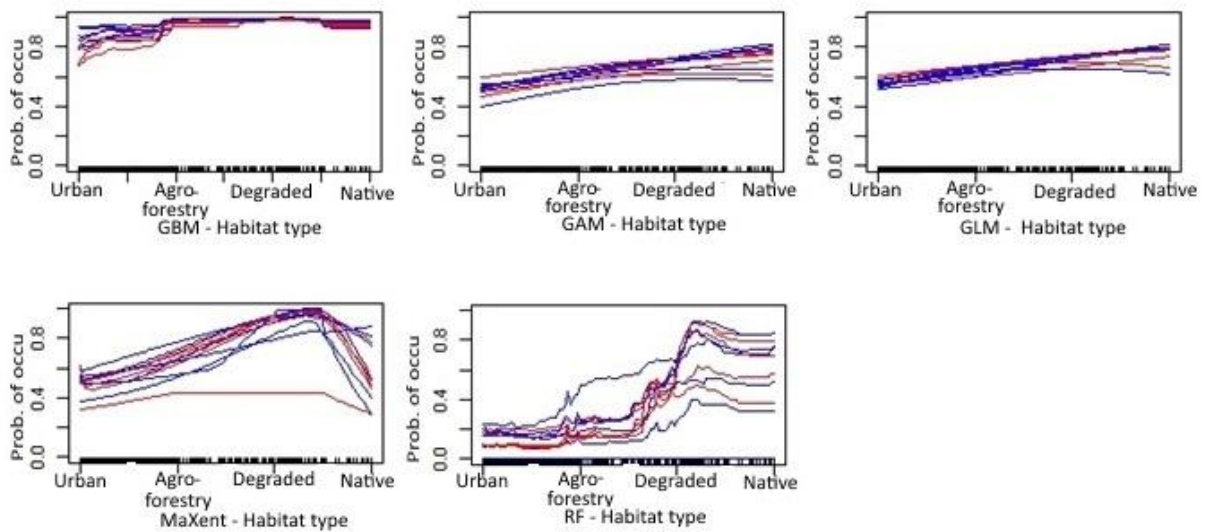
d. Response curve of variable 'Slope' with 10 runs for each algorithm (x axis represents 'Slope' and y axis represents 'probability of occurrence').



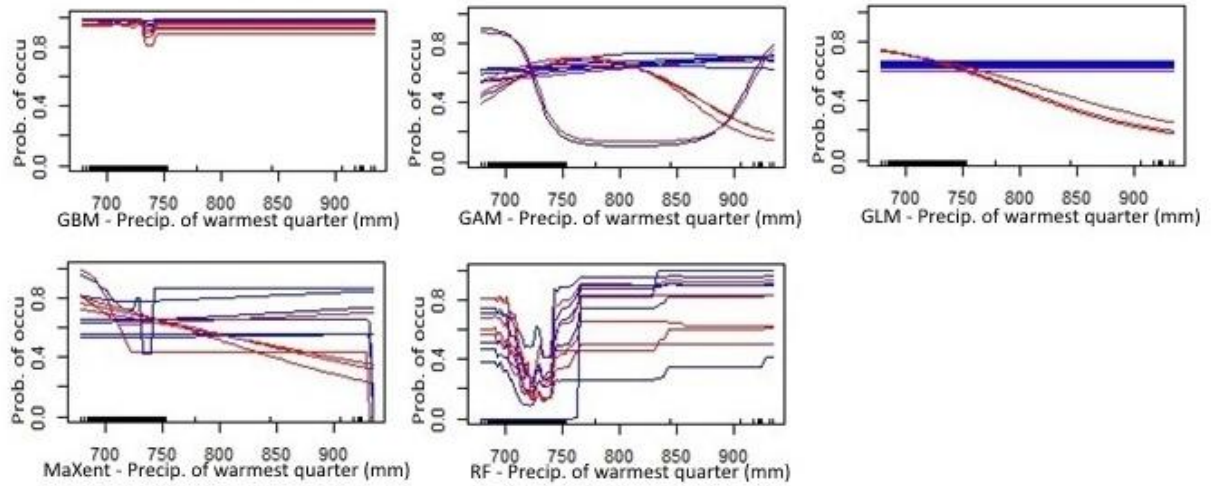
e. Response curve of variable 'Distance from Rivers' with 10 runs for each algorithm (x axis represents 'Distance from Rivers' and y axis represents 'probability of occurrence').



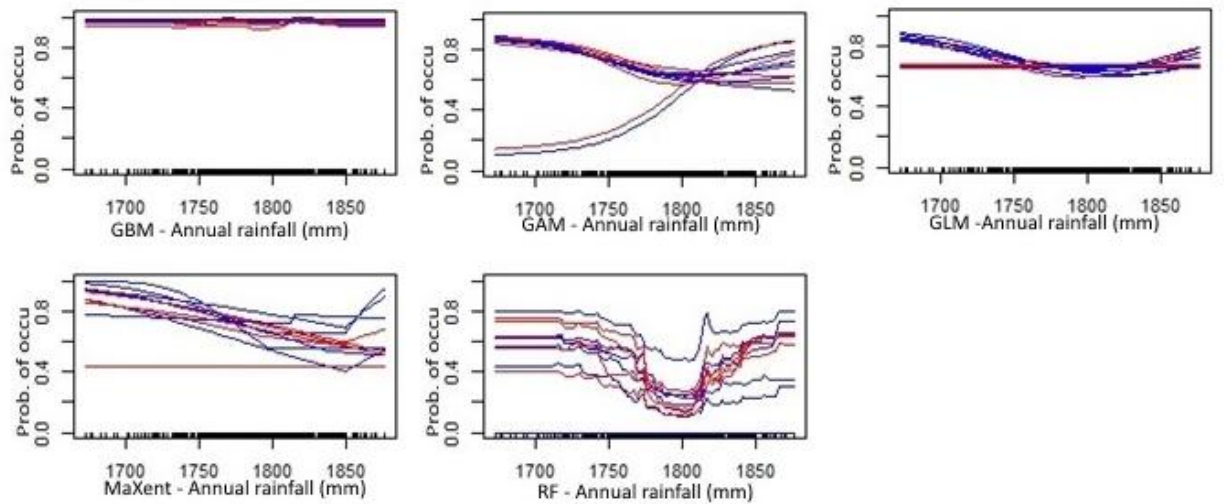
f. Response curve of variable 'Temperature Seasonality' with 10 runs for each algorithm (x axis represents 'Temperature Seasonality' and y axis represents 'probability of occurrence').



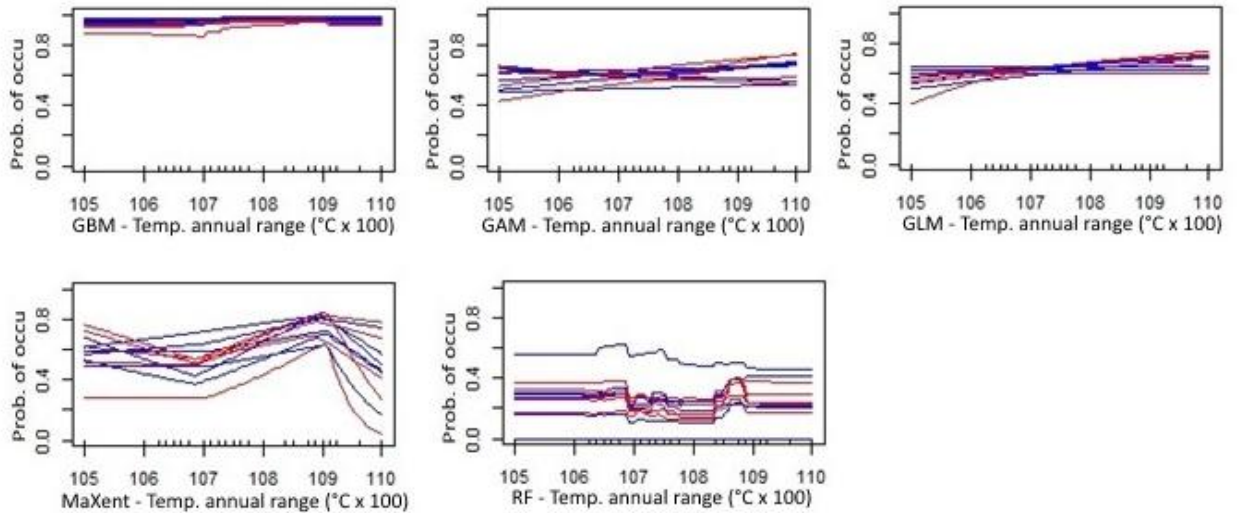
g. Response curve of variable 'Habitat Type' with 10 runs for each algorithm (x axis represents 'Habitat Type' and y axis represents 'probability of occurrence').



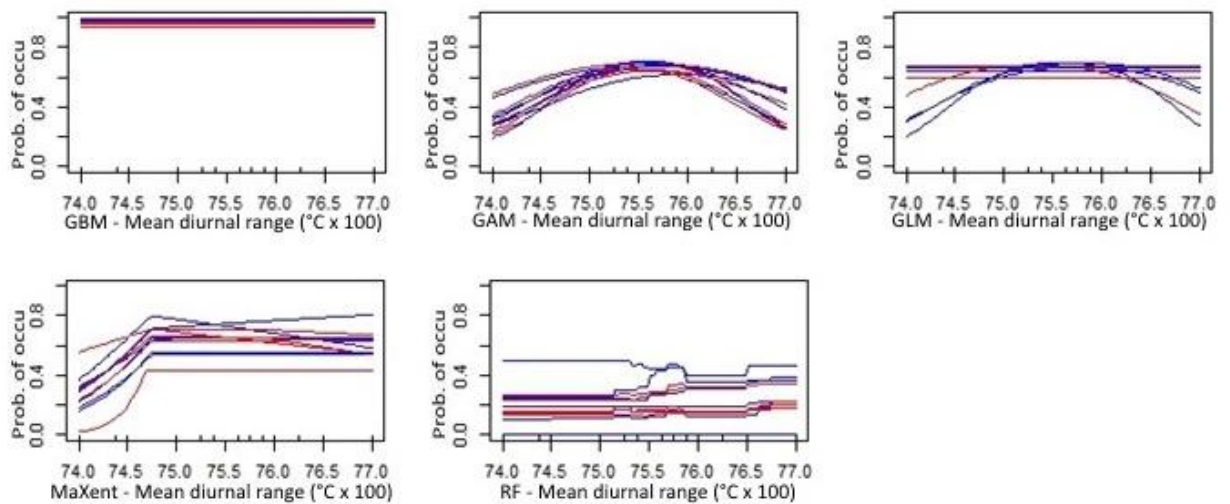
h. Response curve of variable 'Precipitation of Warmest Quarter' with 10 runs for each algorithm (x axis represents 'Precipitation of Warmest Quarter' and y axis represents 'probability of occurrence').



i. Response curve of variable 'Annual precipitation' with 10 runs for each algorithm (x axis represents 'Annual precipitations' and y axis represents 'probability of occurrence').



j. Response curve of variable 'Temperature Annual Range' with 10 runs for each algorithm (x axis represents 'Temperature Annual Range' and y axis represents 'probability of occurrence').



k. Response curve of variable 'Mean Diurnal Range' with 10 runs for each algorithm (x axis represents 'Mean Diurnal Range' and y axis represents 'probability of occurrence').

Figure 2.3 (a-k) Variable response curves for each environmental variable, with separate plots for each algorithm. Each graph shows the predicted probability of occurrence of lemurs in response to the environmental variable, for one of the five algorithms (GBM, GAM, GLM, MaxEnt and RF), with a response curve for each model run (10 repeats for each algorithm).

The selected consensus model was considered an excellent fit, with an AUC of 0.98. A prediction threshold of 0.47 was used to maximise the sensitivity and specificity of the model, which were 100% and 87% respectively. This threshold was used to convert probability of habitat suitability (fig 2.4) to presence/absence distribution (fig 2.5). The model predicts a suitable habitat range of 239km² for *E. mongoz* on Anjouan (56% of the island). An area of 6km² of highly suitable habitat (>80% probability of suitability) was predicted. The variables that contributed most to the model were aspect, distance from forest, distance from roads and urban areas, and slope (table 2.3).

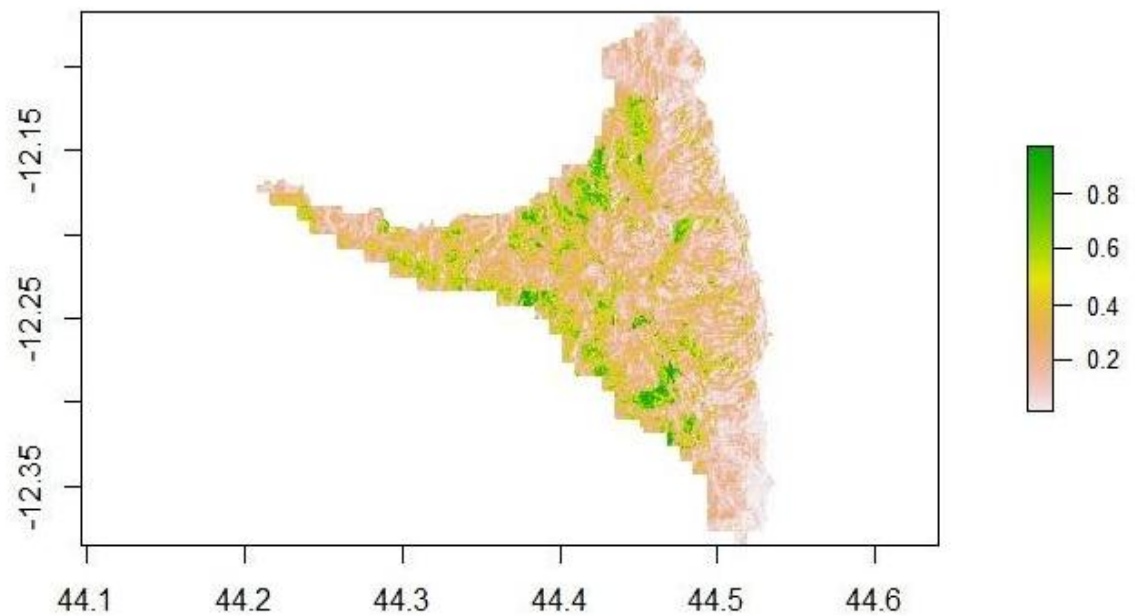


Figure 2.4 Projected habitat suitability map for *E. mongoz* on Anjouan. The scale bar represents probability of habitat suitability: dark green areas indicate a higher suitability.

