NOTTINGHAM TRENT UNIVERSITY

HABITAT UTILIISATION OF TWO SYMPATRIC DIURNAL LEMUR SPECIES IN RESPONSE TO HUMAN DISTURBANCE: A COMPARISON OF COQUEREL'S SIFAKA (*PROPITHECUS COQUERELI*) AND COMMON BROWN LEMUR *(EULEMUR FULVUS)* IN THE MAHAMAVO REGION, NORTHWEST MADAGASCAR.

By

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Abstract

The lemurs of Madagascar make up 20% of the world's primate species and are considered one of the most threatened mammal taxa on earth with an estimated 95% of all species currently facing extinction. Species responses to increasing levels of anthropogenic disturbance are generally thought to be negative but remain poorly understood, particularly in regards to primate species and lemurs. This study aimed to assess and compare how two sympatric lemur species the Coquerel's sifaka (*Propithecus coquereli*) and the Common Brown lemur (*Eulemur fulvus*), are utilising their habitat in response to anthropogenic disturbance. Species disturbance, habitat use and activity budgets were assessed across two forest fragments with differing levels of human disturbance in the remote dry forests of Northwest Madagascar. Findings show that the distribution of each species does not appear to differ significantly across disturbed and undisturbed habitats, or in relation to distance from human disturbance (villages, roads and camps). However, a significantly larger amount of *P. coquereli* were observed compared with *E. fulvus*, 61 and 19 groups respectively. *P. coquereli* were found more often on introduced trees, as well as in higher percentage canopy cover, taller trees and higher positions in the tree, compared with *E. fulvus*. Additionally, analysis of activity budgets found *P. coquereli* observed in disturbed habitats spent on average, increased time feeding and decreased time resting and in locomotion, compared with those in undisturbed forest habitats. Findings suggest *P. coquereli* are responding more positively to increased human disturbance in the Mahamavo region, compared to *E. fulvus.* The ability to successfully determine and understand the responses of endangered primate species to anthropogenic disturbance is key to their conservation, and survival in a world dominated by human activity.

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Chapter 1: Introduction, Literature Review and Aims

1.1 Introduction

Twenty-first century wildlife is living in a progressively human-dominated landscape (Ciuti *et al.,* 2012). Where human populations have exploded, the demand for resources has accelerated (Primack and Sher, 2016) and the encroachment of humans on wild animal habitats has increased (White and Ward, 2011). The ability to understand the impact that increasing levels of anthropogenic pressures and human disturbance is having on the behaviour of species, particularly forest dwelling primates, is critical to their effective management and future conservation strategies to ensure their survival (Arrigo-Nelson, 2006).

Species responses to human encroachment and increased anthropogenic disturbance are largely viewed as negative, but in general remain poorly known or understood (Irwin e*t al.,* 2010a). It is known however that primates are among the vertebrate's orders most affected by anthropogenic disturbance due to their high dependence on rainforest ecosystems (Isaac and Cowlishaw, 2004). However, a lack of research currently exists exploring species specific responses for primates (de-Almeida-Rocha *et al.,* 2018). This is made harder when phylogenetic relatedness and ecological similarity cannot be used to determine responses (Irwin *et al.,* 2010a). With an estimated 60% of all primate species currently threatened with extinction (Estrada *et al.,* 2017), the need for individual species-specific research exploring responses is critical for the survival of many species into the future (de-Almeida-Rocha *et al.,* 2018).

The lemurs of Madagascar represent more than 20% of the world's primate species (Schwitzer *et al.,* 2014), and are among the most threatened mammal taxa on earth, with an estimated 95% of all species facing extinction (Schwitzer *et al.,* 2013). Despite receiving high research attention relatively few studies examine their responses to anthropogenic disturbance (Irwin *et*

al., 2010a; Schwitzer *et al.,* 2007). Again, highlighting the growing need for species-specific research to enhance the effectiveness of future conservation actions.

The following study aims to assess and compare how two sympatric diurnal lemur species, Coquerel's sifaka (*Propithecus coquereli*) and Common Brown lemur (*Eulemur fulvus*), both International Union for Conservation of Nature (IUCN) threatened species, are utilising their habitat in response to anthropogenic disturbance in the rapidly changing landscape of Northwest Madagascar. This will be achieved through the assessment and comparison of three different elements; Species distribution, habitat use and activity budgets.

This study aims to contribute to the current understanding of how endangered primate species, specifically lemur species, are responding and adapting to the increased pressures associated with anthropogenic disturbance. The increasing understanding of these ecological mechanisms will allow for more effective conservation for these species (Irwin, 2006), and similar others at risk, to ensure their long-term survival in a human-dominated world.

1.2 Literature Review

1.2.1 Anthropogenic Disturbance

The loss of the earth's biodiversity, the variability among living things (Myers *et al.,* 2000), is the biggest environmental issue facing humanity to date. Threatening ecosystem goods and services in addition to general human well-being (Ceballos *et al.,* 2015). It is believed the earth is entering a sixth 'mass extinction' event, where by 2050 an estimated 30 to 50 percent of all species could be extinct or heading towards extinction (Thomas *et al.,* 2004). Extinctions are a 'natural' process with background rates estimated at two mammal extinctions per 10,000 species, per hundred years (Primack and Sher, 2016). However, current estimates for the last century show extinction rates to be hundred times higher than background rates (Ceballos *et al.,* 2015). This acceleration has been linked with the rise in human populations and a

subsequent upsurge in resource exploitation, and the destruction of ecosystems and habitats due to anthropogenic activities (Primack and Sher, 2016).

World human populations currently stand at an estimated 7.6 billion (Worldometers, 2018), exploding from one billion since the industrial revolution, in the mid nineteenth century. As a result of increased birth rates and declines death rates populations are projected to reach over 10 billion by the end of the twenty-first century (Primack and Sher, 2016) (Figure 1.1).
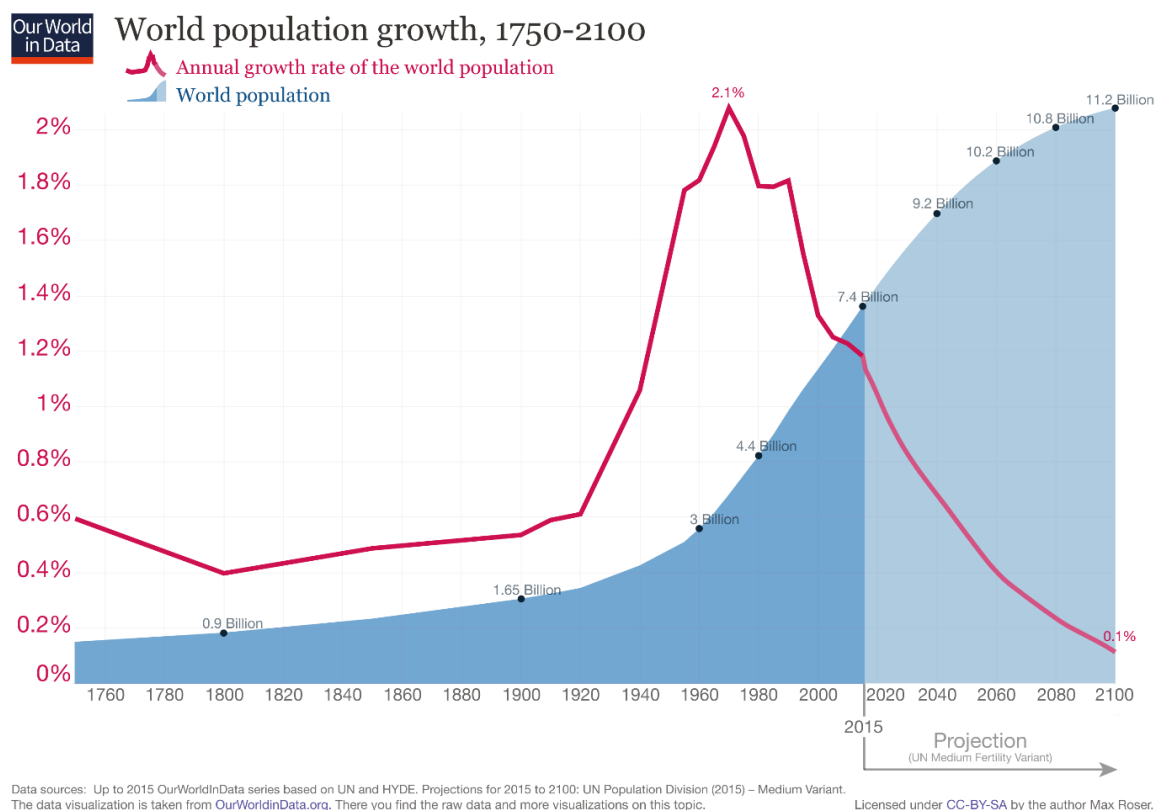
Figure 1.1: Graph showing global human population growth from the mid-18th century to the end of the 21st century (Roser and Ortiz-Ospina, 2018).

Humans and their activities dominate ecosystems and habitats worldwide, applying pressures to wildlife through; habitat loss, degradation and fragmentation, exotic species and hunting. Human activities such as agriculture (de Almeida-Rocha *et al.,* 2017), urbanisation (McKinney, 2002) and resource extraction (Peres and Lake, 2003), cause the modification of natural landscapes, putting huge threats on species worldwide (Brown *et al.,* 2013). Land-use changes

such as these cause widespread habitat loss and degradation, the leading cause of biodiversity loss at ecosystem, species and genetic levels (Primack and Sher, 2016).

Anthropogenic disturbance or human disturbance, defined as disturbance caused or produced by humans and their activities (Irwin *et al.,* 2010a), has been found to affect species presence, density and distribution on an ecosystem level (McKinney, 2002; Sagot *et al.,* 2016), while also influencing behaviour and ecology on a species-specific level (Ciuti *et al.,* 2012). Specifically habitat change for urban development and agriculture has been associated with changes in species spatial and temporal responses (Mammals, San Francisco Bay: Reilly *et al.,* 2016), distribution (Carnivores, Southern California: Ordenana *et al.,* 2010), personality (Spotted hyaena, *Crocuta crocuta:* Greenberg and Holekamp, 2017), predator risk perception (Guanaco, *Lama guanicoe:* Cappa *et al.,* 2017) and survival rate (Brown bear, *Ursus arctos:* Lamb *et al.,* 2017). These changes are being seen in species across the globe, and all taxa. Additionally, a recent study from Hardesty-Moore *et al.,* (2018), outlined how increasing levels of human disturbance pose threats to migratory species, including mammals, birds and fish.

Generally human disturbance is thought to negatively impacting wildlife, driving species decline. Ciuti *et al.,* (2010) for example, found elk (*Cervus elaphus*) behaviour to be negatively influenced by human disturbance, triggering increased vigilance and decreased foraging. Some species however appear to be responding and adapting to increasing levels of human disturbance, showing the ability to coexist with humans. Samia *et al., (*2015) suggested this coexistence could be explained by species tolerance. Providing a meta-analysis of birds, mammals and lizards, three major taxa, Samia *et al.,* (2015) found that overall, disturbed populations of all three showed more tolerance to human disturbance than those less disturbed populations, suggesting a degree of tolerance. Similarly, some species have been seen to perceive human infrastructures, such as roads, as 'safe' environments due to open areas adjacent facilitating the detection of predators (Cappa *et al.,* 2017). Suggesting some species are more likely to be influenced by human disturbance than others, therefore quantifying the

impact of anthropogenic disturbance on species is a high priority for conservation (Ciuti *et al.,* 2010).

1.2.2 Madagascar

Islands, where human populations are high, are particularly susceptible to the effects of anthropogenic disturbance (Primack and Sher, 2016). Showing historically higher extinction rates (Sax and Gaines, 2008), due to high levels of endemism and smaller population sizes (Primack and Sher, 2016).

Madagascar is the fourth largest island in the world (Irwin *et al.,* 2010a), found within the Indian ocean off the south-east coast of Africa. An island ecosystem that has, and is continuing to be put under intense unsustainable pressure by anthropogenic disturbance and pressures (Myers et al., 2000). As of 2016 the human population stood at around 24 million, increasing year on year. The island has been labelled as one of the world's hottest biodiversity hotspots by the Conservation International, and a number one conservation priority (Ingram and Dawson, 2005). As a result of high concentrations of endemism at all taxonomic levels (Fritz-Vietta et al., 2011), including 93% of fauna and flora (Valentine and Birtles, 2004) and 95% of vertebrate species (Ganzhorn et al., 2001; Myers et al., 2000).

Forests habitats across the island have seen extreme change in recent decades due to anthropogenic activity. Remaining intact forest has been seen to reduce from 106,600 km^2 in 1990, to an estimated 92,200 km^2 in 2010 (Schwitzer *et al.,* 2014). Now, with only 10-20% of Madagascar's intact primary forest cover remaining (Figure 1.2), it is thought if such rates of forest loss continue all of Madagascar's primary vegetation will disappear by 2067 (Moat and Smith, 2007), along with its forest dependant species. The clearance and conversion of land for agriculture, through practises such as slash-and-burn, to meet the demand of growing human populations, remains the leading driver of deforestation and forest loss across the island.
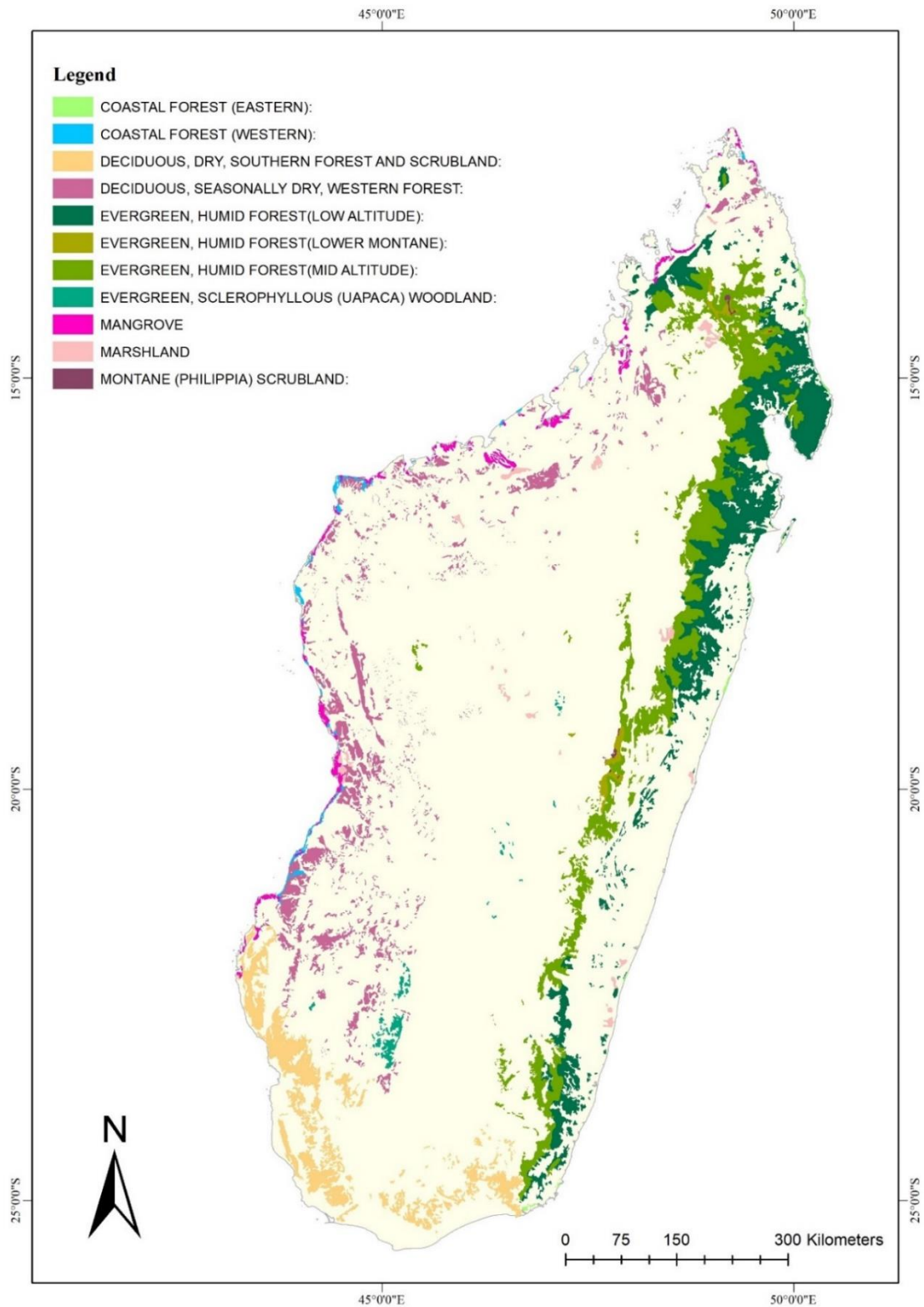
Figure 1.2: Remaining primary vegetation across Madagascar (Adapted from Moat and Smith, 2007)

1.2.2.1 Anthropogenic Disturbance in Madagascar

61% of Madagascar's human population lives outside of urban areas, leading to increasing levels of human disturbance and encroachment on wild animal habitats (Irwin et al., 2010a). Such pressures have been shown to have a significant impact on the ecology and behaviour of a variety of taxa across Madagascar, including carnivores (Farris *et al.,* 2015), lizards (D'Cruze and Kumer, 2010), bats (Cardiff *et al.,* 2012), amphibians (Vallan, 2002) and birds (Watson *et al.,* 2004).

Largely this impact is seen as negative, affecting species richness, abundance and occupancy. As found by Farris *et al.,* (2015) who explored the effects habitat loss and human encroachment on Madagascar's native carnivores. Finding that as habitat degradation increased, occupancy and encounter rates of native carnivores decreased. Similarly, D'Cruze and Kumar, (2010) and Vallan, (2002) found habitat disturbance and deforestation to be associated with decreases in species richness in reptiles and amphibians respectively. Behaviour has also been shown to be impacted by increased levels of human disturbance. Cardiff *et al.,* (2012) assessed the behavioural responses of Madagascar endemic bat species *Rousettus madagascariensis* to human presence. Summarising as presence became more frequent, bat colonies showed increasingly negative behavioural responses such as, increased flight activity and alertness. Which could ultimately pose a threat to the conservation of these endemic mammals.

Excluding lemurs, a lack of research currently exists exploring species-specific responses by Malagasy taxa. With human populations increasing an estimated 2.7% annually (Irwin e*t al.,* 2010a), leading to growing pressures on wildlife. The need for this type of research is high, and critical if conservationists wish to prevent the loss of Madagascar's endemic biodiversity.

1.2.3 Primates

The mammalian order Primates currently consists of 16 families and 72 genera. Of which are widely distributed across primarily the southern hemisphere, through Central and South America, Africa and southern Asia (Figure 1.3). Primates range from primitive lemurs to highly advanced humans (Martin, 2012), and are ideal species for ecological study, due to their size, diurnal habits and ability to be comfortably observed and followed by human researchers (Terborgh, 2015).
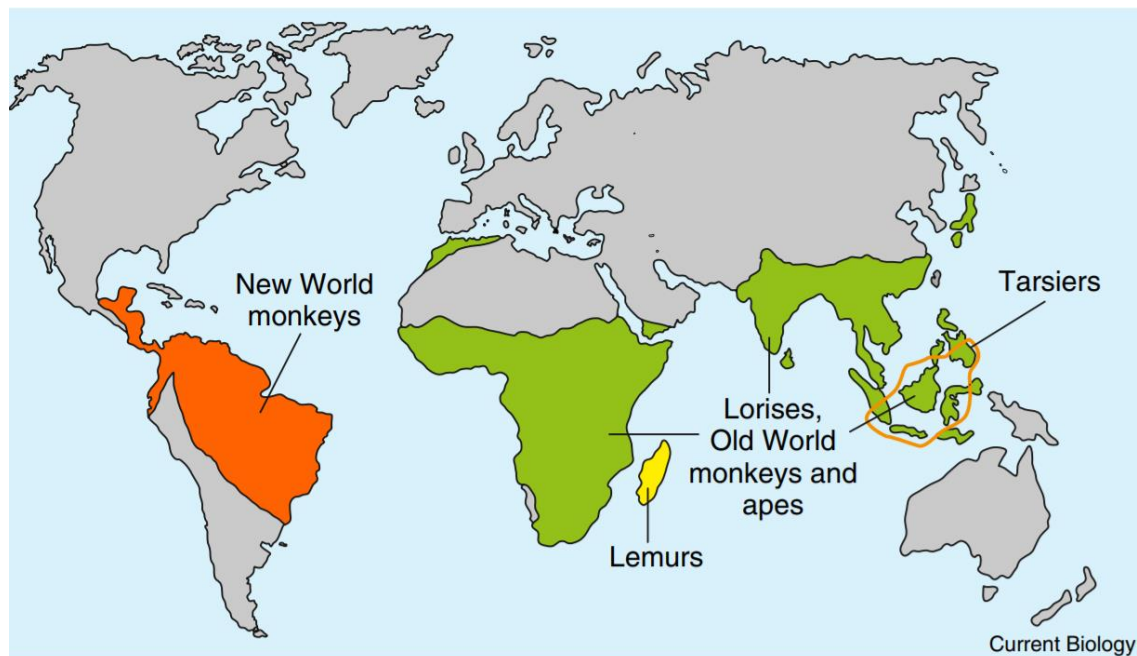
Figure 1.3: Global primate distribution (Martin 2012)

1.2.3.1 Global Primate Responses to Anthropogenic Disturbance

Primates have been shown to be highly sensitive to habitat changes, hunting and anthropogenic disturbance, making them one of the most impacted vertebrate orders (de Almeida-Rocha *et al.,* 2017). This is thought to be due partly to their high dependence on intact tropical rainforest ecosystems (Isaac and Cowlishaw, 2004).

There is increasing evidence being produced supporting this, with studies across new and old world primate populations and communities showing responses to increased levels of anthropogenic disturbance. A meta-analysis from de Almeida-Rocha *et al.,* (2017), quantified the effects of anthropogenic habitat modification on primate communities in the tropics. Finding that overall human induced habitat modification in tropical forests has a negative effect. Causing significant reductions in species richness and abundance. Analysis also found species responses are highly associated with four major biogeographical realms, showing potential evolutionary resilience to disturbance. Furthermore, increasing levels of human disturbance have been shown to impact primate risk perception. Milkula e*t al.,* (2018) upon examination found the flight initiation distance (FID) or fleeing distance in *Chlorocebus pygerythrus* (Vervet monkeys) to be significantly negatively impacted by human disturbance/presence.

Although anthropogenic impacts are usually detrimental to primates, there is some evidence suggesting that positive or neutral effects are possible, at least on a limited basis (Kamilar and Tecot, 2016). Recent research has been exploring the idea that some primate species are showing the ability to adapt and cope with some levels of anthropogenic disturbance in their habitat. A study from Rodrigues, (2017) found female *Ateles geoffroyi* (Spider monkeys) to respond to anthropogenic disturbance and its impact on food availability through fission-fusion dynamics. However, further research is needed into this area to identify if these responses are long or short term. Similarly, while exploring the influence of anthropogenic edge effects in Costa Rica, a study from Bolt *et al.,* (2018) found neutral responses by three primate species. Encounter rates of *Ateles geoffroyi, Cebus capucinus* and *Alouatta palliata,* were found to not differ between anthropogenically disturbed and undisturbed habitats, showing species hold an ability to withstand habitat change and modification.

It is important to remember that the responses explored here have only been studied in the short term, and it is known that for long-lived primates a lag time exists between habitat disturbance and change in behaviour and ecology (Worman and Chapman, 2006). Meaning long term

studies are needed to fully understand the impact habitat and human disturbance is having on the long-term survival of primate species. Particularly as it currently stands that 60% of all primate species are threatened with extinction (Estrada *et al.,* 2017), making them the mammal order with the highest proportion of species under threat.

1.2.4 Lemurs of Madagascar

The infraorder Lemuriformes comprises of five families and 15 genera made up of over 100 described species, all endemic to Madagascar (Schwitzer *et al.,* 2013). Considered one of the world's highest primate conservation priorities, Madagascar's lemurs represent 20% of the world's primate species, 30% family-level diversity (Schwitzer *et al.,* 2014) and 100% primate endemism (Mittermeier *et al.,* 2010). An estimated 95% of lemur species are currently threatened with extinction (Schwitzer *et al.,* 2014), due to habitat destruction, hunting and live capture (Mittermeier *et al.,* 2010). With such high levels of endemism and endangered species research on the behaviour, ecology and genetics of this infraorder is needed to fully grasp the basic requirements to ensure the future survival of the lemurs.

1.2.4.1 Lemur Responses to Anthropogenic Disturbance

Lemurs are the Madagascan taxa to have received the most research attention, despite this however few studies have explored their responses to increased anthropogenic disturbance (Irwin *et al.,* 2010a). Those studies that have, have documented changes to lemur abundance and distribution (Craul *et al.,* 2008; Rasoamanarivo *et al.,* 2015; Iris *et al.,* 2018), health (Junge *et al.,* 2011; Singleton e*t al.,* 2015), genetic diversity (Craul *et al.,* 2008) and behaviour (Seiler, 2012) in response to increased human disturbance and pressure.

Such responses are often found to be negative, particularly in response to lemur health. A study from Junge *et al.,* (2011) exploring the impact of anthropogenic disturbance on *Indri indri* health found those living in disturbed forests have increased susceptibility to parasitism and may experience physiological changes. Likewise, Singleton *et al.,* (2015) provided evidence

that habitat degradation impacts the physiology and health of populations of *Lemur catta.* Increasing levels of disturbance and subsequent habitat fragmentation have also been found to impact presence and genetic diversity of certain lemur species. Craul *et al.,* (2009) investigated the effects of human induced forest fragment on the larger-bodies *Lepilemur edwardsi,* finding lower genetic diversity in populations found in fragments compared with those in found in a nearby national park.

However, recent research has revealed some species of lemur exhibiting the ability to coexist with humans and inhabit anthropogenically disturbed habitats. A study from Hending *et al.,* (2018) confirmed the presence of five species of lemur in vanilla plantations, one of Madagascar's principle export crop. Similarly, de Winter *et al.,* (2018) found populations of *Varecia variegata* to inhabit both disturbed and less disturbed sites, a promising find for a species that is characterised by its drastic decline. Such research as presented again outlines the importance of species-specific research into responses to human disturbance.

1.2.4.2 *Propithecus* Genus

The sifaka, genus *Propithecus,* are one of three genus within the Indriidae family, distributed throughout the periphery of the island. The ranges of this genus differ, with some quite large (e.g. *P. diadema* and *P. verreauxi*), and others (e.g. *P. perrieri, P. candidus* and *P. coronatus*) being restricted and having some of the smallest primate ranges on earth (Mittermeier *et al.,* 2010). This genus, like all lemurs, is under intense threat from human activity (Bailey *et al.,* 2015), and all are considered threaten. Various studies have found human disturbance to affect the distribution, genetic diversity (Bailey *et al.,* 2015), feeding ecology (Arrigo-Nelson, 2006; Irwin, 2006) and general behaviour (McGoogan, 2011) of various species within the genus.

A study from Arrigo-Nelson, (2006) investigating the impact of habitat disturbance on *P. edwardsi,* found those living in anthropogenically disturbed habitats to spend increased time feeding and decreased time interacting socially compared with those in pristine forests. Results which indicate issues with long term reproductive success with those living in disturbed habitats. Likewise, Irwin, (2006) when exploring the impacts of forest fragmentation and

disturbance on *P. diadema*, found those seen in fragmented and disturbed forests to show decreased social cohesion and reduced home range size. Additionally, a study from McGoogan, (2011) fond *P. coquereli* in Ankarafantsika National Park to be edge avoiders, with only 5% of sightings in disturbed edge habitat. These studies present the survival, in the short term, of *Propithecus* species in disturbed forests, however ecological trade-offs are seen through changes in ecology and behaviour, which could place the long-term survival of these species at risk (Irwin, 2006).