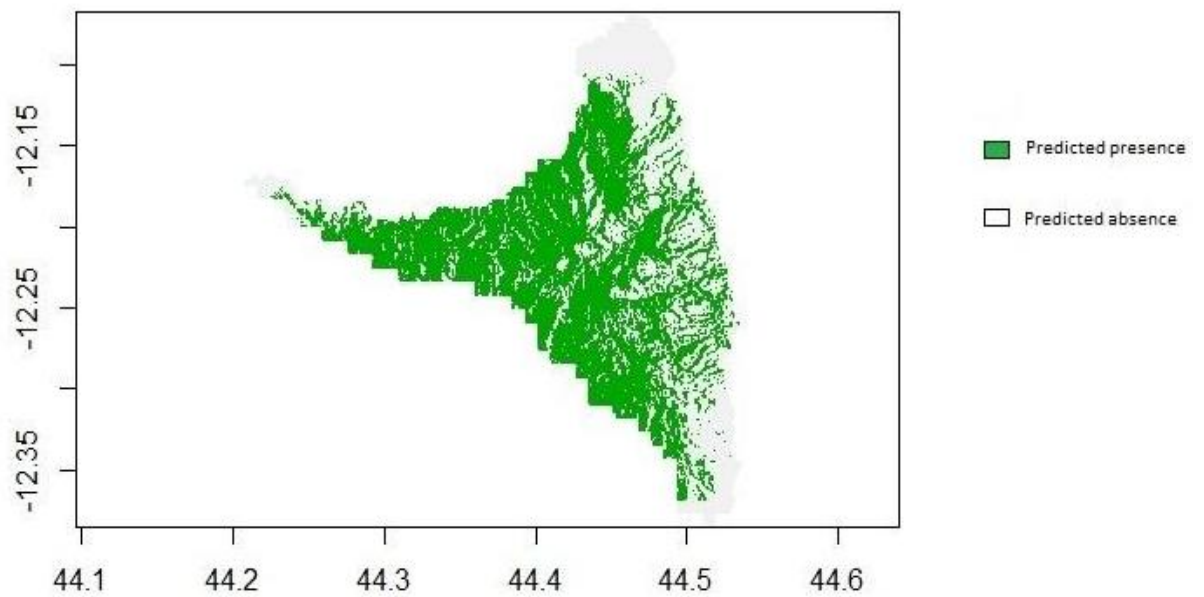


Figure 2.5 Binary projection for *E. mongoz* distribution. Green represents cells in which the species was predicted to be present based on the occurrence probability threshold.

Table 2.3 Results of the variable importance test.

Variable	Variable Importance
Aspect	0.34
Distance from forests	0.21
Distance from roads and urban areas	0.12
Slope	0.13
Distance from rivers	0.07
Temperature seasonality	0.06
Habitat	0.05
Precipitation of warmest quarter	0.03
Annual precipitation	0.02
Temperature annual range	0.01
Mean diurnal range	0.02

2.4 Discussion

In this chapter, I have used species distribution modelling with a consensus approach to predict habitat suitability for *E. mongoz* on Anjouan. The consensus model predicted an area of 239 km² of suitable habitat on Anjouan (56% of the island). This suggests that the species has a potentially wide range. Of the predicted area of suitable habitat, 6 km² is predicted to be highly suitable (>80% probability of suitability). The environmental variables that contributed most to the model were aspect, distance from forests (natural and degraded forest), distance from roads and urban areas, and slope. Habitat type and bioclimatic variables were of low importance in the model. The habitat suitability map indicates that areas of most suitable habitat are located in the Moya forest, the Vouani region, Trindrini and Lingoni regions on the southwest side; in the northwest from Moimoi to Patsy; and more centrally in the Nyantranga area and the valley adjacent to Chandra and Tsembehou. Based on the landcover map, these areas incorporate all habitat types and mostly consist of agroforestry, degraded forest and natural forest. Overall the results support my prediction that *E. mongoz* would have a wide range, and indicate that *E. mongoz* is flexible in its use of habitat on Anjouan.

The variable importance tests predict that habitat suitability decreases with distance from forests, which indicates that both natural and degraded forest offer suitable habitat for the species. The most recent study of *E. mongoz* on the Comoros reported larger group sizes in degraded forest than in other habitat types, which was suggested to indicate higher food availability in this habitat (Nadhrou et al. 2017). Degraded forest on Anjouan forms a buffer around the small remaining area of native forest and contains a mix of native and exotic food resources. *E. mongoz* is therefore able to survive in both forest types.

The variable importance tests also predict that the most suitable habitat occurs at an intermediate distance from roads and urban areas. Based on the land cover map, agroforestry tends to occur closer to roads and urban areas, therefore this result suggests that agroforestry can also offer suitable habitat for *E. mongoz*. Surveys in 1997 reported the presence of *E. mongo* in close proximity to many villages, with some local reports of crop foraging (Clark 1997). *E. mongoz* is known to use agroforestry (Tattersall 1976, 1998, Nadhrou et al. 2017) and was also frequently observed feeding on agroforestry crops during my study. Primates with flexible diets are able to obtain a higher diversity of food

items in urban areas due to ready availability of human foods or crop foods (Maibeche et al. 2015). *E. mongoz* exhibits dietary flexibility (Rasmussen 1999) and therefore may be more adaptable to anthropogenic habitat; additionally, as a predominantly frugivorous species, it is able to exploit the abundance of fruit crops produced in agroforestry.

It is possible that sampling bias may have been introduced into the model as a result of the large number of presence points collected opportunistically, and this may also have contributed to the importance of distance from roads and urban areas in the model. Although clustered points were removed from the model, some opportunistic data may have been biased towards more accessible and frequently visited areas. This may also be reflected by the negative relationship between slope and habitat suitability, which indicates that the steepest areas are less suitable for lemurs. The remaining natural forest is restricted to steep slopes at high elevation, as these areas are least accessible by people. As lemurs are using natural forest, the result may not mean that steep areas are unsuitable, and may be due to false absences in the model due to the difficulty of sampling on steep slopes. It may however also be the case that suitable habitat occurs in less steep zones due to the occurrence of suitable degraded forest and agroforestry.

Aspect was of high importance in the model, with more suitable habitat predicted on west-facing slopes than on the east side of the island. Aspect can influence vegetation characteristics at a site by affecting levels of solar radiation, which determines soil moisture and temperature (Geiger 1965, Oke 1987, Bennie et al. 2008); therefore habitat quality could be affected by lower levels of solar radiation on the east side. However, it is more likely that the lower habitat suitability on the east is the result of more intense anthropogenic land use. There is a more gradual incline towards the central ridge on the east, therefore land is more accessible, which may have resulted in more intense human activity. Habitat on this side consists of more non-forest (urban areas and plantation) containing smaller, more isolated patches of agroforestry, and an absence of degraded forest. Agroforestry is included in areas of predicted suitable habitat on the island, but the smaller more isolated patches of this habitat on the east may contain a lower quality and quantity of food (Arroyo-Rodríguez and Mandujano 2006). There is little connectivity between agroforestry patches in the east and the central area of more suitable habitat. Lack of connectivity between patches of agroforestry may render these uninhabitable

(Ramanamanjato and Ganzhorn 2001). *E. mongoz* was seen foraging in urban areas on the island but these are likely to have been accessible from suitable habitat.

Distance from rivers, habitat type, temperature seasonality, precipitation and temperature range variables were of lower importance in the model. The variable importance test indicates a slight positive relationship between distance from rivers and habitat suitability. Field observations suggested that suitable habitat occurred near to rivers and streams, as lemurs were often seen or reported close to rivers, where vegetation was more continuous and relatively dense. Riparian vegetation can act as corridors for lemurs between forest fragments (Eppley et al. 2015) and our field observations suggested that rivers may form corridors connecting patches of agroforestry. However, my results may reflect sufficient availability of suitable habitat on the island, such that lemurs do not depend on riparian corridors. Habitat type was of low importance in the model, and this variable does not have a strong relationship with habitat suitability, although the response curves suggest a slight increase in habitat suitability in degraded or native forest. This demonstrates that the species is flexible in its use of habitat, but may confirm the importance of degraded and native forest on the island. Temperature seasonality, precipitation and temperature range variables were of low importance in the model and did not have clear relationships with habitat suitability. Temperature seasonality was correlated with elevation, therefore temperature seasonality may vary according to elevation on the island. The species is able to survive at high elevations and in the lowlands, and as a cathemeral species, changes its activity patterns according to season and elevation (Rasmussen 1999, Curtis et al. 1999, Curtis and Rasmussen 2003). Cathemerality has been linked to temperature in Anjouan (Tattersall 1976) and this behavioural strategy may enable the species to cope with different bioclimatic conditions.

Overall, the results suggest that the species has a wide tolerance to environmental variables and uses all habitat types on the island. As *E. mongoz* is ecologically flexible, it has been able to expand its niche with changing land use (Eppley et al. 2017) and has adapted successfully to degraded and agroforestry habitats. Ecological flexibility may be a factor in the successful colonisation of Anjouan by *E. mongoz*. Introduced species may be better at exploiting resources than native species (Sakai et al. 2001), which may have enabled *E. mongoz* to exploit new agroforestry habitat. Introduced species are also able to expand their niche due to absence of competitors (Bolnick et al. 2010). On Anjouan, the endemic *Pteropus*

seychellensis comorensis (Seychelles fruit bat), and *Pteropus livingstonii* (Livingstone's Fruit Bat) have some dietary overlap, but *E. mongoz* seems not to be limited by competition for resources. As an ecologically flexible, introduced species, *E. mongoz* is therefore able to occupy a broad niche on the island.

The large predicted range on Anjouan has positive implications for the conservation of the species. *E. mongoz* is currently listed as Critically Endangered on the IUCN Red List based on a suspected reduction in size of the population on Madagascar of 80% or more over a three-generation period, as well as continuing decline in area, extent and quality of habitat in Madagascar (Andriaholinirina et al. 2014). Using the results of this chapter, the status of the species could be re-assessed against IUCN Red List evaluation criterion B (geographic range), to incorporate the Comoros population. For a species to be listed as Endangered according to criterion B, based on geographic range in the form of area of occupancy (AOO), an AOO of between 10km² and 500km² is required, as well as two of three sub-criteria relating to fragmentation, continuing decline in population parameters and extreme fluctuations in population parameters (IUCN 2012). The predicted area of suitable habitat on Anjouan is 239 km², which meets the criteria for listing in the Endangered category. For a full assessment based on this criterion, further monitoring would be required to investigate decline or fluctuations in demographics in the Comoros, as well as surveys to determine area of occupancy on Mohéli and Madagascar. My result however suggests that the population on Anjouan is less threatened than the Madagascar population, and hypothetically, inclusion of the Comoros population in a species status assessment based only on area of occupancy could enable the down-listing of the species to Endangered or Vulnerable. Due to the continued population decline and unceasing threats to the species in Madagascar, down-listing may not be advisable; however, this encouraging result demonstrates the conservation value of the Comoros population.

2.5 Conclusion

The species distribution model predicts a large area of suitable habitat for *E. mongoz*, with a smaller area of optimal habitat. It can be inferred that they have a wide tolerance to habitat type, using natural and degraded forest and agroforestry, which may be close to urban areas. These results are encouraging for the conservation of the species, as they suggest that it is less threatened on the Comoros than in Madagascar, and support claims that the

Comoros population may act as a genetic reservoir for future conservation work. The large estimated range predicted by the consensus model is encouraging as this suggests that suitable habitat occurs across the island. However, as the predicted area of highly suitable habitat is much smaller, the species could benefit from habitat management such as reforestation and creation of corridors to improve connectivity between all the patches of suitable habitat.

3. Chapter three. Population size and habitat use of the mongoose lemur, *E. mongoz*, on Anjouan, Comoros.

The population of *E. mongoz* on the Comoros could be an important insurance or source population for the species, as it is highly threatened in Madagascar, however, information on the status of this population is lacking. In this chapter, I aim to obtain a population estimate for *E. mongoz* on Anjouan, and to investigate microhabitat requirements, in order to inform conservation management for the species. I used distance sampling to estimate population density on the island. I used hierarchical *N*-mixture modelling to predict the effect of habitat on abundance of *E. mongoz*, using data collected on transect surveys and vegetation surveys. A density of 23 lemurs per km² and a population size of 9919 (95% CI 5541-17755) lemurs were estimated on the island. Density of *Syzygium aromaticum* (clove) and species richness were found to have a significant effect on lemur abundance. The population estimate suggests that *E. mongoz* is less threatened on Anjouan than on Madagascar. The results suggest that species richness is a microhabitat requirement and species rich degraded forest and agroforestry are important habitats, which may provide a diversity of fruit resources.

3.1 Introduction

Identifying population trends and providing accurate information on population size allows conservation priorities to be determined. This can be achieved by conducting a conservation status assessment such as the IUCN Red List assessment, which is an essential tool in species conservation (Vie et al. 2009). For example: if a species population has declined by 90% or more over ten years or three generations, the species will be listed as Critically Endangered on the IUCN Red List (IUCN 2012). Based on this information, a conservation action plan can be implemented to mitigate causes of decline.

Conservation action plans often include habitat management, because loss of habitat is a significant driver of species population decline (Brooks et al. 2002). Habitat characteristics are linked to abundance and population trends (Krausman 1999) because a species has specific habitat requirements for its survival (the ecological niche) (Hutchinson 1957). Investigating habitat associations, or the relationship between habitat characteristics and

species abundance is a time and cost-efficient method of identifying habitat requirements of the species (Krausman 1999). Knowledge about the habitat requirements of a species is needed for effective conservation management (Morrison et al. 1998, Manly et al. 2002, Buckland et al. 2008), and to ensure that resources are not wasted (Sillett et al. 2012). For example, this can enable identification of areas of habitat to protect (Maeda 2001) or plant species and habitat types to include in reforestation or habitat restoration.

Habitat associations may vary according to spatial scale, and habitat use is recommended to be investigated at different scales (Wiens et al. 1987). Habitat can be characterised at different spatial scales; e.g., biogeographic scale (contains different climates, vegetation and species), regional scale (contains different habitat patches and local populations), local scale (a patch that many individuals can occupy) and individual scale (the space that a single individual occupies) (Wiens et al. 1986). Habitat spatial scales can also be grouped into two categories: macrohabitat (incorporating geographic, landscape and patch) and microhabitat (patch and finer scale habitat features) (Block and Brennan 1993, Krausman 1999). Patch-scale characteristics have a significant influence on species abundance (Mazerolle and Villard 1999). These include features such as vegetation composition and structure (Mazerolle and Villard 1999).

Eulemur mongoz is found in the Comoros and Madagascar, and is listed as Critically Endangered in Madagascar by the IUCN Red List assessment (Andriaholinirina et al. 2014), but its status is unknown in the Comoros. It has been suggested that the population could act as a future source for translocation to Madagascar (Clark 1997, Nadhrou et al. 2017), however, this is based on preliminary surveys. Additionally, given the level of threat to the Madagascar population, the Comoros population needs to be protected to safeguard the future of the species. A status assessment is required to determine if action needs to be taken to protect the Comoros population and to ascertain if it has the potential to act as a reservoir population.

My study investigates the effect of patch-scale characteristics on abundance, to identify microhabitat use of *E. mongoz*. My study has two aims: first, to investigate the relationship between habitat patch characteristics and *E. mongoz* abundance in order to identify potentially important habitat characteristics for the species, and second, to obtain a population estimate for *E. mongoz* on Anjouan. This will contribute to status assessment,

help to determine the need for conservation action to protect the *E. mongoz* population on Anjouan, and inform conservation action relating to habitat management. A population estimate will also provide baseline figures for ongoing population monitoring. I investigate habitat use at the microhabitat level, to complement the information on macrohabitat obtained in the second chapter of my thesis. I will use distance sampling to obtain the population estimate, and I will test the effect of habitat characteristics on abundance using hierarchical *N*-mixture modelling.

My study aims to answer the following questions:

- 1) Which habitat patch characteristics influence lemur abundance; specifically, are density of native species, non-native species or plant species diversity important?
- 2) What is the current estimated population size of *E. mongoz* on Anjouan?

As I discussed in chapter 1, *E. mongoz* is reported to use anthropogenic habitat and may be ecologically flexible. Surveys conducted in the 1980s indicated that density was higher in native forest than in anthropogenic regrowth (degraded forest and agroforestry) (Tattersall 1998), whereas recent surveys reported larger group sizes in degraded forest (Nadhrou et al. 2017). This may suggest that the species is adaptable in its habitat use and has shifted to more anthropogenic habitat use following loss of native forest habitat. I predict that density of native plant species will not be an important habitat requirement for *E. mongoz* because the species is ecologically flexible and a habitat generalist.

3.2 Methods

3.2.1 Data collection

Twenty-three transects of between 500m-1000m were established across the island (see section 2.2.1).

Transects were surveyed using a distance sampling protocol (see section 2.2.1). For the hierarchical modelling and distance sampling analysis, each 1000m transect was subdivided into two transects of 400m and 500m in length, and the intervening 100m section was discarded to ensure independence. Transects were subdivided to increase sample size and to obtain habitat covariates at a finer scale. Transects that were originally less than 700m

were not subdivided. This resulted in a total of 38 transects of between 400m-700m (fig. 3.1).

For the purposes of hierarchical modelling and distance sampling, the number of groups of lemurs observed on each transect survey was recorded, as well as the number of lemurs in each group. At the start of each transect, time, temperatures and altitude were recorded.

Vegetation surveys were conducted along the same transects, on separate occasions to the lemur surveys. The number of individuals of each plant species within 5m of each side of the transect and with a diameter at breast height (dbh) of more than 5cm, was recorded. It was considered that plants of >5cm dbh could produce food items for lemurs, e.g. young leaves. Plant species were identified by trained ecologists.

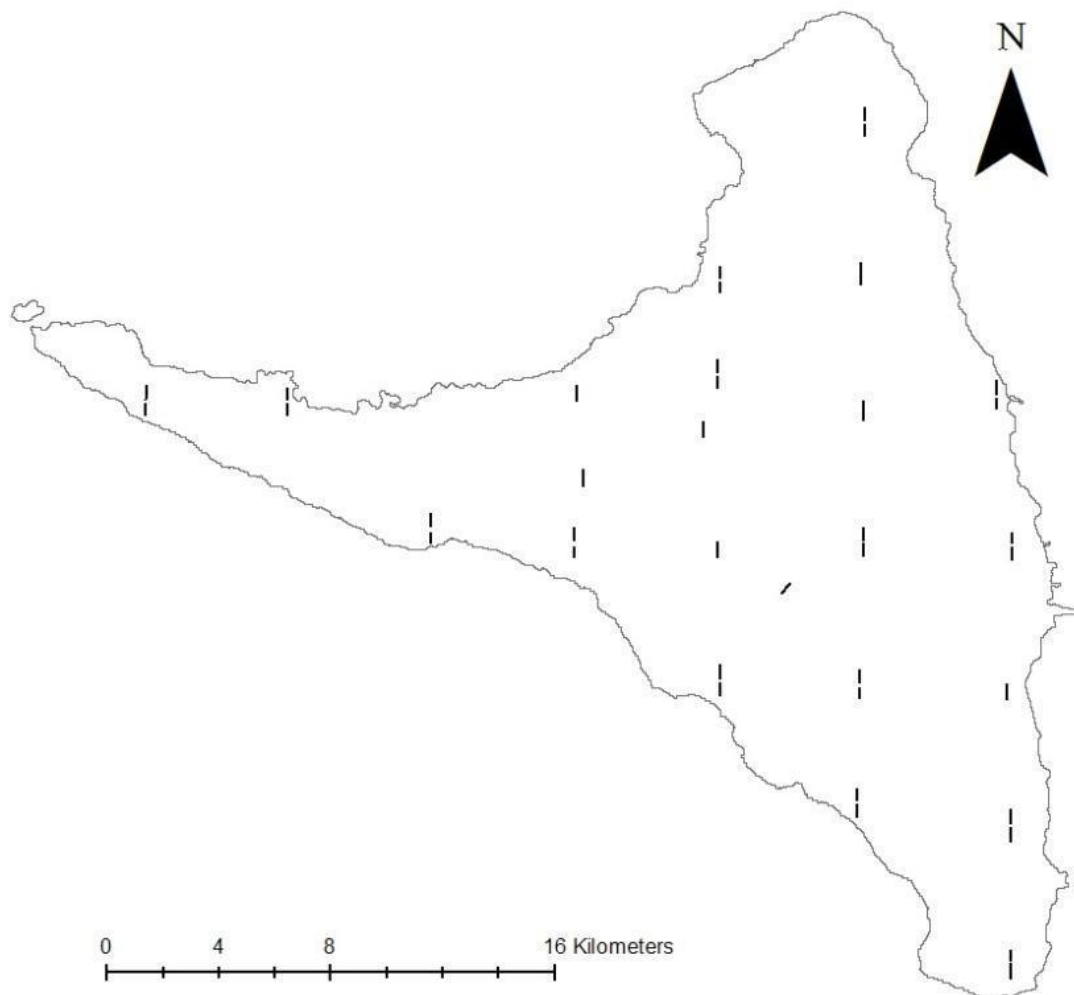


Figure 3.1 Map of Anjouan showing locations of sub-divided transects, indicated by black lines.

3.2.2 Statistical analysis

3.2.2.1 Abundance modelling

Binomial N -mixture modelling was used to estimate abundance and detection probabilities, and to model the effects of covariates on abundance. This was conducted using R package *unmarked* (Fiske and Chandler 2011). N -mixture modelling is a method of hierarchical modelling of the spatial variation in true abundance of a species (variation that does not result from the sampling method) (Royle 2004a), and of the probability of detecting the species during surveys (Kéry and Royle 2016). This is achieved by hierarchical modelling of the effects of observation-level covariates on the detection process and the effects of site-level covariates on species abundance (Royle 2004a). The hierarchical model consists of two linked GLMs; a poisson regression to model the state process (variation in abundance), and a logistic regression to model the observation process (detection probability), using replicated count data. In my study, surveys may result in imperfect detection of lemurs due to factors such as weather conditions. Time of survey, temperature and date were selected as observation-level covariates as these may influence lemur activity. Lemur abundance at a site can be influenced by factors such as vegetation characteristics and altitude, therefore these were used as site-level covariates in this study. N -mixture modelling enables abundance estimation without identifying individuals (Royle 2004b, Mazerolle et al. 2007). It requires spatially replicated count data (Royle 2004a), therefore repeat transect surveys were conducted.

The N -mixture model assumes that the population being sampled is closed to recruitment, mortality and movement (Royle 2004b); that there are no false-positive errors; that individuals are detected independently of each other; that all individuals at a site have an identical detection probability; and that abundance follows the distribution specified in the model (Kéry and Royle 2016). Sampling was conducted within a single season to meet the assumption of closure. There are no false positives in the data: only observations that were certain to be lemurs were included, this was easily verifiable as there were no other primates on the island with which *E. mongoz* could be confused. As *E. mongoz* occurs in groups, number of observations of groups rather than individuals were used as the count

variable in order to meet the assumptions of independent and identical detection. Goodness of fit tests were conducted to ensure that the abundance fit the model distribution.

For the site-level covariates, vegetation data from each transect were compiled. From this data, the following site-level covariates were derived for each transect: density ha^{-1} of trees, plant species diversity (Shannon-Wiener index), plant species richness, density ha^{-1} of native trees, density ha^{-1} of non-native trees, and densities ha^{-1} of the six most common plant species recorded on transects (including four fruiting species that lemurs were observed to use for food): *Musa* spp., *S. aromaticum*, *Cyathea boivinii* (native fern), *C. nucifera*, *Gliricidia sepium* (exotic shrub used for forage and fencing in agriculture) and *M. indica*. Altitude was also included as a site-level covariate. Temperature, time of day and date were included as observation-level covariates. Date was converted to Julian date for analysis.

Multicollinearity for site-level and observation-level covariates were tested separately with Spearman's rank order correlation coefficient, and least informative variables with correlation values of >0.60 were excluded (density of trees, plant species diversity, density of non-native trees, density of *C. boivinii*) from the analysis. The site-level covariates included in the global model were plant species richness, density of native trees, density of *M. indica*, density of *Musa* spp., density of *C. nucifera*, density of *S. aromaticum* and density of *G. sepium*. All observation-level covariates were included in the model. Covariate data were scaled to minimise collinearity (Logan 2010).

The *dredge* function in *MuMIn* R Package (Barton 2018) was used to select the most parsimonious model from the global model by an information theoretic approach, using corrected Akaike Information Criterion values corrected for small sample size (AICc) as sample size (n) / number of parameters (k) was less than 40 (Burnham and Anderson 2002). A parametric bootstrapping Chi Square goodness of fit test was used to determine model adequacy. Three alternative abundance models (Poisson, negative binomial and zero-inflated Poisson) were compared using AIC (Kéry and Royle 2016).

3.2.2.2 Distance sampling

Distance sampling analysis was conducted using *Distance* 7.1 release 1 (Thomas et al. 2010). Distance sampling is a method of estimating density of an object (usually an animal) based

on probability of detection on a line transect (Thomas et al. 2010). Probability of detection is modelled as a function of distance from the line; the distribution of distances of animals to the line is used to estimate the proportion of animals being detected (Thomas et al. 2010). The method makes the following key assumptions: all objects on the line are detected; objects have not moved in response to the observer before detection; and distance measurements are accurate (Thomas et al. 2010).

As the species occurs in groups, objects were specified as clusters (groups) and cluster sizes (number of individuals in each observed group) were included in the observation data layer. As recommended by Buckland *et al.* (2001), four models were considered in the analysis: uniform, half-normal and hazard rate key functions for detection (detection functions) with cosine, simple polynomial and hermite polynomial expansions (adjustment terms). Goodness of fit of the model was found to increase after truncating the data at 5%, which is recommended when the dataset contains extreme outliers (Buckland et al. 1993, 2001). The best model was selected based on Akaike Information Criteria values corrected for small sample sizes (AICc) (Sugiura 1978, Burnham and Anderson 2002).