One thing these studies and others of their kind have in common is they explore the impact of disturbance and subsequent responses from species in one area of the species total range. Populations of the same species in different regions may be influenced by different disturbances, and may show different responses, trade-offs and adaptations. Due to this, detailed species- and region-specific research is needed in order to adapt conservation efforts to specific populations.

1.2.4.3 *Eulemur* Genus

The *Eulemur* genus, often referred to as the 'little brown jobs' (Tattersall and Sussman, 2016), are a diverse, widely distributed and generalised genus, showing high levels of ecological flexibility (Schwitzer, *et al.,* 2007). Also referred to as the true lemurs, 12 species of *Eulemur* are recognised, found across the island of Madagascar in a wide variety of habitats (Mittermeier *et al.,* 2010). Despite this however all species are threatened by deforestation, habitat fragmentation and other human activities.

Eulemur are, like other primates and lemurs, forest-dwelling primates relying on intact primary forest (de Almeida-Rocha *et al.,* 2017), and as such are negatively impacted by forest loss and disturbance (Kamilar and Tecot, 2016) because of human disturbance. There is increasing evidence supporting this, with recent research examining hormone levels in relation to habitat disturbance. Balestri e*t al, (*2014) found *E. collaris* in disturbed forests to exhibit higher levels of faecal stress hormone, glucocorticoid, compared with those in nearby intact forests. Ultimately impacting the physiology of the species. Similarly, a study from Tecot, (2012) on

E. rubriventer, found those in anthropogenically disturbed habitats did not show behavioural and physiological responses to seasonal changes in food availability and climate, in contrast to those in undisturbed. On a larger scale geographical ranges and distributions of all *Eulemur* species have been found to be influenced by anthropogenic activity. Kamilar and Tecot, (2016) using species distribution modelling found the distributions of five *Eulemur* species (*E. collaris, E. fulvus, E. flavifrons, E. ruffrons a*nd *E. snfordi*), to be reduced once anthropogenic factors such as, distance from settlements, villages and croplands, were added to the model. Interestingly, the same model supported the idea that *E. cinereiceps* increased distributions once anthropogenic factors were added.

Despite evidence supporting the idea that *Eulemur* are negatively impacted by human disturbance and activity, some do believe that the genus's ecological flexibility and plasticity may allow populations of *Eulemur* to persist in disturbed areas for longer than other lemurs with less ecological and behavioural adaptability (Donati *et al.,* 2015). Supporting this, Schwitzer *et al.,* (2007) found while assessing habitat utilisation*,* that *E. m. flavifrons* use primary and secondary forest habitats types differently, showing a degree of habitat specialisation and adaptability.

Nevertheless, as Irwin *et al.,* (2010a) stated, it is not possible to rely on phylogenetic relatedness and ecological similarity to determine species responses to anthropogenic disturbance. Meaning species specific research is needed, as even the examples above show that species of the same genus can respond differently.

1.3 Research Aim and Objectives

The aim of this study is to assess and compare how two sympatric diurnal lemur species the Coquerel's sifaka (*Propithecus coquereli*) and the Common Brown Lemur (*Eulemur fulvus*) are utilising their habitat in response to human disturbance across two forest fragments in the Mahamavo region of Northwest Madagascar.

The specific research objectives for this study are as follows:

1) Species Distribution: Assess and compare the distributions of *P. coquereli* and *E. fulvus* across the two forest fragments, in relation to habitat type and distance from human disturbance.

2) Habitat Utilisation: Assess and compare how *P. coquereli* and *E. fulvus* are using their habitat, in terms of tree species, tree height, lemur height and canopy cover, in response to anthropogenic disturbance.

3) Activity Budget: Assess the impact of human disturbance on the behavioural repertoire and activity budget of *P. coquereli* across the two forest fragments and different habitat types.

Chapter 2: Materials and Methods

2.1 Study Site

This study was conducted in the dry forests of Mahamavo, Northwest Madagascar at a site currently occupied by the conservation organisation Operation Wallacea (Opwall) (Figure 2.1). Opwall have been working in the area for the past ten years carrying out long-term ecological monitoring and working closely with local people.

Opwall's site spans across two main forest fragments; the Mariarano classified forest and Matsedroy. The latter Matsedroy forest is smaller and more fragmented, with an estimated area of 11km^2, in comparison to the Mariarano forest with an estimated area of 31km^2 (Figure 2.2). High occurrences of deforestation have seen the fragments being separated by an agricultural matrix, which lemurs are unlikely to cross (Pers. Obs.).
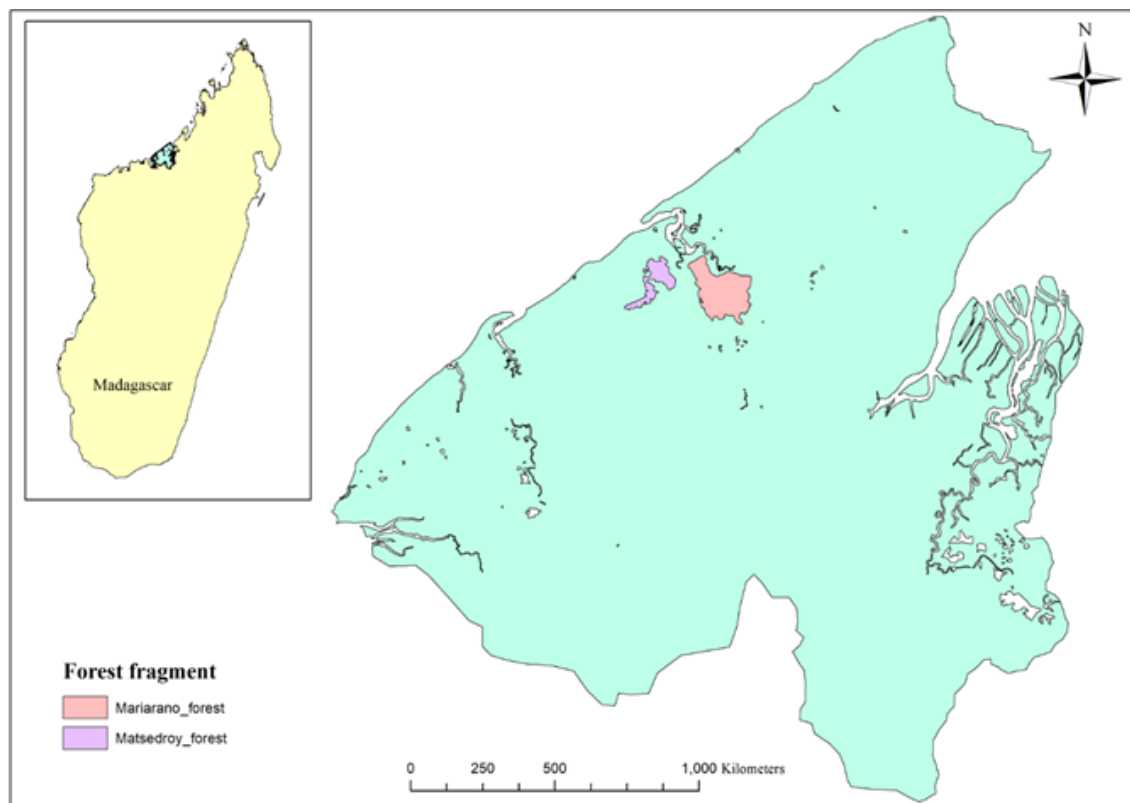
Figure 2.1: Map showing the location of the study site in the Mahamavo region, in the Northwest of Madagascar. Two main forest fragments are highlighted (Map produced in ESRI ArcGIS 10.3).

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Across both fragments the site is considered rural Madagascar with a relatively low human population density; however, this is thought to be increasing year on year. Various small villages exist across the two fragments, the main one being Mariarano, which is situated next to base camp and inhabits approximately 2,000 people. Making the Mariarano fragment have higher levels of human disturbance and activity. The village is accessible by a sand track with weekly services connecting the village to the nearest city of Mahajanga. Excluding the wet season when tracks are impassable. Villages across the commune are then further connected by narrow dirt tracks with the main transport being walking and zebu cart.
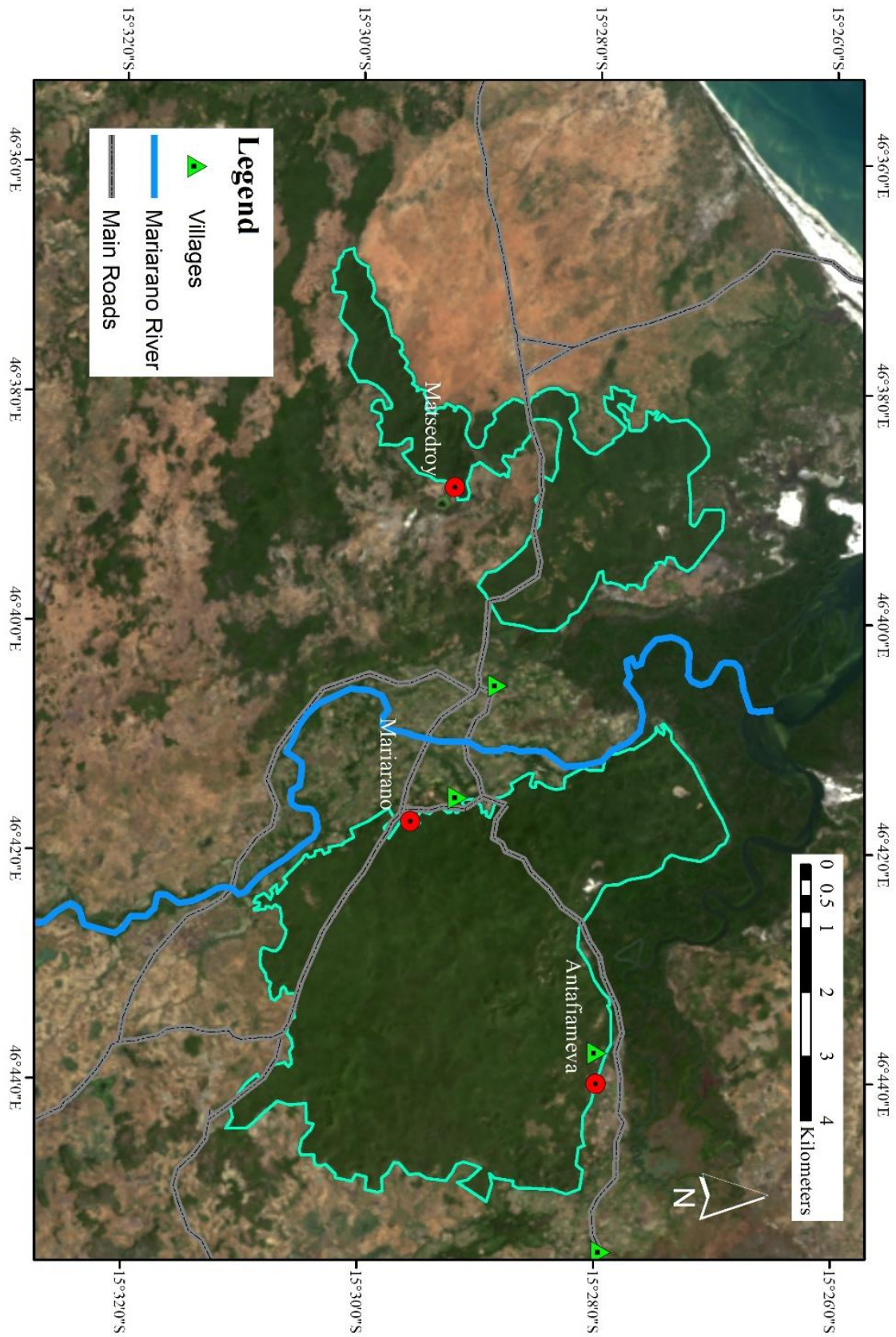
Figure 2.2: Satellite map showing the study site. Including camps, indicated in red, villages in green. As well as main roads/tracks and the Mariarano river. (Produced in ESRI ArcGIS 10.3)

2.2 Study Species

2.2.1 Coquerel's sifaka (*Propithecus coquereli*)

Propithecus coquereli, is one of nine species of sifaka within the *Indriidae* Family (Figure 2.3). A medium sized diurnal lemur found throughout the tropical dry lowland forests of north-western Madagascar (Figure 2.4). Found in troops of three to ten individuals, this arboreal primate is considered primarily folivorous (Bailey *et al.,* 2015), but also noted to feed on flowers and fruit (Mittermeier et al., 2010), depending on food availability and season. Sexual dimorphism does is not seen to occur within this species.

Since 1996, *P. coquereli* has been Listed as 'Endangered' on the International Union for Conservation of Nature (IUCN) Red List (Andriaholinirina *et al.,* 201a). However, a recent IUCN Red list meeting called for the up listing of all species of *Propithecus,* including *P. coquereli* to 'Critically Endangered'. Due to projected population declines of >50% over three generations (Andriaholinirina *et al.,* 2014a). An estimated 200,000 individuals are thought to remain throughout its range (Mittermeier *et al.,* 2010).

Across their distribution this species is facing serious decline due to habitat degradation and fragmentation because of slash-and-burn agricultural practices for cattle grazing and rice cultivation. Local taboos (fadys) regarding the hunting of *P. coquereli* is found in the Mariarano area (Rambinintsoa *et al.,* 2006). The immigration of neighbouring villagers into the region however, has been linked with increased hunting pressures on this species for food (Rambinintsoa e*t al.,* 2006).

Figure 2.3: Coquerel's sifaka (*P. coquereli)* with infant

Figure 2.4: Map showing the distribution of *P. coquereli* throughout northwest Madagascar (Andriaholinirina *et al.,* 2014a).