3.3 Results

3.3.1 Vegetation survey

The vegetation data were used to obtain site-level vegetation covariates for hierarchical modelling. For each transect, the density of six common species, density of trees, plant species diversity (Shannon-Wiener index), plant species richness, density of native trees and density of non-native trees were calculated. The averages for each vegetation covariate across transects are shown in table 3.1. A total of 84 different plant species were identified on vegetation surveys, of which 29 were native (35%) and 55 introduced (65%). The ten most common plant species identified in the surveys are shown in table 3.2.

Table 3.1 Mean and standard deviation of each vegetation covariate across transects

Covariate	Mean (\bar{x})	Standard Deviation
Density of trees (ha^{-1})	53.92	38.79
Species richness	8.18	4.12
Density of native species (ha^{-1})	12.93	35.32
Density of non-native species (ha^{-1})	41	28.97
Density of <i>S. aromaticum</i> (ha^{-1})	5.66	5.77
Density of <i>C. nucifera</i> (ha^{-1})	3.6	3.13
Density of <i>M. indica</i> (ha^{-1})	2.73	2.32
Density of <i>Musa</i> spp. (ha^{-1})	14.23	23.04
Density of <i>G. sepium</i> (ha^{-1})	2.76	6.29
Density of <i>C. boivinii</i> (ha^{-1})	5.07	15.49
Shannon-Wiener index	1.47	0.43

Table 3.2 The ten most common plant species identified on transects. The results were based on total density across all transects

Species	Density (ha^{-1})	Status
<i>Musa</i> spp.	151	Introduced
<i>Syzygium aromaticum</i>	55	Introduced
<i>Cyathea boivinii</i>	50	Native
<i>Cocos nucifera</i>	34	Introduced
<i>Gliricidia sepium</i>	27	Introduced
<i>Mangifera indica</i>	27	Introduced
<i>Cananga odorata</i>	21	Introduced
<i>Jatropha curcas</i>	20	Introduced
<i>Pterocarpus indicus</i>	12	Introduced
Other <i>Syzygium</i> spp.	10	Introduced

3.3.2 Effect of habitat on abundance

A total of 130 transect surveys were conducted on 38 transects (with 2-8 repeat surveys per transect), in which 22 groups containing a total of 74 lemurs were recorded. The three

alternative models were tested for over-dispersion. The Poisson distribution showed signs of over-dispersion in the global model, therefore was not selected for model fitting. The negative binomial and zero-inflated Poisson distributions both fit the abundance model. The zero-inflated Poisson resulted in a lower AIC than the negative binomial, but as this difference was small (3.15) and the negative binomial model produced more realistic abundance predictions, the negative binomial distribution was selected. The most parsimonious model was chosen (table 3.3), this included temperature as the detection covariate, and species richness and density *S. aromaticum* as site covariates. Abundance of lemurs was found to significantly increase with increasing plant species richness ($b= 0.92$, $z=3.74$, $P<0.01$) and with increasing density of *S. aromaticum* ($b=0.80$, $z=3.34$, $P<0.01$). There was no significant effect of temperature on detection of lemurs ($b=0.13$, $z=0.58$, $P=0.56$).

Table 3.3 Model selection table for the hierarchical model (k = number of parameters, AICc= AIC corrected for small sample size; Delta AICc= difference in AICc to that of the best candidate model; AICc Weight =Likelihood of model being the best candidate model).

Site covariates	Obs covariates	K	AICc	Delta AICc	AICc Weight
Species richness + density of <i>S. aromaticum</i>	Temperature	5	108.8	-	0.20
Species richness + density of <i>S. aromaticum</i> + density of <i>G. sepium</i>	Temperature	6	111.5	2.63	0.05
Density of <i>Musaspp.</i> + density of <i>S. aromaticum</i> + species richness	Temperature	6	111.6	2.78	0.05
Density of <i>S. aromaticum</i> + species richness	No covariate	4	111.7	2.86	0.05
Density of <i>S. aromaticum</i> + density of <i>M. indica</i> + species richness	Temperature	6	111.7	2.88	0.05
Density of trees + density of <i>S. aromaticum</i> + species richness	Temperature	6	111.7	2.90	0.05
Density of <i>C. nucifera</i> + density of <i>S. aromaticum</i> + species richness	Temperature	6	111.8	3.01	0.05
Density of <i>S. aromaticum</i> + species richness	Temperature + time	6	113.8	4.95	0.02
Density of <i>S. aromaticum</i> + density of <i>G. sepium</i> + species richness	No covariate	5	113.9	5.07	0.02
Density of <i>Musa spp.</i> + density of <i>S. aromaticum</i> + species richness	No covariate	5	114.1	5.32	0.01

3.3.3 Density estimate

The total survey effort for distance sampling was 78.5 km. The uniform model with a cosine adjustment term best fit the data, with the lowest AICc (Table 3.4). The model ran without error and goodness of fit tests indicated good model fit ($\chi^2 = 0.36$, $df = 4.00$, $p = 0.99$). The detection curve shows a decreasing detection probability with distance from transect, with no evasive movements before detection (Fig. 3.3). The model estimated a density of 23 lemurs per km^2 , and an abundance of 9919 (95% CI 5541-17755) lemurs within the total land cover of Anjouan. This was based on an expected group size of 3.97 individuals (95% CI 3.69-4.26). The sample size of 22 lemur groups recorded on transects is fewer than the recommended sample size of 40-80 for distance analysis (Buckland et al. 2001), therefore this may have effected precision, and could explain the wide confidence intervals for the abundance estimate.

Table 3.4 Model selection for distance analysis.

Model	AICc	Density (lemurs ha^{-1})	Coefficient of Variation (%)	Abundance	Lower 95% CI	Upper 95% CI
Uniform/cosine	148.51	0.23	29.72	9919	5541	17755
Uniform/simple polynomial	149.83	0.19	27.51	8075	4698	13878
Half-normal	148.94	0.23	30.76	9605	5263	17529
Hazard rate	150.65	0.29	52.68	12164	4421	33468

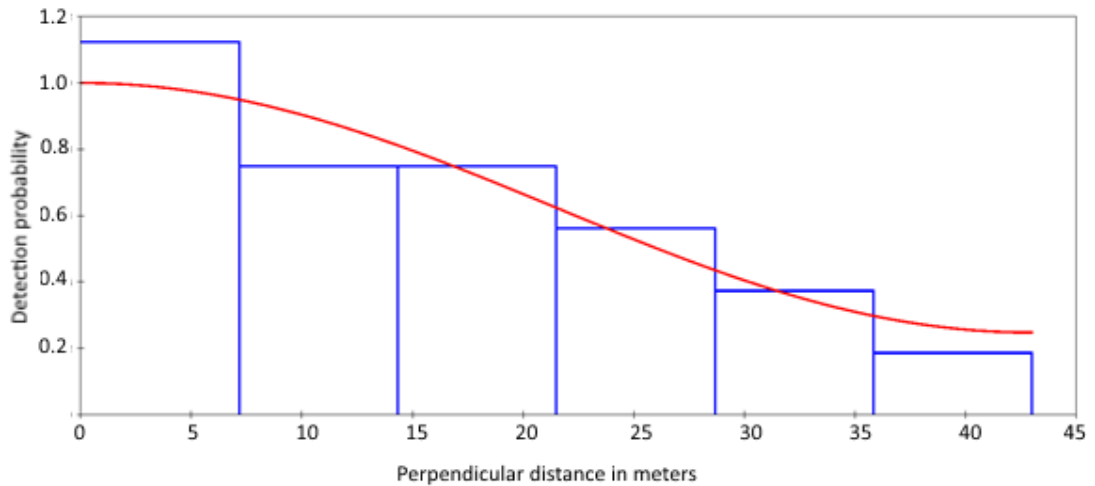


Figure 3.2 Graph showing the probability of detecting *E. mongoz* on transects. Probability of detecting *E. mongoz* on transects is shown as a function of perpendicular distance from the transect. The red line represents the detection function and the histogram represents observations of lemurs. Probability of detection decreases gradually with increasing distance from the transect, which shows that the data met the assumptions of distance sampling.

3.4 Discussion

In this study, hierarchical modelling identified a positive relationship between lemur abundance and density of *S. aromaticum*, as well as species richness. Distance sampling resulted in an estimate of 9919 (95% CI 5541-17755) lemurs on Anjouan. The results of the investigation of habitat use support my prediction that density of native species would not be an important microhabitat requirement, as neither density of native or non-native plant species were significantly related to lemur abundance. This suggests that *E. mongoz* uses non-native habitat, and as an adaptable species, it is not limited by habitat type.

S. aromaticum is a widely available source of food for *E. mongoz*. *S. aromaticum* flower buds are harvested by local farmers to produce cloves, an important commercial crop on Anjouan. The species has one fruiting cycle per year, the timing of which varies across Anjouan (I. Saïd pers. comm.); fruiting generally takes place in the wet season and flowers are in bud in the dry season. During surveys, lemurs were observed to feed on fruits, flowers and young leaves of *S. aromaticum*. Fruits are a source of carbohydrates and lipids, while protein, minerals and vitamins are obtained from flowers, seeds and leaves, with additional

carbohydrates from nectar (Curtis 2004). Therefore, *S. aromaticum* meets different nutritional requirements at different times of year, and is likely to be a convenient fruit source during the wet season.

A closely related species, *Eulemur fulvus*, consumes flowers of *Albizia lebbek* on Mayotte, and these have been suggested to be an important source of protein for milk production during lactation for this species (Tarnaud 2004). Parturition in *E. mongoz* on Anjouan took place at the end of the dry season, thus, lactation overlapped with *S. aromaticum* flower availability. It is therefore possible that *S. aromaticum* flowers and buds are an important protein source for *E. mongoz* during lactation as well.

The significant relationship between *S. aromaticum* and abundance of *E. mongoz* may represent the use of degraded forest and agroforestry by this lemur. *S. aromaticum* was found to occur in both agroforestry and degraded forest. Abundance of *E. mongoz* also has a significant positive relationship with species richness, and it is possible that *S. aromaticum* is associated with species rich habitat. The importance of species richness as a microhabitat requirement may also indicate greater habitat suitability of natural and degraded forest, as species richness is generally greater in old growth forest than agroforestry (Turner et al. 1997, Bobo et al. 2006), therefore species richness of native forest would be expected to decrease with increasing degradation. As neither density of native species or density of non-native species had a significant effect on abundance of *E. mongoz*, the species seems not to depend on native plant species or native forest. The model results suggest that species richness is a more important microhabitat requirement than density of native or exotic plant species. *E. mongoz* was observed to use all forest types (native, degraded and agroforestry), therefore is not restricted to native forest; and may be selecting the most species rich areas of all habitat types.

Species diversity may be important because it ensures a greater availability of food resources for *E. mongoz*. *Eulemur* species have varied diets, for example *E. flavifrons* females were recorded feeding on 37 plant species during lactation (Volampeno et al. 2011b) and *E. macaco* has been recorded feeding on 104 plant species (Simmen et al. 2007). Previous studies identified that *E. mongoz* has a varied diet and opportunistic feeding strategy (Curtis 2004, Nadhurou et al. 2017) and during my study it was also observed to feed on a diverse range of food items in different habitats. In agroforestry, it was observed to feed on a

variety of crops, including *M. indica* fruits and flowers, *Musa* spp. fruits and flowers, *A. altilis* fruits, *A. heterophyllum* fruits, *C. nucifera* flowers, *Annona muricata* (soursop) fruits, *A. lebbeck* flowers, *Spondias dulcis* (ambarella) fruits and *Litchi chinensis* (lychee) fruits (Ormsby, unpublished data). Species rich agroforestry can therefore provide good habitat on Anjouan, as it produces a variety of crops that are used as food resources by *E. mongoz*.

Ecological flexibility may have enabled *E. mongoz* to use degraded forest and agroforestry habitat. Ecological flexibility increases the adaptability of primates to habitat degradation (Donati et al. 2011). *Eulemur* species are known to be flexible, and able to adapt to new habitats as a result (Ossi and Kamilar 2006). Dietary flexibility involves changing digestive strategy (Chapman et al. 2002); e.g., shifting the proportion of frugivory or folivory in the diet (Sato et al. 2016). Overall, *Eulemur* species are reported to have relatively low levels of dietary flexibility (Sato et al. 2016). However, *E. mongoz* was found to exhibit dietary flexibility in Ampijoroa, where monthly food budget shifted from 6.7% fruit and 46.7% new leaves in December, to 82.4% fruit in February, then 71% nectaries and 0% fruit in June (Rasmussen 1999). In Anjamena, western Madagascar, the diet of *E. mongoz* varies in response to changes in food availability (Curtis 2004) but remains predominantly frugivorous. It was suggested that seasonal fluctuations in fruit availability at Anjamena are not great enough to necessitate dietary shifting at this location (Sato et al. 2014). Dietary information from these populations suggests that the species can exhibit dietary flexibility under variable conditions, and this is likely to have helped *E. mongoz* to adapt to the more plant species-rich anthropogenic habitats on Anjouan.

Behavioural flexibility is found to be high in *Eulemur* species, which can compensate for lower dietary flexibility and increase access to fragmented or variable food resources (Sato et al. 2016). This includes strategies such as habitat shifting (Campera et al. 2014), increasing ranging (Volampeno et al. 2011a), increasing time spent feeding over a 24-hour period (Curtis et al. 1999, Donati et al. 2007, 2009) and altering group size (Donati et al. 2011). *E. mongoz* alters its activity pattern under different seasonal and environmental conditions (Tattersall 1976, Curtis et al. 1999). Variation in group size has also been recorded in the species, and this is suggested to show seasonal patterns (Tattersall 1976, Curtis and Zaramody 1998). On Anjouan, *E. mongoz* may be using behavioural strategies such as increased ranging to access seasonal fruit resources, as some farmers reported presence of lemurs in their farms only at certain times of year, for example during mango season. It was

also reported that group sizes are larger in degraded forest on Anjouan (Nadhrou et al. 2017) suggesting that there are sufficient food resources in this habitat to support larger groups (Curtis and Zaramody 1998, Nadhrou et al. 2017). Therefore, behavioural flexibility may play a role in the species ability to use degraded forest and agroforestry on Anjouan, and these habitats could also benefit the species by providing sufficient food resources.

Habitat degradation can reduce the availability of fruit resources for frugivorous primates (Estrada and Coates-Estrada 1996, Donati et al. 2011). Availability of fruit resources can also be restricted by phenological patterns of plant species (Bollen and Donati 2005). The phenology of exotic plant species may differ from that of native species, which can increase food resources in habitat containing introduced species (Gérard et al. 2015). The inclusion of exotic fruit crops in agroforestry and degraded forest on Anjouan could be mitigating the effects of deforestation on *E. mongoz* by providing a greater variety of fruit resources, and a more continuous supply of food throughout the year, due to varying phenology of the diverse exotic plant species. During my study, it was observed that *S. aromaticum* and *L. chinensis* produced fruit during the wet season; *A. muricata* and *S. dulcis* were fruiting during the dry season; and *M. indica* began fruiting towards the end of the dry season and into the wet season. Locals report that the fruiting season varies according to species and region such that throughout the year there will be fruit available somewhere on the island, for example the mango season takes place at different times on the north, east and south-west sides of the island. The availability of fruit throughout the year that was observed in agroforestry may indicate a relatively consistent temporal availability of ripe fruit, and therefore more easily digestible food for *E. mongoz* (Riley et al. 2013).

Crop fruit can offer advantages over natural forest fruits, such as being easier to digest and easier to find due to being in more open habitat and the generally large size of cultivated fruits (Forthman-Quick and Demment 1988, McLennan and Ganzhorn 2017). *Theobroma cacao* (Cacao pulp), which is consumed by crop raiding Tonkean macaques in Indonesia, contains more digestible carbohydrates and has a higher energy content than the forest fruits in their diet; it is also available throughout the year (Riley et al. 2013). Cultivated foods eaten by chimpanzees in Bulindi, Uganda, contain higher levels of carbohydrates and lower levels of insoluble fibre than wild foods, making them easier to digest (McLennan and Ganzhorn 2017). Crops may contain lower levels of protein and lipids and therefore are not always more nutritious (Riley et al. 2013, McLennan and Ganzhorn 2017). However, fruits of

plants in Madagascar have been found to contain lower levels of nitrogen than species from the New World and Old World (Donati et al. 2017); it is therefore possible that the exotic fruit eaten by *E. mongoz* in agroforestry contains higher nitrogen levels than fruit in Anjouan's natural forest. *E. mongoz* eats both mature and immature fruit, but immature fruit is harder to digest (Waterman 1984, Curtis 2004). A study of diet and nutrient intake of lemurs on Anjouan is required to determine if there is a difference in diet quality between native and exotic habitat.

There have been a multitude of studies on the potential role of agroecosystems in conservation (e.g., Gezon and Freed 1999, Vaughan et al. 2007). Agroforestry can be a solution that benefits both people and wildlife (Estrada et al. 2012, Gérard et al. 2015, Guzmán et al. 2016); by providing food, habitat or corridors for wildlife, and alternative resources to natural forest for people (Gérard et al. 2015). Introduced fruit trees grow faster than native forest, therefore agroforestry can be used in reforestation; it can also be used to connect forest fragments (Gérard et al. 2015).

There is also a growing body of evidence that demonstrates that agroecosystems can benefit primates. They are suggested to be important habitat for several primate species in Mesoamerica (Estrada 2006) and are known to provide habitats for 57 primate taxa around the world (Estrada et al. 2012). *Hapalemur meridionalis* (bamboo lemur) is folivorous and uses invasive swamp tree for feeding and resting (Eppley et al. 2015). *E. macaco* feeds on exotic fruits throughout the year at Ambato Massif (Colquhoun 1998). Introduced *M. indica* forms a large part of the diet of *E. flavifrons* in Ankarafa, Madagascar (Volampeno et al. 2011b, 2013). Chimpanzees are known to feed on agricultural fruit crops when less fruit is available in the forest (McLennan 2013). Shade *Coffea* sp. (coffee) plantations are used as habitat and corridors between forest fragments by mantled howler monkeys (Williams-Guillen et al. 2006) and provide habitat to Andean night monkeys due to abundance of *Prunus integrifolia* in the plantations (Guzmán et al. 2016). Several species of lemurs have been found in *Vanilla planifolia* (vanilla) plantations in Madagascar, and it has been suggested that these plantations have a role in connecting natural forest fragments (Hending et al. 2018). The results of my study suggest that on Anjouan, *E. mongoz* is able to persist in degraded forest and agroforestry if there is sufficient species richness, and adds to the evidence that agroecosystems can benefit primates.

Across the island, a population size of 9919 (95% CI 5541-17755) individuals was estimated for *E. mongoz*. The level of threat of extinction to a taxon is assessed according to at least one of five criteria for the IUCN Red List (population size reduction, geographic range, small population size and decline, very small or restricted population, and analysis of the probability of extinction) (IUCN 2012). *E. mongoz* is currently listed as Critically Endangered under all five categories (Schwitzer et al. 2013). Criterion C, based on population size and decline, requires a population size of between 2500 and 10,000 mature individuals, and an estimated continuing decline of 10% in three generations, for a species to be classified as Vulnerable (a high risk of extinction in the wild) (IUCN 2012). Based on the population estimate obtained here for *E. mongoz* on Anjouan, this population would be listed as Vulnerable depending on the level of decline. The population trend on Anjouan is not known, therefore ongoing monitoring is required to determine the status on the island using this criterion. However, these results are encouraging, as they suggest the potential for the down-listing of the species if the Anjouan population were incorporated into the overall species status assessment. The inclusion of the Mohéli population in a re-assessment could bring the overall population estimate for the species to >10,000 individuals, which could allow it to be listed as Near Threatened. A population estimate and trend data for the Mohéli population is therefore also required. Large group sizes have previously been reported on Mohéli (Nadhrou et al. 2017) where the species is also found in agroforestry (Tattersall 1976, 1998, Nadhrou et al. 2017). The large population estimate for *E. mongoz* on Anjouan could be attributed to the availability of species rich agroforestry and degraded forest. On Mohéli, habitat largely consists of agroforestry. The ability of the species to use this habitat suggests that the species could be doing well on Mohéli.

Although the population estimate could allow down-listing of the species, the implications of this should be considered. The population in Madagascar remains highly threatened by ongoing habitat destruction, and conservation action here is essential; listing the species as Critically Endangered ensures that this remains a priority. The results of my study demonstrate that the population on the Comoros requires ongoing protection and monitoring because as an important genetic reservoir and an insurance population it could play a key role in future conservation management of the species, e.g., through translocations. Therefore, while it may not be advisable to down-list the species, the Comoros population should be included in the species action plan, to ensure its conservation and long-term safeguarding of the species.

3.5 Conclusion

The results of my study indicate that plant species richness is a microhabitat requirement for *E. mongoz*, and that habitat in which *S. aromaticum* is dominant is important for the population on Anjouan. It is likely that species richness is a more important microhabitat characteristic than density of any specific plant species, because *E. mongoz* is ecologically flexible and adaptable, as evidenced by their successful colonisation of the Comoros Islands after introduction. The result suggests that areas of species rich non-native habitat may have mitigated the effects of deforestation for *E. mongoz* on Anjouan. *E. mongoz* can obtain a diversity of food resources from degraded forest and agroforestry, therefore use of species rich agroforestry could be applied to management plans for this species, and habitat quality could be improved by increasing species richness. Based on these results, appropriate conservation management for the species might involve reforestation with a diversity of native and non-native species within agroforestry, or incorporating agroforestry species in reforestation of native forest, to create species rich habitat for *E. mongoz* that continues to benefit local farmers. The population estimate suggests that Anjouan supports a large population of *E. mongoz*, and is consistent with previous suggestions that this population could act as an important reservoir for the species. The result also indicates the potential for down-listing of the species on the IUCN Red List, however, ongoing monitoring is required to investigate population trends. I recommend that the species is included in the species action plan, to ensure long-term conservation of the species.

4. Chapter 4. General discussion

4.1 Summary of results

Prior to my study, it was not known how the *E. mongoz* population on Anjouan was responding to ongoing deforestation and there was no population estimate for the island. The main aims of my study were to obtain information on the status of *E. mongoz* on Anjouan and investigate habitat use at different spatial scales to identify potential conservation needs. My study has produced the first population estimate and distribution map for *E. mongoz* on Anjouan and provides further information on habitat use on the island.

In chapter two, species distribution modelling predicted a large area of suitable habitat on Anjouan, therefore *E. mongoz* has a large potential range on the island. This suggests that the species has been able to adapt to land use change. The model indicates that native and degraded forest are macrohabitat requirements, and also suggests that more anthropogenic habitat such as agroforestry is included in predicted suitable habitat. The species is therefore not restricted to a particular habitat type on the island.

In chapter three, hierarchical modelling identified that density of *S. aromaticum* and species richness are microhabitat requirements, and that there was no effect of densities of native or exotic species on abundance of *E. mongoz*. This suggests that the species is not dependent on native forest, and that species rich agroforestry can provide important habitat for *E. mongoz* on Anjouan. A population estimate of 9919 (95% CI 5541-17755) individuals was obtained for the island.

Overall the results of my thesis suggest that *E. mongoz* on Anjouan requires species rich habitat in either native forest, degraded forest or agroforestry, and is therefore flexible in its use of habitat. My results are particularly important from a conservation perspective because they suggest that on Anjouan the use of species rich agroforestry has acted as a buffer against the effects of deforestation on this species. My thesis contributes to a growing body of evidence of the beneficial role that agroecosystems can play in primate conservation. The large range and population estimate on Anjouan could potentially allow

down-listing of the species on the IUCN Red List if it is included in the next status assessment. My results suggest that the Comoros population is less threatened than the Madagascar population, supporting previous suggestions that it could act as a source for future translocations to Madagascar; this population is therefore vital to the conservation of the species.

4.2 Conservation and management implications

The results of my study contribute to Dahari's CEPF funded biodiversity project, and will be incorporated with results of biodiversity surveys to identify important areas for biodiversity on Anjouan, where the NGO can direct its conservation work to protect threatened species on the island. The large range and population estimate predicted by my study suggest that *E. mongoz* is doing well on Anjouan. However, as the species distribution model predicted a smaller area of optimal habitat, the species could benefit from conservation intervention in the form of habitat management and reforestation.

As *E. mongoz* uses agroforestry and selects species rich habitat, a suitable conservation strategy would be a reforestation programme, involving planting of both native and exotic agroforestry species (e.g. Gérard et al. 2015). This could be applied to create corridors between fragments of native and degraded forest, and existing agroforestry. Corridors containing exotic species are successfully used by other species of lemur in Madagascar (Eppley et al. 2015, Andriamandimbarisoa et al. 2015). On the east of the island, planting to increase species richness of agroforestry could be done to increase habitat suitability. Dahari is currently working with local farmers to reforest agricultural areas at high elevations in the central region, incorporating exotic crop species with native species, so that both farmers and endemic wildlife will benefit. My study suggests that this strategy is appropriate for *E. mongoz* as it will create species rich habitat close to central native and degraded forest. Extending this across the island would be beneficial for lemurs and other island fauna in the long-term.

Previous studies have indicated that farmers perceive lemurs to cause crop damage on Anjouan (Nadhrou et al. 2017) and farmers are known to use poison or throw stones to deter them (Tattersall 1998, Nadhrou et al. 2017). Therefore the use of agroforestry by *E. mongoz* may have human-wildlife conflict implications. Farmers' perceptions of the levels of

crop loss they are experiencing due to lemurs, as well as measurement of crop damage by lemurs, are required for effective mitigation of potential conflicts (Hill 2004, Hill and Webber 2010), therefore this should be investigated further. Enrichment planting in farms is a recommended mitigation strategy (Hill 2017), therefore reforestation in farms should create resources for both farmers and lemurs to reduce impact of lemurs on crops. Planting of buffer zones consisting of exploitable habitat around farms is another recommended strategy (Riley et al. 2013).

The results of my study are positive in terms of the current status of *E. mongoz* on Anjouan, and suggest that inclusion of this population in future status assessments could enable the species to be down-listed from Critically Endangered to Vulnerable on the IUCN Red List (IUCN 2012). If the Mohéli population is also included, the status could potentially be down-listed to Near Threatened. As the species has been established on the Comoros for hundreds of years (Pastorini et al. 2003) and has adapted to the environment, it could now be considered as a naturalised species (Hettinger 2001). It could therefore be argued that the Comoros population should be included in the Red List assessment and action plan for the species, to ensure its protection. However, a caveat to this is that the population in Madagascar remains highly threatened, and protecting the habitat in Madagascar is of high importance; down-listing could detract from this. The best approach may be to include the Comoros population in the next action plan so that it is managed and protected, but not to reduce the overall status of the species. As the species is highly threatened in Madagascar, protection of the Comoros population is essential. An action plan for *E. mongoz* on the Comoros should therefore be put in place.