2.2.2 Common Brown Lemur (*Eulemur fulvus*)

Eulemur fulvus (Figure 2.5), is also considered a medium sized lemur found in lowland and montane rainforest, as well as moist evergreen in the east, and dry deciduous forests in the north west (Figure 2.6) (Garbutt, 2007). This species lives in troops of three to 12 individuals (Mittermeier *et al.,* 2010). Home range sizes for this species are thought to be highly influenced by habitat type.

Eulemur, the true lemur genus, are largely considered to be generalists, opportunistic frugivore-folivores with a high degree of ecological flexibility and adapt well to a of variety habitat types

(Schwitzer *et al.,* 2007; Sato *et al.,* 2016). *E. fulvus* are considered cathemeral, making them active during the day and night (Schwitzer *et al.,* 2007). Sexual dimorphism does not occur in the species (Garbutt, 2007).

Classified as 'Near Threatened' on the IUCN Red List (Andriaholinirina *et al.,* 2014b), this species faces a variety of threats similar to that of *P. coquereli*, including decline in suitable habitat and exploitation though unsustainable hunting pressure. Unlike *P. coquereli*, *E. fulvus* does not have a local taboo surrounding hunting which may impact the species within the Mariarano area.

Figure 2.5*: Common Brown Lemur (E. fulvus).*
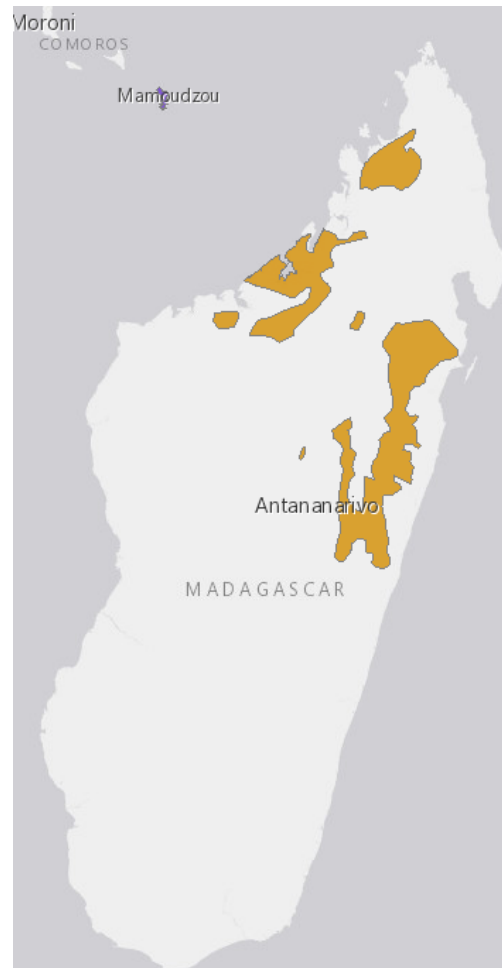
Figure 2.6: Map showing the distribution of *E. fulvus* across Madagascar (Andriaholinirina *et al.,* 2014b).

Despite these species, *P. coquereli* and *E. fulvus,* inhabiting the same geographical region and habitat types in the west of the island the species do differ both behaviourally and ecologically. With differing diets, ranging and activity patterns and social structures. These differences could be key in determining the species responses to human disturbance across the fragments.

2.3 Data Collection

2.3.1 Search Routes

Data collection occurred during the dry season, 2nd July – 20th July 2018, where there was little chance of rain. With day time temperatures ranging from 25-30°C, dropping to around 18°C during the evenings. Search routes predetermined by Opwall at Mariarano, Matsedroy and Antafiameva camps (R1-4, R1-4 and R1-2 respectively), were used to opportunistically search for both species, travelling at 1km/h. Routes were randomised and completed two or three times during this period to increase data reliability. Being completed at least once in the morning around 7am and once in the afternoon, around 1pm, to fit with the activity patterns of the species (Kun-Rodrigues *et al.,* 2014). Opportunistic data were also collected to and from these routes. Data collections sheets in Appendix 1.1 were used to collect all data.

Where possible troops were identified, using distinguishing features such as ear notches and face markings, to avoid pseudo-replication and increase reliability of the results. Unless troops could be successfully identified, each troop was treated as independent, meaning data for all troops encountered were taken. This method worked as this study was not exploring intergroup behaviour but assessing how the species as a whole are utilising their habitat.

2.3.2 Habitat Utilisation

2.3.2.1 Habitat type

For this study habitats were categorised into four primary types: 'Reserve Forest', 'Marginal Land', 'Degraded Land' and 'Other' (Sauther *et al.,* 2006) (Table 2.1).

Table 2.1: Habitat type description (Source: Adapted by Sauther *et al.,* 2006).

Description

Reserve Forest	Intact gallery forest (Figure 2.7)
Marginal Land	Land heavily subjected to deforestation and/or grazing by cattle. This habitat includes all agricultural land and any area cleared, as well as main paths and tracks through reserve forest (Figure 2.8 and Figure 2.9)
Degraded Land	Human inhabited/altered land. Including villages and camps (Figure 2.10).
Other	Habitat types that doesn't fit in any of the above.

Figure 2.7: Example of reserve forest habitat within the Mariarano forest fragment (Photograph: C. Chell)

Figure 2.8: Example of Marginal land habitat type. Intact reserve forest that has been subjected to human disturbance through the formation of a road/track (Photograph: C. Chell).

Figure 2.9: Another example of Marginal land. Land subjected to low levels of tree cutting (Photograph: C.Chell)

Figure 2.10: Example of Degraded habitat type, human altered/inhabited land. This example shows Mariarano Base Camp (Photograph: C.Chell).

2.3.2.2 Tree Species

Tree species were identified, to genus or species level, by trained botanists in the field. Where this was not possible samples were taken and later identified. Due to dense foliage within parts of the study area identification of tree species could not always occur, when this was the case the tree species was recorded as 'Unknown'. Tree species were then later categorised into 'Native' and 'Introduced'.

2.3.2.3 Canopy Cover

Canopy cover was measured as a percentage and calculated using the canopy cover grid method. This method involved placing a premade 5x5 grid over photos of the canopy from below (Figure 2.11). Photos were taken using the same camera, settings and position each time to ensure reliability. The number of squares containing foliage would be counted, adding partial squares together, then the percentage calculated using the following formula:

$$\frac{\# \, of \, squares \, covered}{\# \, of \, squares \, total} \times 100 \; = \% \, Canopy \, Cover$$
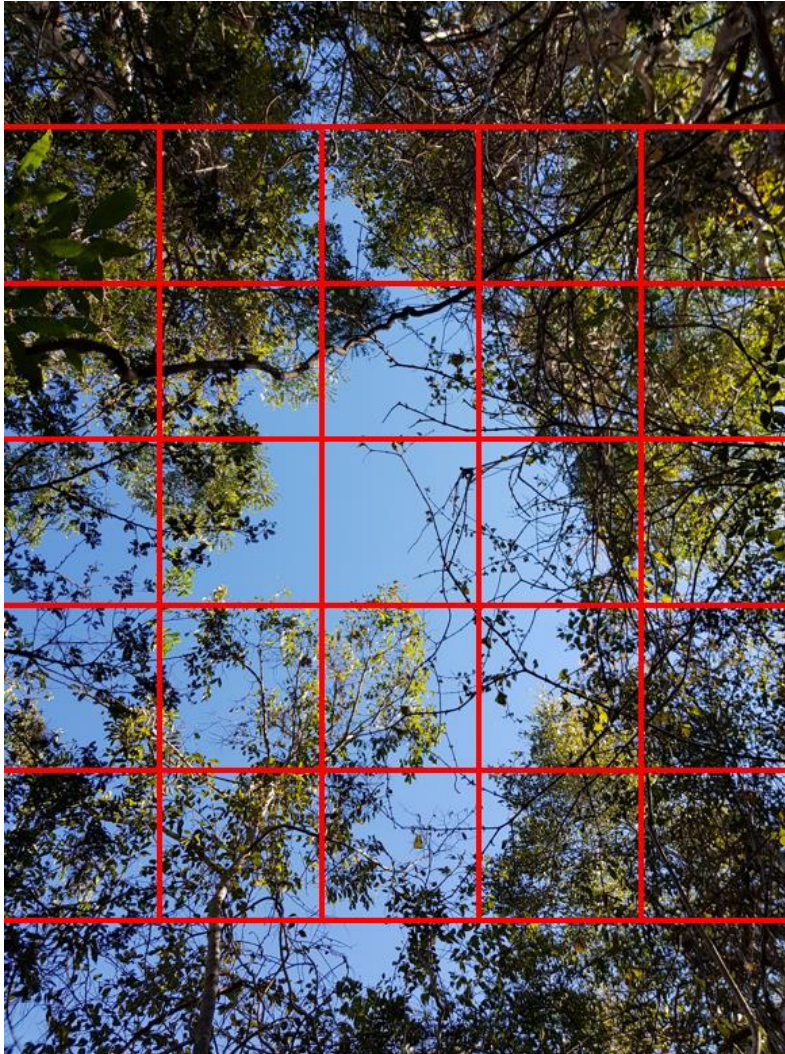
Figure 2.11: Showing the canopy cover grid technique used to work out percentage canopy cover.

2.3.2.4 Tree and Lemur Height

Upon sighting of a troop of *P. coquereli* or *E. fulvus* an estimation was taken on the height, in metres (m), of the tree the troop were observed in. If individuals of the same troop were observed across numerous trees an average height of all trees was taken.

Additionally, an average estimation was taken on the height of the troop as a whole in the tree. If only one individual was observed, an estimation was made of that individuals height alone. All estimations were taken in metres (m), by trained staff.

2.3.2.5 Behavioural Observations

Behavioural observations were recorded on *P. coquereli* only, in the form of a 10-minute continuous focal sample (Altman, 1974), on one, two or three members of the troop. Behaviours were defined using a species-specific ethogram (Adapted from Wallace *et al.,* 2016) (Table 2.2). Data were collected using an additional collection sheet (Appendix 1.2).

The ethogram was divided into state and event behaviours, with duration and frequency recorded respectively. State behaviours included the collection of data on the activity budget of the individual observed, i.e. feeding, resting, locomotion, etc. These behaviours were defined as continuous and mutually exclusive. Event behaviours, i.e. defecation, self-scratch, communication and head hob, were approximated as a point in time and measured as a frequency (Martin and Bateson, 2007). For this study only data taken on state behaviours, specifically resting, locomotion and feeding were used for further statistical analysis.

10-minute continuous focal sampling was used to maximise the number of troops located on each search route, as well as acting as a reliable time to collect data before individuals and/or troops fled, due to troops being semi-habituated.

Inter-Observer Reliability (IOR) tests were conducted to establish the reliability of the observational data collected (Caro *et al.,* 1979). The outcome of this IOR was 96.3%, showing a high level of agreement and reliability.

Table 2.2: Behavioural ethogram for *P. coquereli* (Adapted from Wallace *et al.,* 2016).

Behaviour	Description	Code
State behaviours		
Locomotion	Movement across landscape or through trees with head higher than the rest of the body- arboreal locomotion	**L**
	Movement of the individual across the ground	**LT**
Self- Grooming	The individual is licking and/or combing parts of its own body	**SG**
Allo-grooming	Two or more individuals licking or combing each conspecifics body or body parts in a reciprocated manner	**AG**
Groomed by other	The individual is being licked and/or combed by another conspecific, but not reciprocating towards the other individual	**GBO**
Groom other	The individual is licking and/or combing another conspecific, but the conspecific is not reciprocating the grooming effort	**GO**
Groom infant	Grooming is being directed towards the infant by the mother or a conspecific	**GI**
Feeding	Putting leaves and other food items into mouth and swallowing, also includes foraging, i.e. looking for food.	**F**
Vigilance	The individual is visibly alert with a rigid posture and eyes focused on cause of disturbance:	
	Unknown cause	**V**
	Conspecific	**Vc**
	Animal (e.g. dog)	**Va**
	Human	**Vh**
Resting	No movement, three or four hands holding on to or resting on tree branches. Head relaxed (not vigilant). Body is relaxed and motionless	**R**
Scenting	Rubbing scent glands onto trees/branches (scent glands are under chin and wrists)	**S**
Suckling	Baby sucking on the mother's teat, breastfeeding milk	**Suc**
Copraphagy	Faecal matter ingestion	**FI**
Out of sight	Focal animal moved out of view, behind a tree or beyond eye sight	**OOS**
Play	Individual is engaging in spontaneous, harmless activity with a conspecific, in a relaxed state. The play is not aggressive nor has the purpose of causing intentional injury.	**Pl**
Event behaviours		
Defecation	The expelling of urine or faecal matter from the body	**Def**
Self-scratch	The individual scratches its body with a forelimb or hindlimb momentarily.	**SS**
Communication	Low pitched rumble which occurs in a long, continuous duration	**Cr**
	Soft, quieter grunts performed in a steady, repeated pattern. Sounds like several beat noises in a row and movement/vibration of the body is noticeable when noise is produced.	**Cg**
	Tutting noises produced in a continuous, repetitive pattern at a more frequent rate than grunting. Movement/vibration of the body is noticeable when the noise is produced.	**Ct**
	Another communicative noise produced that does not fit the above criteria	**Co**
	Loud, vocal echoing call which can be heard from a distance. May be used as an alarm call or territorial signal.	**AC**
Head nod	The individual nods its head downwards in a forceful/aggressive manner	**HN**

2.5 Statistical analysis

All data collected were inputted into a Microsoft© Excel (2013) spreadsheet and coded for analysis. All statistical analysis were conducted using RStudio R (RStudio Team, 2016), to a significance level of <0.05. Graphical outputs are produced using R and Microsoft© Excel. Firstly, all data was explored using basic data exploration to identify outliers. From this it was found that the samples size for the degraded habitat type, n=2, was too small for further statistical analysis. The decision was made to combine the degraded and marginal habitat types, as they both represent disturbed habitats.

ArcCatalog and ArcMap (versions 10.3) were used through-out this report. GPS waypoints were plotted onto raster files of the Mahamavo and Mariarano area, to gather a visual representation of the distribution of each species. The distance from each of these waypoints to human disturbance, i.e. camps, roads and village centroids, was calculated and used in further analysis.