4.3 Further research

The results of my study can be built on with further research in several areas. In chapter three, I identified information on habitat use, which suggests that *S. aromaticum* could be an important species, and that species rich habitat is a microhabitat requirement. Species rich agroforestry and degraded forest are therefore important habitat types. Further research could be carried out on habitat selection at the home range level, in order to identify how the species is using these habitats. This could be conducted with a use-availability study whereby use of food resources in the home range is quantified and compared to availability of resources (Manly et al. 2002, Thomas and Taylor 2006). Investigation of habitat selection

could be combined with a study of diet and nutrition. These studies would help to identify the quality of agroforestry habitat in terms of diet and nutrition, and it could also quantify impact of crop foraging on farmers, and it would help to inform habitat management. It could also tie into investigations of ecological flexibility of *E. mongoz*, for example, comparing the level of dietary flexibility in this population with that of the Madagascar populations, and investigation of the role of flexible behavioural strategies such as seasonal range shifting in the species' use of anthropogenic habitat in the Comoros.

As discussed in section 4.2, use of agroforestry by *E. mongoz* may result in conflicts with farmers. This should therefore be investigated further and mitigation strategies identified if necessary. Additionally, as an introduced species, it could also have negative impacts on endemic species on the island (Sakai et al. 2001) such as *Pteropus livingstonii* (Livingstone's fruit bat) and *P. seychellensis comorensis* (Seychelles fruit bat) with which there may be dietary overlap. This could also be investigated further.

My study suggests that *E. mongoz* is successful in anthropogenic habitat, however it is not certain that this is sustainable. A previous study reported a low recruitment index (29%) but with no difference between habitat types (Nadhrou et al. 2017). This should be investigated further with a larger study of recruitment and survival to determine population viability.

My results suggest that the *E. mongoz* population on Anjouan is doing well based on the IUCN Red List criteria. However, information is still missing about the Mohéli population, and the status of the species on Madagascar is informed by survey data from 2008. Therefore the Mohéli population should be studied, and new surveys of the species on Madagascar could be conducted for an up-to-date assessment. Ongoing monitoring on Anjouan is also required to obtain data on population trends for future status assessments, and for use in measuring impact of reforestation and conservation action.

5. References

- Addison, P. F. E., L. Rumpff, S. S. Bau, J. M. Carey, Y. E. Chee, F. C. Jarrad, M. F. McBride, and M. A. Burgman. 2013. Practical solutions for making models indispensable in conservation decision-making. *Diversity and Distributions* **19**:490–502.
- Aguirre-Gutiérrez, J., L. G. Carvalheiro, C. Polce, E. E. van Loon, N. Raes, M. Reemer, and J. C. Biesmeijer. 2013. Fit-for-purpose: species distribution model performance depends on evaluation criteria – Dutch hoverflies as a case study. *PLoS One* **8**:e63708
- Andriaholinirina, N., A. Baden, M. Blanco, L. Chikhi, A. Cooke, N. Davies, R. Dolch, G. Donati, J. Ganzhorn, C. Golden, L.F. Groeneveld, A. Hapke, M. Irwin, S. Johnson, P. Kappeler, T. King, R. Lewis, E.E. Louis, M. Markolf, V. Mass, R.A. Mittermeier, R. Nichols, E. Patel, C.J. Rabarivola, B. Raharivololona, S. Rajaobelina, G. Rakotoarisoa, B. Rakotomanga, J. Rakotonanahary, H. Rakotondrainibe, G. Rakotondratsimba, M. Rakotondratsimba, L. Rakotonirina, F.B. Ralainasolo, J. Ralison, T. Ramahaleo, J.F. Ranaivoarisoa, S.I. Randrianahaleo, B. Randrianambinina, L. Randrianarimanana, H. Randrianasolo, G. Randriatahina, H. Rasamimananana, T. Rasolofoharivelo, S. Rasoloharijaona, F. Ratelolahy, J. Ratsimbazafy, N. Ratsimbazafy, H. Razafindraibe, J. Razafindramanana, N. Rowe, J. Salmona, M. Seiler, S. Volampeno, P. Wright, J. Youssouf, J. Zaonarivelo & A. Zaramody. 2014. *Eulemur mongoz*. The IUCN Red List of Threatened Species 2014:e.T8202A16117799. <http://dx.doi.org/10.2305/IUCN.UK.2014-1.RLTS.T8202A16117799.en>. (10/11/2018)
- Andriamandimbiarisoa, L., T. S. Blanthorn, R. Ernest, J.-B. Ramanamanjato, F. Randriatafika, J. U. Ganzhorn, and G. Donati. 2015. Habitat corridor utilization by the gray mouse lemur, *Microcebus murinus*, in the littoral forest fragments of southeastern Madagascar. *Madagascar Conservation & Development* **10**:144.
- Andriatsarafara, R. 1988. *Note sur les rythmes d'activité et sur le régime alimentaire de Lemur mongoz Linnaeus, 1766 à Ampijoroa*. L'Equilibre des écosystèmes forestiers à Madagascar: actes d'un séminaire international. IUCN, Gland, Switzerland, and Cambridge, UK.
- Araujo, M.B, and M. New. 2007. Ensemble forecasting of species distributions. *Trends in Ecology and Evolution* **22**:42–47.
- Ardestani, E. G., M. Tarkesh, M. Bassiri, and M. R. Vahabi. 2015. Potential habitat modeling for reintroduction of three native plant species in central Iran. *Journal of Arid Land* **7**:381–390.

- Arnold, M. L. 1992. Natural hybridization as an evolutionary process. *Annual Review of Ecology and Systematics* **23**:237–261.
- Arnold, M. L., and A. Meyer. 2006. Natural hybridization in primates: One evolutionary mechanism. *Zoology* **109**:261–276.
- Arroyo-Rodríguez, V., and S. Mandujano. 2006. Forest fragmentation modifies habitat quality for *Alouatta palliata*. *International Journal of Primatology* **27**:1079–1096.
- Austin, M. P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling* **157**:101–118.
- Barbet-Massin, M., F. Jiguet, C. H. Albert, and W. Thuiller. 2012. Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution* **3**:327–338.
- Barbet-Massin, M., Q. Rome, C. Villemant, and F. Courchamp. 2018. Can species distribution models really predict the expansion of invasive species? *PLoS One* **13**:e0193085
- Barbet-Massin, M., B. A. Walther, W. Thuiller, C. Rahbek, and F. Jiguet. 2009. Potential impacts of climate change on the winter distribution of Afro-Palaearctic migrant passerines. *Biology Letters* **5**:248–251.
- Barton, K. 2018. MuMIn: Multi-model inference. R Package version 1.42.1. <https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf> (5/12/2018)
- Beaumont, L. J., L. Hughes, and A. J. Pitman. 2008. Why is the choice of future climate scenarios for species distribution modelling important? *Ecology Letters* **11**:1135–1146.
- Bennie, J., B. Huntley, A. Wiltshire, M. O. Hill, and R. Baxter. 2008. Slope, aspect and climate: Spatially explicit and implicit models of topographic microclimate in chalk grassland. *Ecological Modelling* **216**:47–59.
- Block, W. M., and L. A. Brennan. 1993. The habitat concept in ornithology. Pages 35–91 in D. M. Power, editor. *Current Ornithology*. Plenum Press, New York, New York, USA.
- Bobo, K. S., M. Waltert, N. M. Sainge, et al. 2006. From forest to farmland: species richness patterns of trees and understorey plants along a gradient of forest conversion in southwestern Cameroon. *Biodiversity and Conservation* **15**: 4097–4117.
- Bollen, A., and G. Donati. 2005. Phenology of the littoral forest of Sainte Luce, southeastern Madagascar. *Biotropica* **37**:32–43.
- Bolnick D.I., T. Ingram, W. E. Stutz, L. K. Snowberg, O.L. Lau, and J. S. Paull. 2010. Ecological release from interspecific competition leads to decoupled changes in population and

- individual niche width. *Proceedings of the Royal Society B: Biological Sciences* **277**:1789-1797.
- Breiman, L. 2001. Random forests. *Machine Learning* **45**:5–32.
- Brooks, T. M., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, A. B. Rylands, W. R. Konstant, P. Flick, J. Pilgrim, S. Oldfield, G. Magin, and C. Hilton-Taylor. 2002. Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology* **16**:909–923.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake. 1993. Distance sampling: estimating abundance of biological populations. Springer-Science + Business Media, B.V., Dordrecht, Netherlands.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. Borchers, and L. Thomas. 2001. *Introduction to distance sampling: estimating abundance of biological populations*. Oxford University Press, Oxford, UK.
- Buckland, S. T., S. J. Marsden, and R. E. Green. 2008. Estimating bird abundance: making methods work. *Bird Conservation International* **18**: S91-S108.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Second edition. Springer-Verlag, New York, New York, USA.
- C. Colquhoun, I. 1998. Cathemeral behavior of *Eulemur macaco* at Ambato Massif, Madagascar. *Folia Primatologica* **69**:22–34.
- Campera, M., V. Serra, M. Balestri, M. Barresi, M. Ravaolahy, F. Randriatafika, and G. Donati. 2014. Effects of habitat quality and seasonality on ranging patterns of collared brown lemur (*Eulemur collaris*) in littoral forest fragments. *International Journal of Primatology* **35**:957–975.
- Chapman, C. A., L. J. Chapman, M. Cords, J. M. Gathua, A. Gautier-Hion, J. E. Lambert, K. Rode, C.E.G. Tutin and L.J.T. White 2002. Variation in the diets of *Cercopithecus* species: differences within forests, among forests, and across species. Pages 325-350 in M. E. Glenn & M. Cords, editors. *The guenons: Diversity and adaptation in African monkeys*. Kluwer Academic/Plenum Publishers, New York, New York, USA.
- Chefaoui, R. M., J. Hortal, and J. M. Lobo. 2005. Potential distribution modelling, niche characterization and conservation status assessment using GIS tools: a case study of Iberian *Copris* species. *Biological Conservation* **122**:327–338.
- Chucholl, C. 2017. Niche-based species distribution models and conservation planning for endangered freshwater crayfish in south-western Germany. *Aquatic Conservation: Marine and Freshwater Ecosystems* **27**:698–705.

- Clark, M. 1997. The mongoose lemur *Eulemur mongoz* on Anjouan, Comores. *The Dodo Journal of the Wildlife Preservation Trusts* **33**:36–44.
- Corsi, F., E. Duprè, and L. Boitani. 1999. A large-scale model of wolf distribution in Italy for conservation planning. *Conservation Biology* **13**:150–159.
- Curtis, D. J. 2004. Diet and nutrition in wild mongoose lemurs (*Eulemur mongoz*) and their implications for the evolution of female dominance and small group size in lemurs. *American Journal of Physical Anthropology* **124**:234–247.
- Curtis, D. J., and M. A. Rasmussen. 2003. Cathemerality in lemurs. *Evolutionary Anthropology* **11**:83–86.
- Curtis, D. J., and A. Zaramody. 1998. Group size, home range use, and seasonal variation in the ecology of *Eulemur mongoz*. *International Journal of Primatology* **19**:811–835.
- Curtis, D., and A. Zaramody. 1999. Social structure and seasonal variation in the behaviour of *Eulemur mongoz*. *Folia Primatologica* **70**:79–96.
- Curtis, D. J., A. Zaramody, and R. D. Martin. 1999. Cathemerality in the mongoose lemur, *Eulemur mongoz*. *American Journal of Primatology* **47**:279–298.
- Domisch, S., M. Kueimmerlen, S. C. Jähnig, and P. Haase. 2013. Choice of study area and predictors affect habitat suitability projections, but not the performance of species distribution models of stream biota. *Ecological Modelling* **257**:1–10.
- Donati, G., N. Baldi, V. Morelli, J. U. Ganzhorn, and S. M. Borgognini-Tarli. 2009. Proximate and ultimate determinants of cathemeral activity in brown lemurs. *Animal Behaviour* **77**:317–325.
- Donati, G., A. Bollen, S. M. Borgognini-Tarli, and J. U. Ganzhorn. 2007. Feeding over the 24-h cycle: dietary flexibility of cathemeral collared lemurs (*Eulemur collaris*). *Behavioral Ecology and Sociobiology* **61**:1237–1251.
- Donati, G., K. Kesch, K. Ndremifidy, S. L. Schmidt, J.-B. Ramanamanjato, S. M. Borgognini-Tarli, and J. U. Ganzhorn. 2011. Better few than hungry: flexible feeding ecology of collared lemurs *Eulemur collaris* in littoral forest fragments. *PLoS One* **6**:e19807
- Donati, G., L. Santini, T. M. Eppley, S. J. Arrigo-Nelson, M. Balestri, S. Boinski, A. Bollen, L. L. Bridgeman, M. Campera, V. Carrai, M. K. Chalise, A. Derby Lewis, G. Hohmann, M. F. Kinnaird, A. Koenig, M. Kowalewski, P. Lahann, M. R. McLennan, A. K. I. Nekaris, V. Nijman, I. Norscia, J. Ostner, S. Y. Polowinsky, O. Schülke, C. Schwitzer, P. R. Stevenson, M. G. Talebi, C. Tan, I. Tomaschewski, E. R. Vogel, P. C. Wright, and J. U. Ganzhorn. 2017. Low levels of fruit nitrogen as drivers for the evolution of Madagascar's primate communities. *Scientific Reports* **7**:14406.