2.5.1 Species Distribution

Data used to assess distribution included; species, habitat type and distance to human disturbance. Due to small sample sizes a Fisher's extract test was performed to test for significance between species and habitat type. Shapiro-Wilks test conducted found all distance data to follow a non-normal distribution (Appendix 2.1) thus requiring non-parametric tests. Mann-Whitney U test was performed to test for differences between the two species and their distance from human disturbance.

2.5.2 Habitat Utilisation

Small samples for tree species meant a Fisher's extract test was performed to test for significance between *P. coquereli* and *E. fulvus,* and tree type. Unknown values (n=23), were not included in statistical analysis.

Due to the late addition of variables to methods, data for canopy cover, tree height and lemur height was smaller (n=44). Shapiro-Wilks test conducted on canopy cover, tree height and

lemur height (Appendix 2.2; 2.3; 2.4) found all data to be non-normally distributed requiring non-parametric tests. Mann-Whitey U tests were carried out to test for differences between the % canopy cover each species were found at, tree height and habitat type, and lemur height and habitat type.

2.5.3 Activity Budget

Data from focal observations were inputted into Microsoft Excel and then transformed into minutes per hour. Observations were collected on either one, two or three members of the troop. For those with two or more observations an average for the troop was calculated.

A Shapiro-Wilks test performed across the data found all 17 of the variables to follow non-normal distribution (Appendix 2.5), thus non-parametric tests were used. Mann-Whitney U tests were conducted to test for differences between the activity budget behaviours, resting, feeding and locomotion, and the two forest fragments and habitat types.

Chapter 3: Results

3.1 Species Distribution

In total 19 data collection days occurred, collecting 80 data points, for *P. coquereli* (n=61) and *E. fulvus* (n=19). This was across the two forest fragments, Mariarano (n=36) and Matsedroy (n=44). Each of these data points represented a troop located. The distributions of these troops across the two forest fragments can be seen in Figure 3.1.

Focusing on each forest fragment Figure 3.2 shows the number of sightings of each species across the two fragments. A near even split can be seen in the sightings for *P. coquereli* within Mariarano and Matsedroy (n= 30 and n= 31 respectively), compared with *E. fulvus* where a smaller number of sightings occurred (n= 6 and n= 13 respectively).
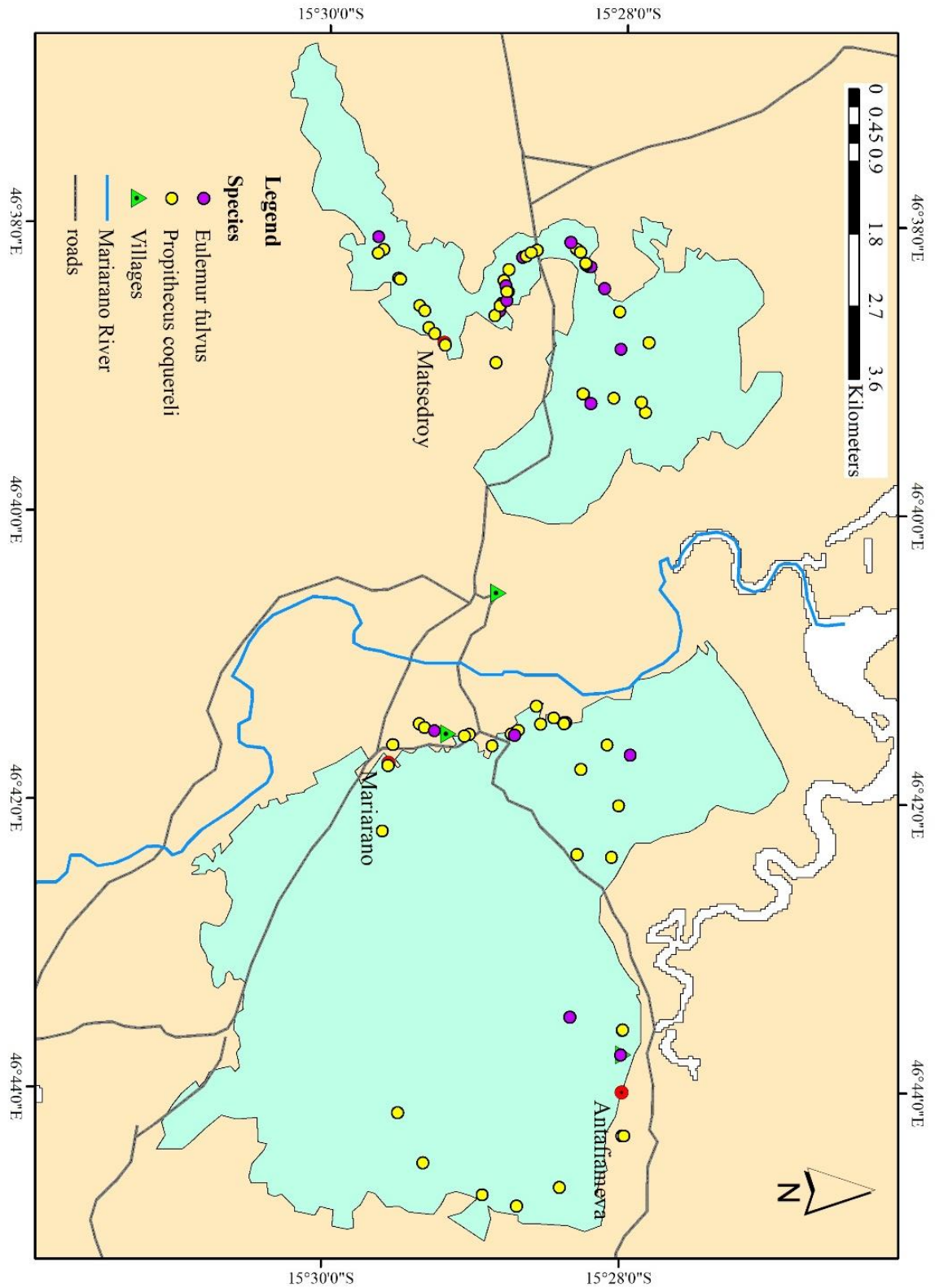
Figure 3.1: Map showing the distribution of each species, *P. coquereli* (n=61) and *E. fulvus* (n=19), across the two forest fragments, Mariarano and Matsedroy (Produced in ESRI ArcGIS 10.3).
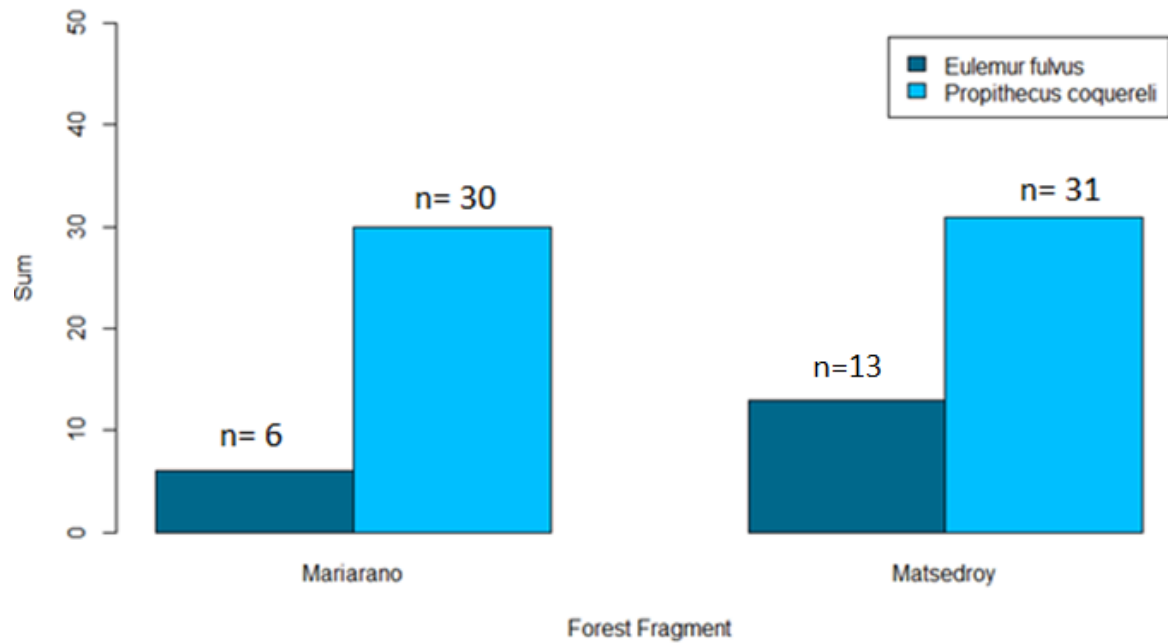
Figure 3.2: Barplot showing number of occurrences of *P. coquereli* and *E.. fulvus* across the Mariarano (n=36) and Matsedroy (n=44) forest fragments.

3.1.1 Distribution Across Habitat Type

It is important to remember here that due to small sample sizes occurrences in degraded and marginal habitats types were combined under one heading, marginal. With this being said the total occurrences in marginal were n=25, compared with n= 55 in reserve. Figure 3.3 Shows the breakdown of these occurrences across both species.
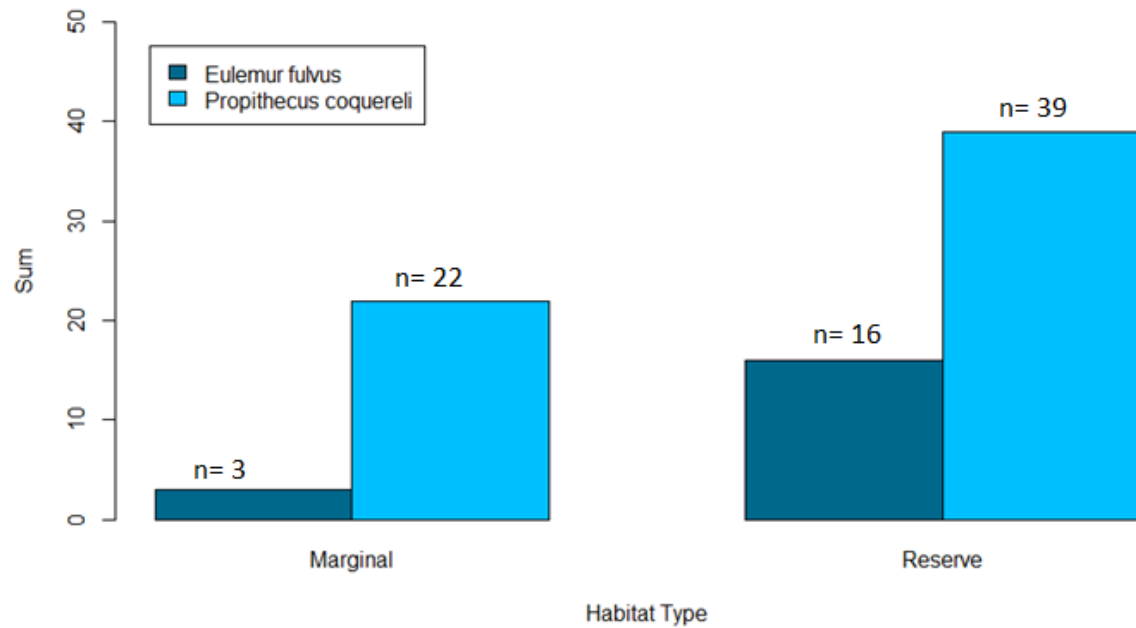
Figure 3.3: Barplot showing the number of occurrences of each species in each habitat type, marginal (n=25) and reserve (n=55).

For each species it can be seen there were an increased number of sightings in the reserve habitat type. A Fisher's extract test performed, found no significant differences between the number of troops for each species sighted across each habitat type (P= 0.155). This result does not support the hypothesis tested.

3.1.2 Distribution and Human Disturbance

Analysis of distance data shows *P. coquereli* on average (m) to be found further away from roads (672.27 ± 84.78), while slightly closer to camps (1506.74 ± 103.3) and significantly closer to village centroids (2521.07 ± 175.03), in comparison with *E. fulvus* (Figure 3.4 and Table 3.1).
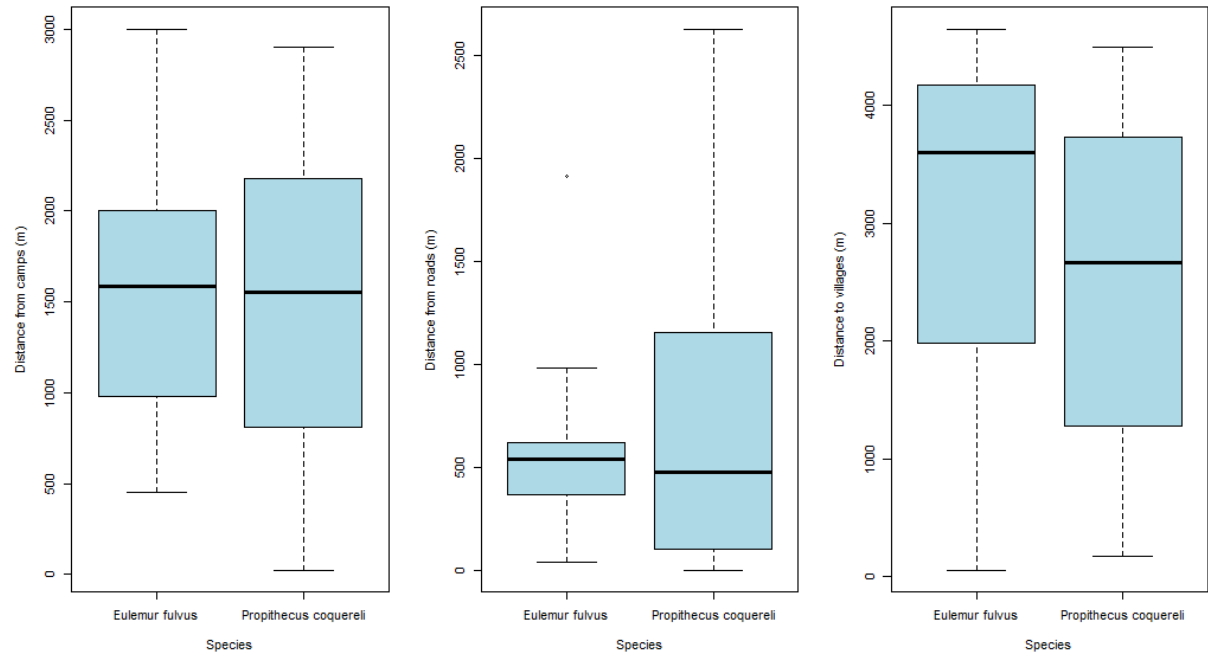
Figure 3.4: Conditional boxplots for distance from camps, roads and village centroids (m), for both species *P. coquereli* (n=61) and *E. fulvus* (n=19), showing means and upper and lower values for each.