- Doulton, H., M. Mohamed, G. Shepherd, S. Mohamed, B. Ali, and N. Maddison. 2015. XIV World Forest Congress, Durban, South Africa, 7-11 September 2015. Competing land-use in a small island developing state: using landscape approaches to manage sustainable outcomes in the Comoro Islands. <https://daharicomores.org/wp-content/uploads/2014/01/WFC2015-paper-Doulton-et-al-Competing-land-use-in-a-small-island-developing-state.pdf> (9/8/2018)
- Duncan, R. P., T. M. Blackburn, and D. Sol. 2003. The ecology of bird introductions. *Annual Review of Ecology, Evolution, and Systematics* **34**:71–98.
- Elith, J., S. Ferrier, F. Huettmann, and J. Leathwick. 2005. The evaluation strip: A new and robust method for plotting predicted responses from species distribution models. *Ecological Modelling* **186**:280–289.
- Elith, J., C. H. Graham, R. P. Anderson, M. Dudík, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. McC. Overton, A. Townsend Peterson, S. J. Phillips, K. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberón, S. Williams, M. S. Wisz, and N. E. Zimmermann. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29**:129–151.
- Elith, J., and J. R. Leathwick. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics* **40**:677–697.
- Eppley, T. M., M. Balestri, M. Campera, J. Rabenantoandro, J.-B. Ramanamanjato, F. Randriatafika, J. U. Ganzhorn, and G. Donati. 2017. Ecological Flexibility as measured by the use of pioneer and exotic plants by two lemurids: *Eulemur collaris* and *Haplemur meridionalis*. *International Journal of Primatology* **38**:338–357.
- Eppley, T. M., G. Donati, J.-B. Ramanamanjato, F. Randriatafika, L. N. Andriamandimbarisoa, D. Rabehevitra, R. Ravelomanantsoa, and J. U. Ganzhorn. 2015. The use of an invasive species habitat by a small folivorous primate: implications for lemur conservation in Madagascar. *PloS one* **10**:e0140981
- Estrada, A. 2006. Human and non-human primate co-existence in the Neotropics: a preliminary view of some agricultural practices as a complement for primate conservation. *Ecological and Environmental Anthropology* **2**: 17-29.
- Estrada, A., and R. Coates-Estrada. 1996. Tropical rain forest fragmentation and wild populations of primates at Los Tuxtlas, Mexico. *International Journal of Primatology* **17**:759-783

- Estrada, A., B. E. Raboy, and L. C. Oliveira. 2012. Agroecosystems and primate conservation in the tropics: a review. *American Journal of Primatology* **74**:696–711.
- Fajardo, J., J. Lessmann, E. Bonaccorso, C. Devenish, and J. Muñoz. 2014. Combined use of systematic conservation planning, species distribution modelling, and connectivity analysis reveals severe conservation gaps in a megadiverse country (Peru). *PLoS One* **9**:e114367
- FAO. 2010. *Global forest resources assessment 2010: Forestry Paper 163*. FAO, Rome, Italy. <http://www.fao.org/3/a-i1757e.pdf> (09/2/2017)
- Ferraz, K. M. P. M. B., B. M. Beisiegel, R. C. De Paula, D. A. Sana, C. B. De Campos, T. G. De Oliveira, and A. L. J. Desbiez. 2012. How species distribution models can improve cat conservation-jaguars in Brazil. *Cat News Special Issue* **7**:38–42.
- Fick, S. E., and R. J. Hijmans. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* **37**:4302–4315.
- Fiske, I., and R. Chandler. 2011. unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software* **43**:1–23.
- Forthman-Quick, D. L., and M. Demment. 1988. Dynamics of exploitation: differential energetic adaptations of two troops of baboons to recent human contact. Pages 25–51 in J. E. Fa & C. Southwick editors. *Ecology and behaviour of food enhanced primate groups*. Alan R. Liss, Inc, New York, New York, USA.
- Franklin, J. 2013. Species distribution models in conservation biogeography: developments and challenges. *Diversity and Distributions* **19**:1217–1223.
- Fuller, L., M. Shewring, and F. M. Caryl. 2018. A novel method for targeting survey effort to identify new bat roosts using habitat suitability modelling. *European Journal of Wildlife Research* **64**:31.
- García, G., and S. M. Goodman. 2003. Hunting of protected animals in the Parc National d'Ankarafantsika, north-western Madagascar. *Oryx* **37**:115–118.
- Geiger, R. 1965. *The climate near the ground*. Harvard University Press, Cambridge, MA, USA.
- Gérard, A., J. U. Ganzhorn, C. A. Kull, and S. M. Carrière. 2015. Possible roles of introduced plants for native vertebrate conservation: the case of Madagascar. *Restoration Ecology* **23**:768–775.
- Gezon, L. L., and B. Z. Freed. 1999. Agroforestry and conservation in northern Madagascar: hopes and hindrances. *African Studies Quarterly* **3**:9–38.

- Green, K. 2013. *Land cover mapping of the Comoros Islands: methods and results*. ECCD, Hombô, Anjouan, Union des Comores. <https://daharicomores.org/wp-content/uploads/2014/09/ECDD-land-cover-mapping-of-the-Comoros-final-report-2014.pdf> (8/8/2017)
- Green, K. E., B. M. Daniel, S. P. Lloyd, I. Said, A. Houmadi, D. M. Salim, S. M'Madi, H. Doulton, and R. P. Young. 2015. Out of the darkness: the first comprehensive survey of the Critically Endangered Anjouan scops owl *Otus capnodes*. *Bird Conservation International* **25**:322–334.
- Guisan, A., O. Broennimann, R. Engler, M. Vust, N. G. Yoccoz, A. Lehmann, and N. E. Zimmermann. 2006. Using niche-based models to improve the sampling of rare species. *Conservation Biology* **20**:501–511.
- Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* **8**:993–1009.
- Guisan, A., W. Thuiller, and N. E. Zimmermann. 2017. *Habitat suitability and distribution models: with applications in R*. Cambridge University Press, New York, New York, USA.
- Guisan, A., R. Tingley, J. B. Baumgartner, I. Naujokaitis-Lewis, P. R. Sutcliffe, A. I. T. Tulloch, T. J. Regan, L. Brotons, E. McDonald-Madden, C. Mantyka-Pringle, T. G. Martin, J. R. Rhodes, R. Maggini, S. A. Setterfield, J. Elith, M. W. Schwartz, B. A. Wintle, O. Broennimann, M. Austin, S. Ferrier, M. R. Kearney, H. P. Possingham, and Y. M. Buckley. 2013. Predicting species distributions for conservation decisions. *Ecology Letters* **16**:1424–1435.
- Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* **135**:147–186.
- Guzmán, A., A. Link, J. A. Castillo, and J. E. Botero. 2016. Agroecosystems and primate conservation: shade coffee as potential habitat for the conservation of Andean night monkeys in the northern Andes. *Agriculture, Ecosystems & Environment* **215**:57–67.
- Hastie, T., and R. Tibshirani. 1999. *Generalized additive models*. Chapman and Hall, London, UK.
- Hending, D., A. Andrianaina, Z. Rakotomalala, and S. Cotton. 2018. The use of vanilla plantations by lemurs: encouraging findings for both lemur conservation and sustainable agroforestry in the Sava region, northeast Madagascar. *International Journal of Primatology* **39**:141–153.

- Hettinger, N. 2001. Exotic species, naturalisation and biological nativism. *Environmental Values* **10**:193-224.
- Hill, C. M. 2004. Farmers' perspectives of conflict at the wildlife–agriculture boundary: some lessons learned from African subsistence farmers. *Human Dimensions of Wildlife* **9**:279–286.
- Hill, C. M. 2017. Primate crop feeding behavior, crop protection, and conservation. *International Journal of Primatology* **38**:385–400.
- Hill, C. M., and A. D. Webber. 2010. Perceptions of nonhuman primates in human-wildlife conflict scenarios. *American Journal of Primatology* **72**:919–924.
- Hirzel, A. H., V. Helfer, and F. Metral. 2001. Assessing habitat-suitability models with a virtual species. *Ecological Modelling* **145**:111–121.
- Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* **22**:415-427.
- Ibouroi, M. T., A. Cheha, G. Astruc, S. A. O. Dhurham, and A. Besnard. 2018. A habitat suitability analysis at multi-spatial scale of two sympatric flying fox species reveals the urgent need for conservation action. *Biodiversity and Conservation* **27**:2395–2423.
- International Monetary Fund. 2010. *Union of the Comoros: Poverty Reduction and Growth Strategy Paper. IMF Staff Country Reports No 10/190*. International Monetary Fund, Washington, D.C., USA
<https://www.imf.org/en/Publications/CR/Issues/2016/12/31/Union-of-the-Comoros-Poverty-Reduction-and-Growth-Strategy-Paper-24013> (2/4/2017)
- IUCN. 2012. *IUCN Red List Categories and Criteria: Version 3.1*. Second edition. IUCN, Gland, Switzerland and Cambridge, UK. <https://portals.iucn.org/library/node/10315> (5/8/2018)
- IUCN Standards and Petitions Subcommittee. 2017. *Guidelines for Using the IUCN Red List Categories and Criteria. Version 13*. IUCN, Gland, Switzerland and Cambridge, UK. <http://www.iucnredlist.org/documents/RedListGuidelines.pdf>(10/1/2018)
- Kearney, M., and W. Porter. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters* **12**:334–350.
- Kearney, M. R., B. A. Wintle, and W. P. Porter. 2010. Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Conservation Letters* **3**:203–213.

- Kéry, M., and J. A. Royle. 2016. *Applied hierarchical modeling in ecology: analysis of distribution, abundance and species richness in R and BUGS*. Academic Press, Boston, MA, USA.
- Krausman, P. R. 1999. Some basic principles of habitat use. *Grazing behavior of livestock and wildlife* **70**:85–90.
- Liu, C., M. White, G. Newell, and P. Griffioen. 2013. Species distribution modelling for conservation planning in Victoria, Australia. *Ecological Modelling* **249**:68–74.
- Logan, M. 2010. *Biostatistical design and analysis using R: a practical guide*. Wiley-Blackwell, Chichester, West Sussex, UK; Hoboken, NJ, USA.
- Lozier, J. D., and N. J. Mills. 2011. Predicting the potential invasive range of light brown apple moth (*Epiphyas postvittana*) using biologically informed and correlative species distribution models. *Biological Invasions* **13**:2409–2421.
- Maeda, T. 2001. Patterns of bird abundance and habitat use in rice fields of the Kanto Plain, central Japan. *Ecological Research* **16**:569–585.
- Maibeche, Y., A. Moali, N. Yahi, and N. Menard. 2015. Is diet flexibility an adaptive life trait for relic and peri-urban populations of the endangered primate *Macaca sylvanus*? *PLOS ONE* **10**:e0118596.
- Malone, E. W., J. S. Perkin, B. M. Leckie, M. A. Kulp, C. R. Hurt, and D. M. Walker. 2018. Which species, how many, and from where: Integrating habitat suitability, population genomics, and abundance estimates into species reintroduction planning. *Global Change Biology* **24**:3729–3748.
- Manly, B. F. L., L. McDonald, D. Thomas, T. L. McDonald, and W. P. Erickson. 2002. *Resource selection by animals: statistical design and analysis for field studies*. Springer Netherlands, Dordrecht, Netherlands.
- Márcia Barbosa, A., R. Real, J. Olivero, and J. Mario Vargas. 2003. Otter (*Lutra lutra*) distribution modeling at two resolution scales suited to conservation planning in the Iberian Peninsula. *Biological Conservation* **114**:377–387.
- Marini, M. Â., M. Barbet-Massin, J. Martinez, N. P. Prestes, and F. Jiguet. 2010. Applying ecological niche modelling to plan conservation actions for the Red-spectacled Amazon (*Amazona pretrei*). *Biological Conservation* **143**:102–112.
- Mazerolle, M. J., L. L. Bailey, W. L. Kendall, J. A. Royle, S. J. Converse, and J. D. Nichols. 2007. Making great leaps forward: accounting for detectability in herpetological field studies. *Journal of Herpetology* **41**:672–689.

- Mazerolle, M. J., and M.-A. Villard. 1999. Patch characteristics and landscape context as predictors of species presence and abundance: A review. *Écoscience* **6**:117–124.
- McCullagh, P., and J. A. Nelder. 1989. *Generalized linear models, Second Edition*. Chapman and Hall, London, UK.
- McLennan, M. R. 2013. Diet and feeding ecology of chimpanzees (*Pan troglodytes*) in Bulindi, Uganda: foraging strategies at the forest–farm interface. *International Journal of Primatology* **34**:585–614.
- McLennan, M. R., and J. U. Ganzhorn. 2017. Nutritional characteristics of wild and cultivated foods for chimpanzees (*Pan troglodytes*) in agricultural landscapes. *International Journal of Primatology* **38**:122–150.
- Mittermeier, R. A., E. E. Louis, M. Richardson, C. Schwitzer, O. Langrand, A. B. Rylands, F. Hawkins, S. Rajaobelina, J. Ratsimbazafy, R. Rasoloarison, C. Roos, P. M. Kappeler, and J. Mackinnon. 2010. *Lemurs of Madagascar*. Conservation International, Arlington, Texas, USA.
- Mooney, H. A., and E. E. Cleland. 2001. The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences* **98**:5446–5451.
- Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1998. *Wildlife-habitat relationships: concepts and applications*. Island Press, Washington, DC, USA.
- Müller, P., A. Velo, E.-O. Raheliarisoa, A. Zaramody, and D. J. Curtis. 2000. Surveys of sympatric lemurs at Anjamena, north-west Madagascar. *African Journal of Ecology* **38**:248–257.
- Nadhrou, B., R. Righini, M. Gamba, P. Laiolo, A. Ouledi, and C. Giacoma. 2017. Effects of human disturbance on the mongoose lemur *Eulemur mongoz* in Comoros: implications and potential for the conservation of a Critically Endangered species. *Oryx* **51**:60–67.
- Oke, T. R. 1987. *Boundary layer climates*. Methuen, London, UK.
- Ossi, K., and J. M. Kamilar. 2006. Environmental and phylogenetic correlates of *Eulemur* behavior and ecology (Primates: Lemuridae). *Behavioral Ecology and Sociobiology* **61**:53–64.
- Pastorini, J., U. Thalmann, and R. D. Martin. 2003. A molecular approach to comparative phylogeography of extant Malagasy lemurs. *Proceedings of the National Academy of Sciences* **100**:5879–5884.