A Mann-Whitney U test revealed no significant differences between the averages distances each species *P. coquereli* (n=61) and *E. fulvus* (n=19), were found to human disturbance; camps, roads and village centre points (W= 587, P= 0.937; W= 606.5, P= 0.764 and W= 697.5, P= 0.184 respectively) (Table….). These findings do not fully support the hypothesis tested.

Table 3.1: Table showing the mean, standard error and Mann-Whitney U results for distance data. Significant level P<0.05. All values rounded to 2 decimal places.

		Both Species (n=80) Mean ± S.E	*P. coquereli* (n=61) Mean ± S.E	*E. fulvus* (n=19) Mean ± S.E	Mann-Whitney U Test
Distance Data (m)	Distance From Camps	1514.45 ± 86.02	1506.74 ± 103.3	1539.21 ± 149.96	P= 0.937
	Distance From Roads	643.55 ± 68.38	672.27 ± 84.78	551.36 ± 94.20	P= 0.764
	Distance From Village Centre	2639.25 ± 155.67	2521.07 ± 175.03	3014.47 ± 331.08	P= 0.184

3.2 Habitat Utilisation

3.2.1 Tree Species

From 80 observations a total of 23 tree species were unable to be identified. Analysis from those that were indicate that both *P. coquereli* and *E. fulvus* were found on average more on native tree species compared with introduced, with interestingly only one sighting of *E. fulvus* on an introduced tree species (Figure 3.5).
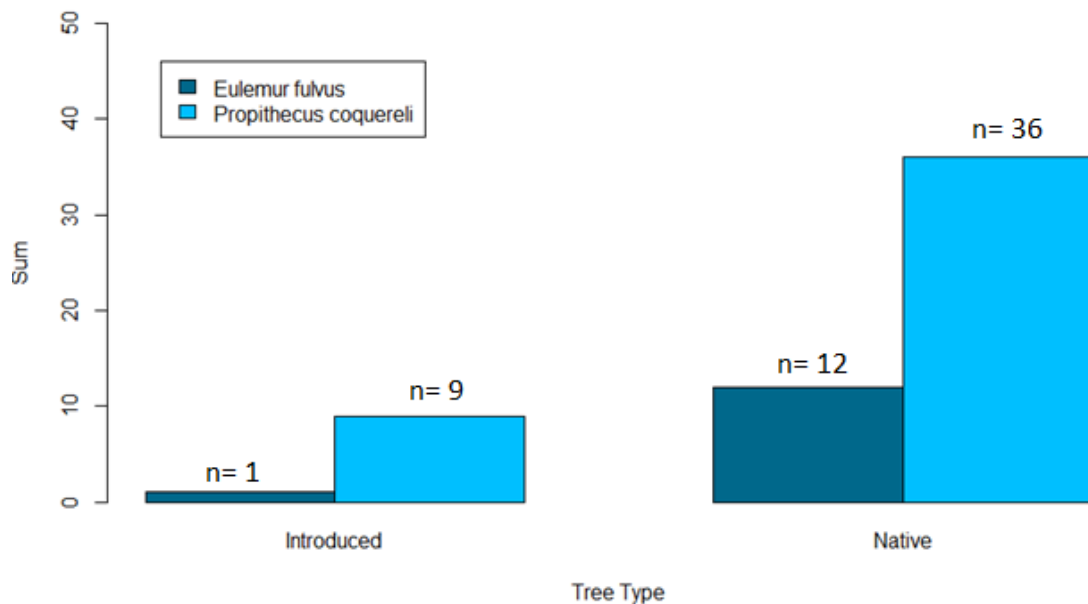
Figure 3.5: Barplot showing the number of occurrences of each species in each tree type, introduced (n=10) and native (n=47).

Due to small sample sizes a Fisher's extract test was performed, finding no significant differences between each species *P. coquereli* and *E. fulvus* and the tree type they were found on (P= 0.429). These results do not fully support the hypothesis tested.

3.2.2 Canopy Cover

E. fulvus were found on average a lower percentage canopy cover at 64.5%, compared with *P. coquereli* 73.4% (Figure 3.6). When comparing the species together across the two habitat types those in the marginal habitat were found at lower canopy cover (67.8%), compared with those in reserve habitat (76.2%) (Figure 3.7).

Results from a Mann-Whitney U test indicated there to be no significant differences between the percentage canopy cover species were found in and habitat type (W=199, P= 0.322). This result does not support the hypothesis tested.
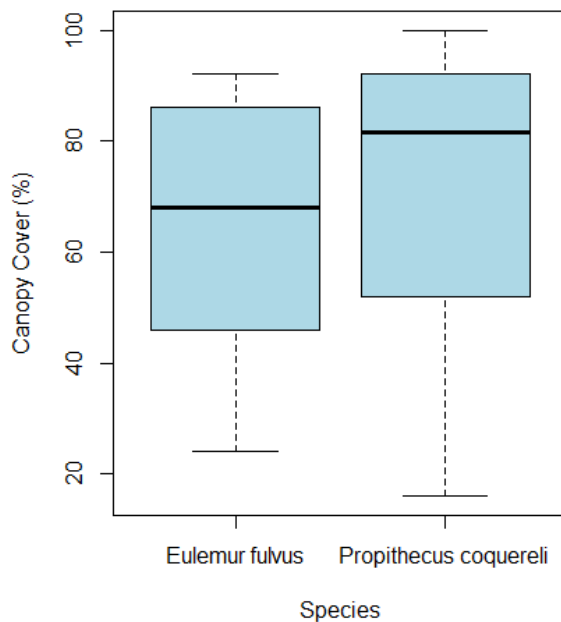
Figure 3.6: Boxplot showing canopy cover (%) for each species, *P. coquereli* (n=36) and *E. fulvus* (n=8).
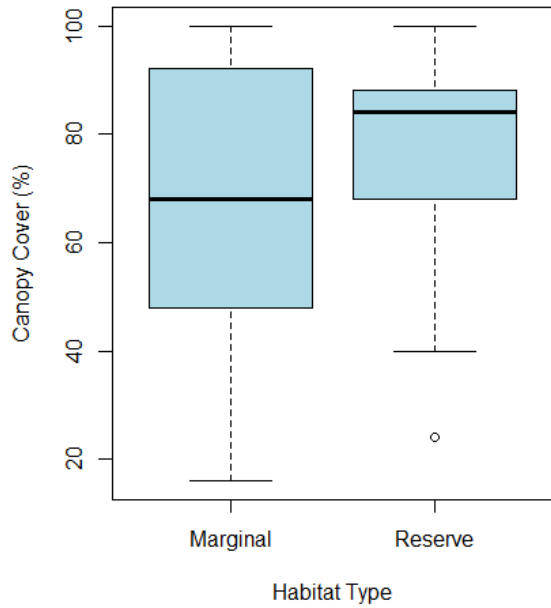
Figure 3.7: Boxplot showing canopy cover (%) for both species across each habitat type, marginal (n-=23) and reserve (n=21).

3.2.3 Tree Height

When comparing the tree height each species were found in, it could be seen that *E. fulvus* were on average found in smaller trees at 9m, compared with *P. coquereli* at 13.2m (Figure 3.8). When comparing both species together against habitat type a Mann-Whitney U test performed found significant differences (P=0.055), with those in marginal habitats (n=23) being found in taller trees at 14.2m, compared with 10.5m in reserve habitats (n=21) (Figure 3.9). These results do not however support that hypothesis tested.
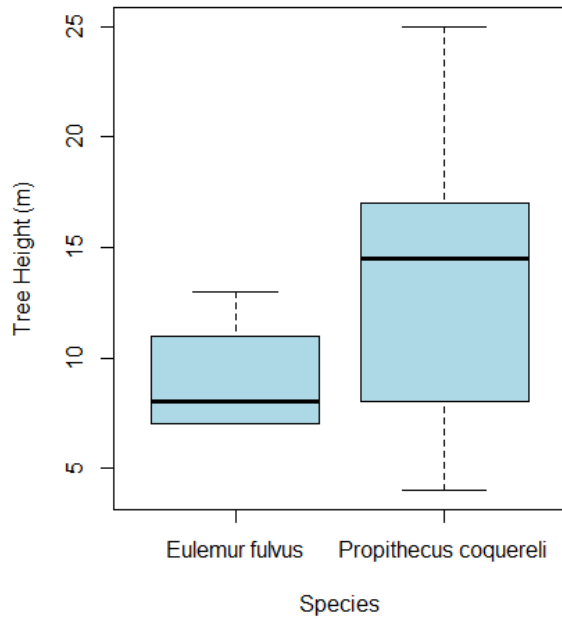
Figure 3.8: Boxplot showing tree height (m) for each species *P. coquereli* (n=36) and *E. Fulvus* (n=8).
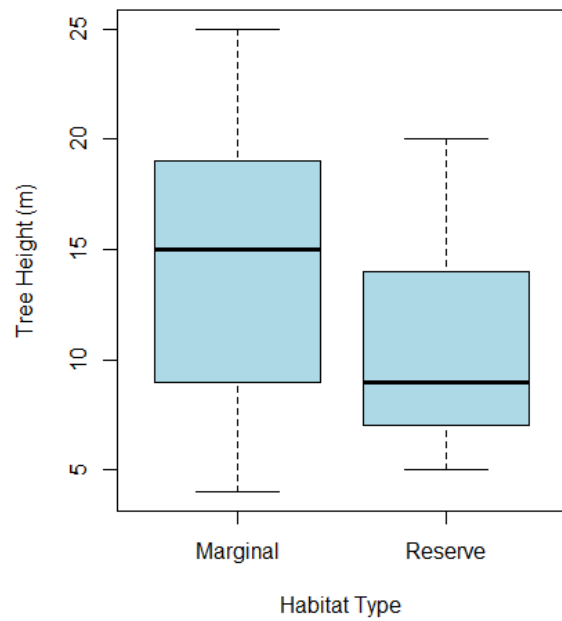
Figure 3.9: Boxplot showing tree height (m) for both species combined across each habitat type, marginal (n=23) and reserve (n=21).

3.2.4 Lemur Height

Results show *E. fulvus* to on average be found at lower heights, 5.5m, compared with *P. coquereli* that were found on average at 9.8m (Figure 3.10). When comparing the height both species were found at again habitat type a Mann-Whitney U test indicated significant differences (P=0.055), with those in marginal habitat types (n=23) being found on average at higher heights, 10.6m, compared with those in reserve habitat types (n=20) at 7.8m (Figure 3.11). These findings do not support the hypothesis tested.
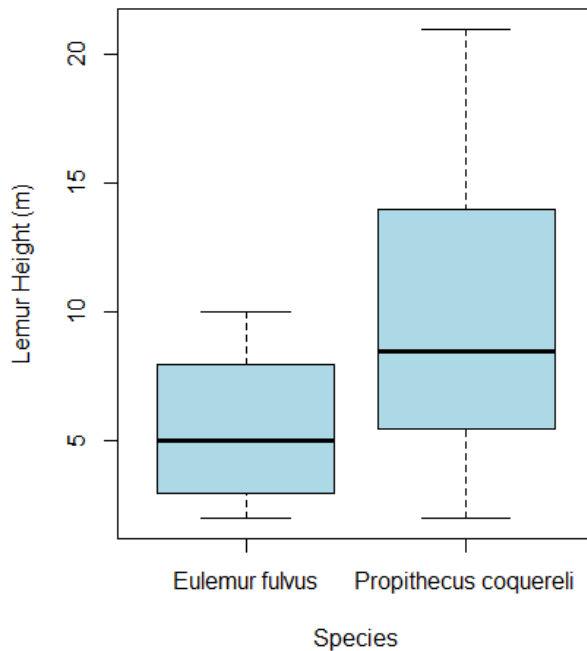
Figure 3.10: Boxplot showing lemur height (m) for each species *P. coquereli* (n=36) and *E. fulvus* (n=8).

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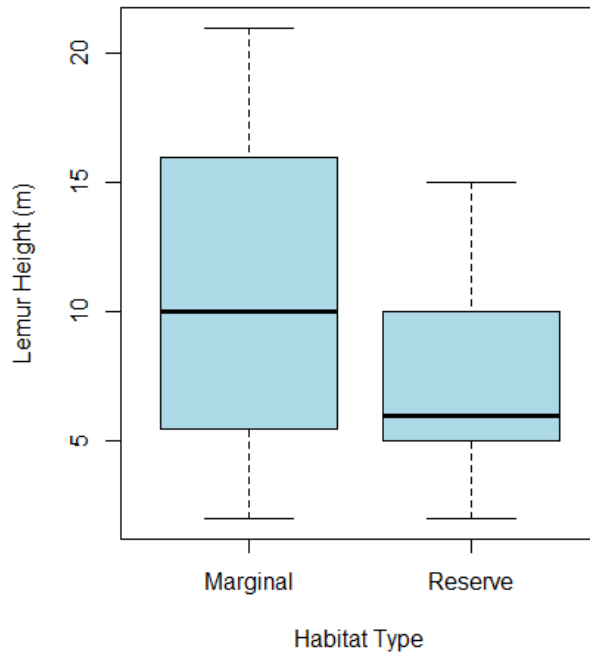
Figure 3.11: Boxplot showing lemur height (m) for both species combined across the habitat types, marginal (n=23) and reserve (n=21).