- Pastorini, J., A. Zaramody, D. J. Curtis, C. M. Nievergelt, and N. I. Mundy. 2009. Genetic analysis of hybridization and introgression between wild mongoose and brown lemurs. *BMC Evolutionary Biology* **9**:32.
- Pereira, J. M., L. Krüger, N. Oliveira, A. Meirinho, A. Silva, J. A. Ramos, and V. H. Paiva. 2018. Using a multi-model ensemble forecasting approach to identify key marine protected areas for seabirds in the Portuguese coast. *Ocean & Coastal Management* **153**:98–107.
- Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* **190**:231–259.
- Poulos, H., B. Chernoff, P. L. Fuller, and D. Butman. 2012. Ensemble forecasting of potential habitat for three invasive fishes. *Aquatic Invasions* **7**:59–72.
- Pulliam, H. R. 1988. Sources, Sinks, and Population Regulation. *American Naturalist* **132**:652–661.
- Pulliam, H. R. 2000. On the relationship between niche and distribution. *Ecology Letters* **3**:349–361.
- QGIS Development Team. 2015. *QGIS Geographic Information System*. Open Source Geospatial Foundation Project. <http://qgis.osgeo.org> (12/4/2017)
- Ramanamanjato, J.-B., and J. U. Ganzhorn. 2001. Effects of forest fragmentation, introduced *Rattus rattus* and the role of exotic tree plantations and secondary vegetation for the conservation of an endemic rodent and a small lemur in littoral forests of southeastern Madagascar. *Animal Conservation* **4**:175–183.
- Rasmussen, M. A. 1999. *Ecological influences on activity cycle in two cathemeral primates, Eulemur mongoz (mongoose lemur) and Eulemur fulvus (common brown lemur)*. Unpublished PhD thesis, Duke University, Durham, North California, USA.
- Razgour, O., J. Hanmer, and G. Jones. 2011. Using multi-scale modelling to predict habitat suitability for species of conservation concern: The grey long-eared bat as a case study. *Biological Conservation* **144**:2922–2930.
- Ridgeway, G. 1999. The state of boosting. *Computing Science and Statistics* **31**:172–181.
- Riley, E. P. 2007. Flexibility in diet and activity patterns of *Macaca tonkeana* in response to anthropogenic habitat alteration. *International Journal of Primatology* **28**:107–133
- Riley, E. P., B. Tolbert, and W. R. Farida. 2013. Nutritional content explains the attractiveness of cacao to crop raiding Tonkean macaques. *Current Zoology* **59**:160–169.
- Royle, J. A. 2004a. Generalized estimators of avian abundance from count survey data. *Animal Biodiversity and Conservation* **27**:375–386.

- Royle, J. A. 2004b. *N*-mixture models for estimating population size from spatially replicated counts. *Biometrics* **60**:108–115.
- Rushton, S. P., S. J. Ormerod, and G. Kerby. 2004. New paradigms for modelling species distributions? *Journal of Applied Ecology* **41**:193–200.
- Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D.E. McCauley, P. O'Neil, I. M. Parker, J. N. Thompson, and S. G. Weller. 2001. The population biology of invasive species. *Annual review of ecology and systematic* **32**:305–332.
- Santos, X., J. C. Brito, N. Sillero, J. M. Pleguezuelos, G. A. Llorente, S. Fahd, and X. Parellada. 2006. Inferring habitat-suitability areas with ecological modelling techniques and GIS: A contribution to assess the conservation status of *Vipera latastei*. *Biological Conservation* **130**:416–425.
- Sato, H., S. Ichino, and G. Hanya. 2014. Dietary modification by common brown lemurs (*Eulemur fulvus*) during seasonal drought conditions in western Madagascar. *Primates* **55**:219–230.
- Sato, H., L. Santini, E. R. Patel, M. Campera, N. Yamashita, I. C. Colquhoun, and G. Donati. 2016. Dietary flexibility and feeding strategies of *Eulemur*: a comparison with *Propithecus*. *International Journal of Primatology* **37**:109–129.
- Sawyer, R. M., Z. S. E. Fenosoa, A. Andrianarimisa, and G. Donati. 2017. The effect of habitat disturbance on the abundance of nocturnal lemur species on the Masoala Peninsula, northeastern Madagascar. *Primates* **58**:187–197.
- Schwitzer, C., R. A. Mittermeier, N. Davies, S. Johnson, J. Ratsimbazafy, J. Razafindramana, E. E. Louis, and S. Rajaobelina. 2013. *Lemurs of Madagascar: a strategy for their conservation 2013-2016*. IUCN SSC Primate Specialist Group, Bristol Conservation and Science Foundation, and Conservation International, Bristol, UK <https://portals.iucn.org/library/efiles/documents/2013-020.pdf> (12/13/2018)
- Seehausen, O. 2004. Hybridization and adaptive radiation. *Trends in Ecology & Evolution* **19**:198–207.
- Shrum, M. 2008. *Preliminary study of the lemur diversity in the Mahavavy-Kinkony Wetland Complex and Ankarafantsika National Park in northwest Madagascar: with emphasis on the reassessment of the status of the mongoose lemur (Eulemur mongoz) and its habitat*. Unpublished MSc thesis, Oxford Brookes University, Oxford, UK.

- Sillett, T. S., R. B. Chandler, J. A. Royle, M. Kéry, and S. A. Morrison. 2012. Hierarchical distance-sampling models to estimate population size and habitat-specific abundance of an island endemic. *Ecological Applications* **22**:1997–2006.
- Simmen, B., F. Bayart, A. Marez, and A. Hladik. 2007. Diet, nutritional ecology, and birth season of *Eulemur macaco* in an anthropogenic forest in Madagascar. *International Journal of Primatology* **28**:1253–1266.
- Sol, D., S. Bacher, S. M. Reader, and L. Lefebvre. 2008. Brain size predicts the success of mammal species introduced into novel environments. *The American Naturalist* **172**:S63–S71.
- Späth, T., M.-L. Bai, L. L. Severinghaus, and B. A. Walther. 2018. Distribution, habitat, and conservation status of the near-threatened Japanese Paradise-Flycatcher (*Terpsiphone atrocaudata periophthalmica*) on Lanyu, Taiwan. *Avian Conservation and Ecology* **13**:7
- Spiers, J. A., M. P. Oatham, L. V. Rostant, and A. D. Farrell. 2018. Applying species distribution modelling to improving conservation based decisions: a gap analysis of Trinidad and Tobago's endemic vascular plants. *Biodiversity and Conservation* **27**:2931–2949.
- Sugiura, N. 1978. Further analysts of the data by Akaike's Information Criterion and the finite corrections. *Communications in Statistics - Theory and Methods* **7**:13–26.
- Sussman, R. W., and I. Tattersall. 1976. Cycles of activity, group composition, and diet of *Lemur mongoz* Linnaeus 1766 in Madagascar. *Folia Primatologica* **26**:270–283.
- Swets, J. A. 1988. Measuring the accuracy of diagnostic systems. *Science* **240**:1285–1293.
- Tarnaud, L. 2004. Ontogeny of feeding behavior of *Eulemur fulvus* in the dry forest of Mayotte. *International Journal of Primatology* **25**:803–824.
- Tattersall, I. 1976. Group structure and activity rhythm in *Lemur mongoz* (Primates, Lemuriformes) on Anjouan and Moheli Islands, Comoro Archipelago. *Anthropological papers of the American Museum Natural History* **53**:4.
- Tattersall, I. 1998. Lemurs of the Comoro Archipelago: status of *Eulemur mongoz* on Moheli and Anjouan, and of *Eulemur fulvus* on Mayotte. *Lemur News* **3**:15–17.
- Tattersall, I. 2006. The concept of cathemerality: history and definition. *Folia Primatologica* **77**:7–14.
- Tattersall, I., and R. W. Sussman. 2016. Little brown lemurs come of age: summary and perspective. *International Journal of Primatology* **37**:3–9.

- Thomas, D. L., and E. J. Taylor. 2006. Study designs and tests for comparing resource use and availability II. *Journal of Wildlife Management* **70**:324-336
- Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. B. Bishop, T. A. Marques, and K. P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology* **47**:5–14.
- Thorn, J. S., V. Nijman, D. Smith, and K. A. I. Nekaris. 2009. Ecological niche modelling as a technique for assessing threats and setting conservation priorities for Asian slow lorises (Primates: *Nycticebus*). *Diversity and Distributions* **15**:289–298.
- Thuiller, W., D. Georges, R. Engler, and F. Breiner. 2016. biomod2: Ensemble Platform for Species Distribution Modeling. R Package version 3.3-7. <https://cran.r-project.org/web/packages/biomod2/biomod2.pdf> (9/8/2018)
- Thuiller, W., B. Lafourcade, R. Engler, and M. B. Araújo. 2009. BIOMOD – a platform for ensemble forecasting of species distributions. *Ecography* **32**:369–373.
- Turner, I. M., Y. K. Wong, P. T. Chew, and Ali bin Ibrahim. 1997. Tree species richness in primary and old secondary tropical forest in Singapore. *Biodiversity and Conservation* **6**: 537-543.
- UNDP. 2014. Sustaining Human Progress: Reducing Vulnerabilities and Building Resilience. Human Development Report 2014. UNDP, New York USA. <http://hdr.undp.org/sites/default/files/hdr14-report-en-1.pdf> (9/4/2017)
- van Schaik, C. P., J. W. Terborgh, and S. J. Wright. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics* **24**:353–377.
- Vaughan, C., O. Ramírez, G. Herrera, and R. Guries. 2007. Spatial ecology and conservation of two sloth species in a cacao landscape in Limón, Costa Rica. *Biodiversity and Conservation* **16**:2293–2310.
- Vie, J.-C., C. Hilton-Taylor, and S. N. Stuart. 2009. Wildlife in a Changing World-An Analysis of the 2008 IUCN Red List of Threatened Species. IUCN: Gland, Switzerland. <https://portals.iucn.org/library/sites/library/files/documents/RL-2009-001.pdf> (12/5/2018)
- Volampeno, M. S. N., J. C. Masters, and C. T. Downs. 2011a. Home range size in the blue-eyed black lemur (*Eulemur flavifrons*): A comparison between dry and wet seasons. *Mammalian Biology - Zeitschrift für Säugetierkunde* **76**:157–164.

- Volampeno, M. S. N., J. C. Masters, and C. T. Downs. 2011b. Life history traits, maternal behavior and infant development of blue-eyed black lemurs (*Eulemur flavifrons*). *American Journal of Primatology* **73**:474–484.
- Volampeno, M. S. N., G. Randriatahina, and C. T. Downs. 2013. Structure and composition of Ankarafa forest, Sahamalaza-Iles Radama National Park, Madagascar: implications for the frugivorous endemic blue-eyed black lemur (*Eulemur flavifrons*). *South African Journal of Wildlife Research* **43**:91–102.
- Waterman, P. G. 1984. Food acquisition and processing as a function of plant chemistry. Pages 177–211 in Chivers D. J., Wood, B. A., Bilsborough A., editors. *Food acquisition and processing in primates*. Plenum Press, New York, New York, USA.
- Wiens, J., J. Addicott, T. Case, and J. Diamond. 1986. The importance of spatial and temporal scale in ecological investigations. Pages 145–153 in J. Diamond and T.J. Case, editors. *Community ecology*. Harper & Row, New York, New York, USA.
- Wiens, J. A., J. T. Rotenberry, and B. V. Horne. 1987. Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. *Oikos* **48**:132-147.
- Williams-Guillen, K., C. McCann, J. C. Martinez Sanchez, and F. Koontz. 2006. Resource availability and habitat use by mantled howling monkeys in a Nicaraguan coffee plantation: can agroforests serve as core habitat for a forest mammal? *Animal Conservation* **9**:331–338.
- Wilson, K. A., M. I. Westphal, H. P. Possingham, and J. Elith. 2005. Sensitivity of conservation planning to different approaches to using predicted species distribution data. *Biological Conservation* **122**:99–112.
- Wilting, A., A. Cord, A. J. Hearn, D. Hesse, A. Mohamed, C. Traeholdt, S. M. Cheyne, S. Sunarto, M.-A. Jayasilan, J. Ross, A. C. Shapiro, A. Sebastian, S. Dech, C. Breitenmoser, J. Sanderson, J. W. Duckworth, and H. Hofer. 2010. Modelling the species distribution of flat-headed cats (*Prionailurus planiceps*), an endangered south-east Asian small felid. *PLoS One* **5**:e9612
- Zaniewski, A. E., A. Lehmann, and J. M. Overton. 2002. Predicting species spatial distributions using presence-only data: a case study of native New Zealand ferns. *Ecological Modelling* **157**:261–280.
- Zaramody, A., and J. Pastorini. 2001. Indications for hybridisation between red-fronted Lemurs (*Eulemur fulvus rufus*) and mongoose lemurs (*E. mongoz*) in Northwest Madagascar. *Lemur News* **6**:28–31.