3.4 Activity Budget

3.4.1 Mean State Behaviours

Focal samples were taken for 51 troops of *P. coquereli,* across the two forest fragments, Mariarano (n=28) and Matsedroy (n=23), as well as across the two habitat types, marginal (n=20) and reserve (n=31). Figure 3.12 below shows the mean time in minutes per hour (min/hr) spent on each state behaviour (Appendix 3.1)) across both fragments and habitat types. Results also indicate a large proportion of tie spent out of sight (OOS) and performing vigilance behaviours.
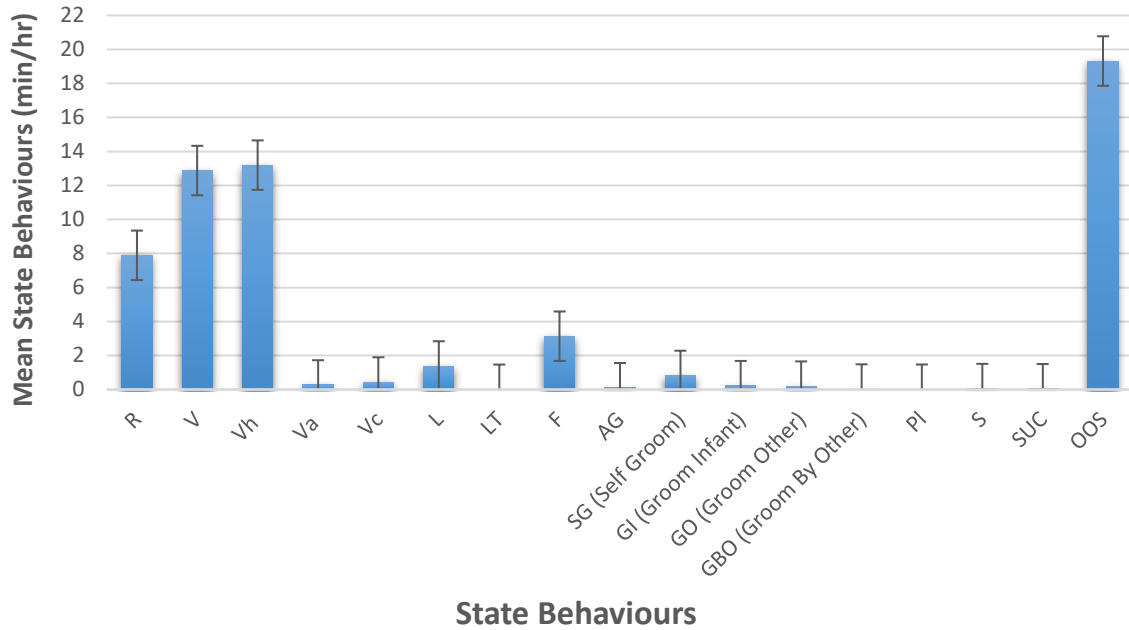
Figure 3.12: Graph showing mean time spent on state behaviours for *P. coquereli* (n=51) in minutes per hour (min/hr) (Appendix 3.1).

3.4.2 Comparison of Forest Fragment

Initial inspection, again focusing on resting, locomotion and feeding behaviours, shows *P. coquereli* in the Mariarano forest fragment (n=28) to on average (min/hr) spend increased time on all behaviours (8.21 ± 2.33; 1.72 ± 0.35 and 4.34 ± 1.34 respectively), compared with those in the Matsedroy forest fragment (n=23) (Figure 3.13, Figure 3.14 and Table 3.2). However, results from a Mann-Whitney U test (Table 3.2) showed no significant differences between forest fragments and the time spent on average performing resting ($W=275$, $P= 01.378$), locomotion ($W=413$, $P=0.086$) and feeding ($W=407$, $P=0.061$) behaviours. These results again do not support the hypothesis tested.
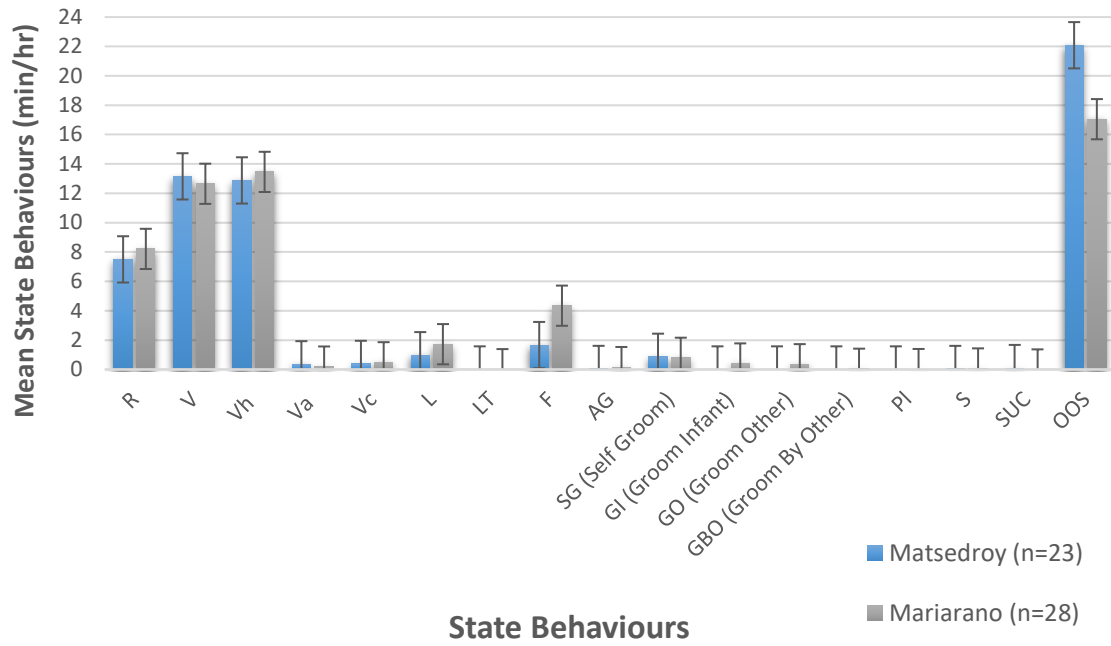
Figure 3.13: Graph showing mean time spent on the state behaviours of *P, coquereli* (n=51) in minutes per hour (min/hr), across both forest fragments.
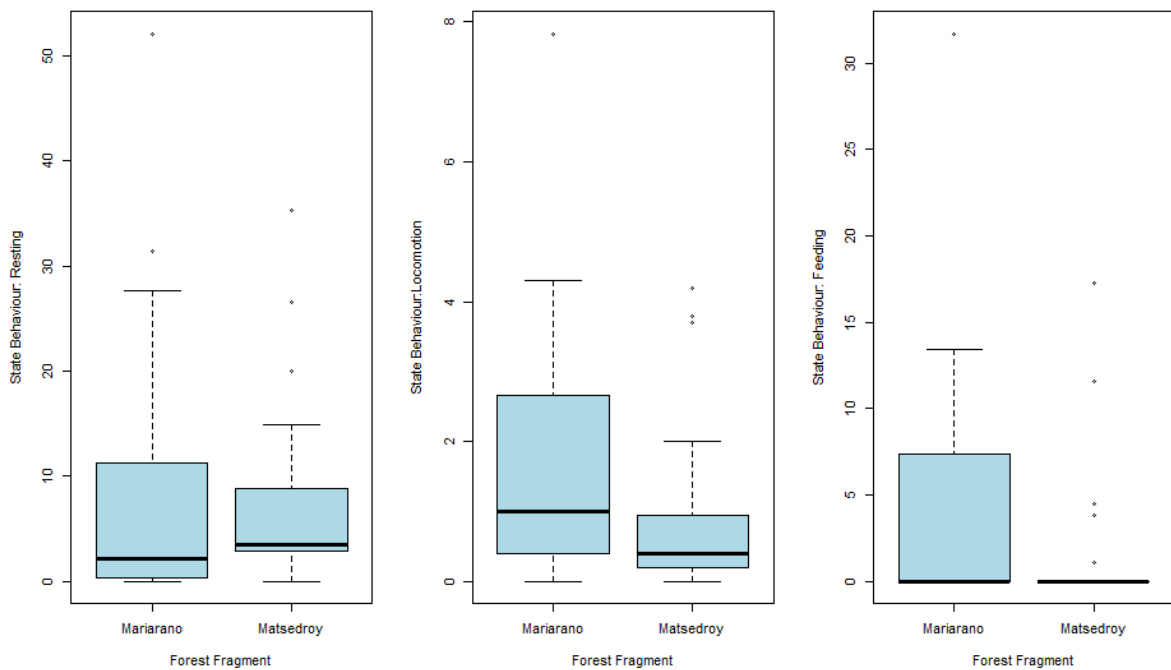
Figure 3.14: Box and whisker plots showing resting, locomotion and feeding behaviours between forest fragments.

Table 3.2: Table showing means, standard error and Mann-Whitney U test results for each activity budget state behaviours across the two forest fragments. Significance level P<0.05.

		Mariarano (n=28) Mean ± S.E.	**Matsedroy (n=23) Mean ± S.E**	**Mann-Whitney U Test**
State Behaviours (min/hr)	Resting	8.21 ± 2.33	7.50 ± 1.89	P= 0.378
	Locomotion	1.72 ± 0.35	0.97 ± 0.26	P= 0.086
	Feeding	4.34 ± 1.34	1.66 ± 0.90	P= 0.061

3.4.3 Comparison of Habitat Type

Initial viewing of the results for resting, feeding and locomotion behaviours specifically show *P. coquereli* in marginal habitats (n=20) to spend on average (min/hr) decreased time resting (6.95 ± 1.86), increased time in locomotion (2.07 ± 0.45) and increased time feeding (5.86 ± 1.76) (Figure 3.15, Figure 3.16 and Table 3.3), compared with those in reserve habitat habitats (n=31).
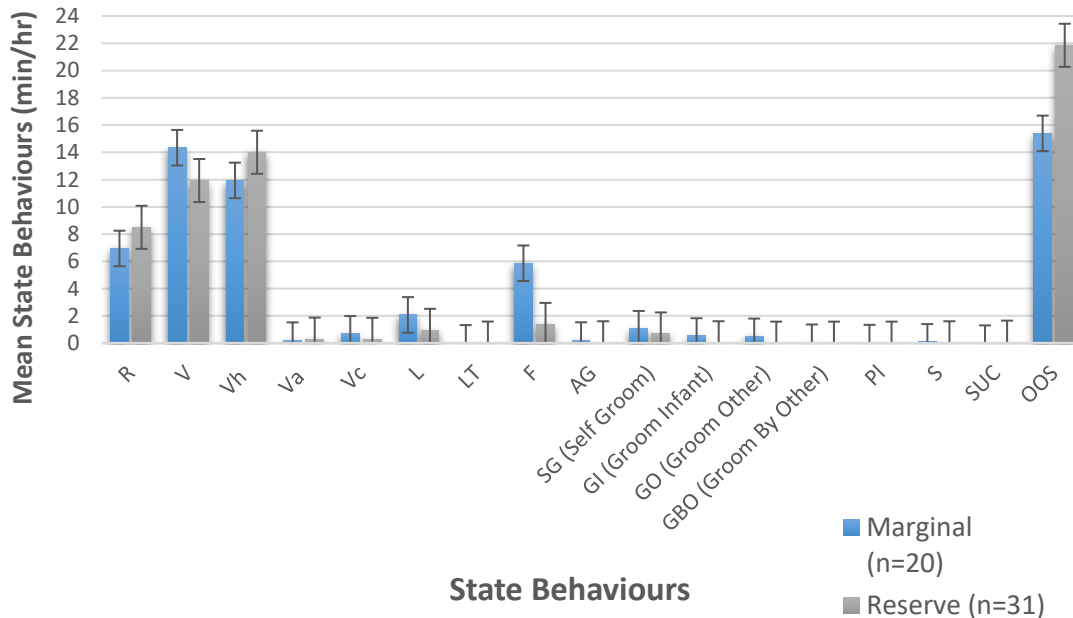
Figure 3.15: Graph showing meaning state behaviours for *P. coquereli* in minutes per hour (min/hr), across the two habitat types, marginal (n=20) and reserve (n=31).
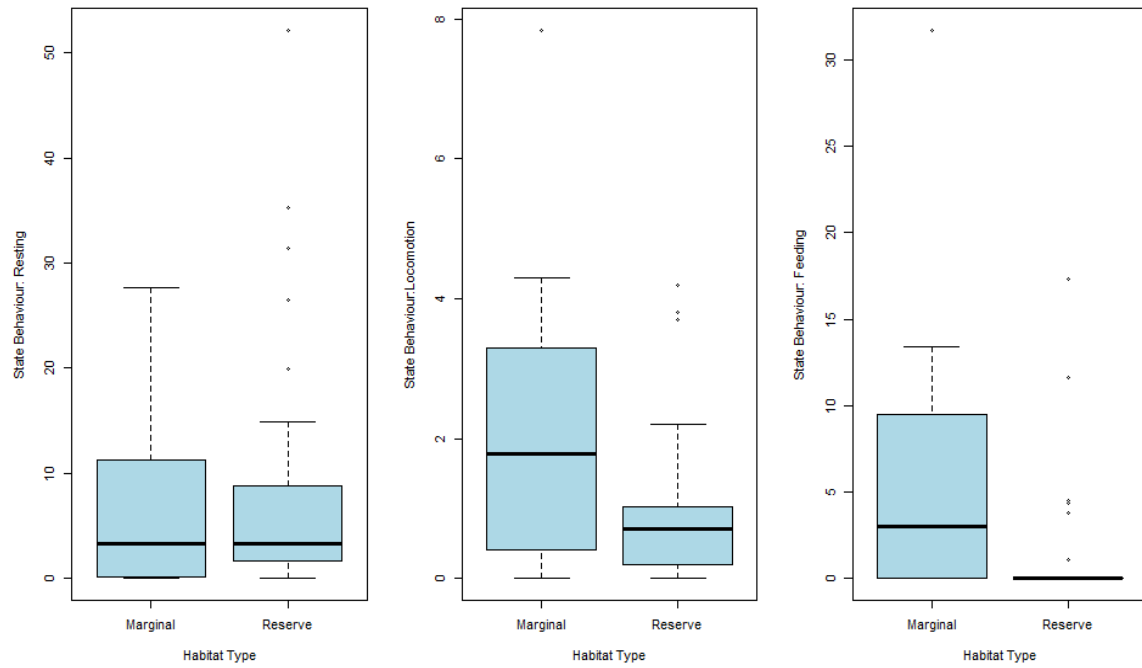
Figure 3.16: Box and whisker plots showing resting, locomotion and feeding behaviours between habitat types.

Results from a Mann-Whitney U tests (Table 3.3) support this by revealing significant differences between habitat type, marginal (n=20) and reserve (n=31), and the time on average spent in locomotion (W=417, P= 0.040) and feeding (W=446, P=0.002) by *P. coquereli*. Despite this these results do not support the hypothesis tested.

Table 3.3: Table showing means, standard error and Mann-Whitney U test results for each activity budget state behaviours, across the two habitat types. Significance level P<0.05. Significant results highlighted.

		Reserve (n=31) Mean ± S.E.	Marginal (n=20) Mean ± S.E.	Mann-Whitney U Test
State Behaviours (min/hr)	Resting	8.50 ± 2.22	6.95 ± 1.86	P= 0.616
	Locomotion	0.94 ± 0.21	2.07 ± 0.45	P= 0.040
	Feeding	1.37 ± 0.68	5.86 ± 1.76	P= 0.002

Chapter 4: Discussion

The purpose of this study was to assess and compare how two species of lemur, *P. coquereli* and *E. fulvus,* are using their habitat in response to human disturbance across two forest fragments in the dry forests of Mahamavo, Northwest Madagascar. This was achieved through the analysis of species distribution, habitat use and activity budget. Overall results indicate that *P. coquereli* are more present across the two fragments and found closer to village centroids. While also being found in higher percentage canopy cover, taller trees and higher in trees, compared with *E. fulvus.* Analysis of activity budgets showed *P. coquereli* in marginal habitats to spend decreased time resting and increased time feeding and in locomotion.

The outputs from this study will provide insights into the ways in which two lemur species are utilising their habitat, which can then be applied to future conservation management strategies for the two species in the area.

4.1 Species Distribution

Human disturbance, and the resulting habitat degradation and fragmentation has been seen to affect species in a variety of ways. Often applying ecological strain on species, which squeezes social groups of the same and different species closer together into smaller areas, which in turn makes them compete for limited resources, such as space and food (Irwin, 2006).

Here we see troops of both species, *P. coquereli* and *E. fulvus*, observed across the Mariarano and Matsedroy forest fragment, with troops of *P. coquereli* seen to occur more frequently (61 and 19 respectively). This is an interesting result as *P. coquereli* is considered critically endangered, with declining populations across its range (Andriaholinirina *et al.,* 2014a), compared to *E. fulvus* that is near threatened (Andriaholinirina *et al.,* 2014b). A near equal amount of *P. coquereli* were observed across the fragments, despite their clear differences in size, 31km^2 and 11km^2 respectively. Some primate's species have shown the ability to tolerate

small home ranges and higher densities, as a result of habitat fragmentation and disturbance (Irwin, 2006). However, frugivore primate species such as *E. fulvus,* must cope with scattered distributions of fruiting resources meaning they require larger home ranges (Estrada and Coates-Estrada, 1996; Rode e*t al.,* 2006). Many frugivorous primates have been seen to disappear from forest fragments and remain restricted to continuous forests due to this dependency on large home ranges. This has been found with *Lophocebus albigena* (gray-faced mangabeys) and *Ateles geoffroyi vellerosus* (Mexican spider monkeys) (Estrada and Coates-Estrada 1996; Tutin e*t al.,* 1997). The low numbers of *E. fulvus* seen here across the fragments, compared with *P. coquereli,* could be explained by this high dependency on large home ranges that frugivores have.

4.1.1 Habitat Type and Distance from Human Disturbance

Assessment of occurrences of each species across the defined habitat types found no statistically significant results, however it could be seen that more troops of both *P. coquereli* and *E. fulvus*, were found in reserve habitat, intact gallery forest, compared with marginal, anthropogenically disturbed habitat. This could be explained by the dependency lemurs have on intact primary forest (de Almeida-Rocha *et al.,* 2017). Despite this however, 36% of *P. coquereli* observations were in marginal habitats. This corresponds with findings from other studies, which has found that habitat choice by species in the *Propithecus* genus is flexible and they are found in both disturbed and undisturbed habitats (Salmona *et al.,* 2014; Johnson et al., 2003; Lehman et al., 2006a). However, McGoogan, (2011) found P. *coquereli* to be strong edge and disturbed habitat avoiders, with 95% of sightings being in the forest interior.

The statistical analysis of species occurrences in relation to distance from human disturbances; camps, roads and village centroids, also found no statistical differences. *P. coquereli* and *E. fulvus* were found to be on average around the same distance from camps and roads. However, when exploring distances from village centroids *P. coquereli* were found on average closer than *E. fulvus*. Supporting conclusions from previous studies which have found *P. coquereli* to

be found closer to or inhabiting anthropogenic areas, such as villages (Salmona et al., 2014). The lack of *E. fulvus* sightings in marginal habitats (15%) and increased distance from human disturbance suggests that such habitat types are of limited value to the species (Schwitzer *et al.,* 2007). These results correspond with past studies which have shown *Eulemur* species to be found in greater densities, and prefer primary undisturbed forests further from human disturbance (Schwitzer et al., 2007; Wilson et al., 1989 and Herrera et al., 2011).

Frugivorous primates are known to have more negative responses to disturbance than folivores (Johns and Skorupa, 1987), and this is considered to be true for lemur species as well (Irwin et al., 2010a; Lehman, 2007; Lehman et al., 2006b; Herrera et al., 2011). This is thought to be due to the leaf quality in disturbed habitats being improved through increased light exposure (Ganzhorn, 1995), which in turn means increased abundance of folivore lemurs in disturbed habitats. This has been seen in other folivores, such as *Hapalemur meridionalis,* which were found to be more likely to feed and use secondary/disturbed vegetation, than the frugivorous *Eulemur collaris* (Eppley *et al.,* 2016). This could explain the increased occurrence of *P. coquereli* across both forest fragments and in marginal habitats.

4.2 Habitat Utilisation

4.2.1 Tree Species

Analysis of the tree species, native or introduced, that each species were observed on found no statistically significant results. However, for both *P. coquereli* and *E. fulvus* a larger proportion of observations were on native trees, 80% and 92.3% respectively. Trees including *Treculia africana madagascariensis, Xanthocercis madagascariensis* and *Tina chapeleriana*. This is expected when more observations were taken for troops in reserve habitat, where native trees such as these are more abundant.

When exploring the proportion of observations made on introduced tree species, *P. coquereli* were sighted more often, compared with *E. fulvus*, 20% and 7.7% respectively. These sightings

were predominantly on *Mangifera indica,* or more commonly known as mango. This corresponds with the expected, with recent research from Salmona *et al.,* 2014 finding *P. coquereli* to be found more frequently in areas dominated by introduced trees such as mango. Furthermore, other folivorous primate species have been documented to use and heavily rely on fast growing exotic introduced tree/plant species. Including *Alouatta caraa* and *Alouatta pigra* (Black howler monkeys) which were reported to use *Eucalyptus* trees and coco plantations as feeding and sleeping sites in anthropogenic landscapes (Zarate *et al.,* 2014; Bonilla-Sanchez *et al.,* 2012).

During the dry season, when this study took place, mango trees do not fruit but produce young buds and leaves. *P. coquereli* and other members of the *Propithecus* genus as folivores are specially adapted to digest these buds and leaves, compared with *E. fulvus* (Arrigo-Nelson, 2006). This explains their presence on these trees during this season. However, during the wet season when the mango trees are fruiting, various species of *Eulemur* have been noted to feed on these fruits (Simmen e*t al.,* 2007), meaning their presence on introduced trees could change seasonally as food availability changes in the area.

4.2.1 Canopy Cover and Tree and Lemur Height

Habitat structure and forest characteristics such as canopy cover and canopy/tree height have been regarded as an important predictor of primate and lemur abundance (Herrera *et al.,* 2011), and overall primate responses (Epply *et a.,* 2016).

Disturbed habitats and forests, such as marginal land, are associated with characteristically low and open canopy in comparison with undisturbed primary reserve habitats (Herrera *et al.,* 2011). Despite the results not being statistically significant, species observed in marginal habitats were in lower canopy cover at 67.8%, compared with those in reserve, at 76.2%, which is what was expected to be seen. When assessing the canopy cover of each species found across both fragments and habitats types, it was found that *E. fulvus* were in lower canopy cover

compared with *P. coquereli* (64.5% and 73.4% respectively). This result does not fit with the predicted as *E. fulvus* were found more often in reserve habitats which based on previous literature is associated with denser and higher percentage canopy cover (Schwitzer *et al.,* 2007). However, canopy cover is a factor often used by primates to determine sleeping sites, with lower percentage canopy cover being used by primates as protection. This has been noted in species such as *Leontopithecus rosalia* (Golden lion tamarin), that are highly susceptible to predation (Hankerson *et al.,* 2007).

Tree height is another key factor considered by primates in the selection of sleeping and feeding sites (Seiler *et al.,* 2013). Disturbed and secondary habitats are associated with smaller trees, however fast growing introduced exotic trees such as *Mangifera indica,* or mango trees, are more likely to inhabit these areas, and are characteristically taller. Statistically significant results found here indicated that those, predominantly *P. coquereli*, found in marginal habitats were found in taller trees, 14.2m, compared with those in reserve habitats, 10.5m. Contrary to this, research from McGoogan, (2011) found troops of *P. coquereli* living nearer to the forest edge in disturbed habitats preferred smaller trees, compared to those in the forest interior that preferred taller trees. In general, across both fragments and habitat types, *E. fulvus* were observed on average in smaller trees, 9m, compared with *P. coquereli,* 13.2m. This fit with past studies which have shown *E. fulvus* to prefer smaller trees, around 10m, compare with other species of *Propithecus* which are found across all tree heights, but predominantly taller trees (Dagosto and Yamashita, 1998). This could be due to *P. coquereli* and other *Propithecus* species preferring taller trees as sleeping sites, which is common for most primate species (Philips and Abercrombie, 2003).

Previous studies have shown *Eulemur* and *Propithecus* species in disturbed secondary forest habitats to spend a larger proportion of their time in the lower parts of the tree. This contrasts those individuals found in less disturbed habitats, of whom have been found to spend increased time in upper parts of the tree canopy (Schwitzer *et al.,* 2007; Dagosto and Yamashita, 1998). Statistically significant results here however indicate that both species *E. fulvus* and *P.*

coquereli were on average observed in higher parts of the tree in marginal disturbed habitats compared with reserve undisturbed habitats. Despite this not being consistent with pervious literature, these results are understandable as the trees in marginal habitats were found to be on average taller. *P. coquereli* were found in higher parts of the tree compared with *E. fulvus,* 9.8m and 5.5m respectively. This again can be described by that fact *P. coquereli* were found in taller trees in general across both habitat types.

4.3 Activity Budgets

Analysis of the activity budgets of *P. coquereli* troops across the two forest fragments, excluding out of sight (OOS) and vigilance behaviours, showed troops to spend the largest proportion of their time,7.89 min/hr, resting then 3.13 min/hr feeding. The largest proportion of time overall, including all behaviours, was spent out of sight and performing vigilance behaviours. This is due to the troops observed being semi-habituated. Within animal behaviour studies researchers are often concerned with the impact their presence has on the study subjects (Crofoot *et al.,* 2010). To minimise these effects researchers habituate their study animals (Williamson and Feistner, 2003). If troops observed here had gone through this habituation process the time spent out of sight and performing vigilance behaviours would have been dramatically reduced and results would have been more reliable.

4.3.1 Comparisons of Forest Fragments and Habitat Types

A comparison across the two forest fragments, Mariarano and Matsedroy found no statistically significant differences in activity budgets. However, it could be seen on closer inspection that on average those in the Mariarano fragment spent slightly more time in locomotion, feeding and resting, compared with those in the Matsedroy fragment. Both fragments are considered disturbed for different reasons, Mariarano due to its high levels of human activity and Matsedroy due to its highly levels of fragmentation due to human disturbance. Due to this, it is

difficult to determine which of these factors, human activity directly or habitat disturbance as a result of human activity, are having more of an impact on the changes seen in the activity budget the troops of *P. coquereli.* Here Mariarano is assumed as the disturbed forest fragment.

Previous studies exploring the activity budgets of *Propithecus* species have presented conflicting results, which could be due to differences between regions, species or populations. Results found here however, show troops in anthropogenically disturbed fragments to spend increased time in locomotion, correspond with those found by McKinney, (2015). It is thought this increased time in locomotion is due to the maintenance of large home ranges in disturbed habitats. The increased time spend feeding and resting by troops in Mariarano does not fit with McKinney, (2015), but does correspond with results found by Arrigo-Nelson, (2006), which explored the activity budgets of *P. edwardsi* in Ranomafana National Park. It was found that troops in disturbed forests during the dry season spent increased time feeding and resting due to food availability and consumption.

Disturbed forest fragments have been focused on here; however, when zooming in and comparing disturbed marginal habitats with reserve forest habitats, statistically significant differences were found. With *P. coquereli* in disturbed marginal habitats spending on average decreased time resting and increased time in locomotion and feeding, compared with those in reserve. This corresponds with past studies that have observed *Propithecus* species in disturbed habitats to spend increased time feeding (Wilson and Ferguson, 2014; Arrigo-Nelson, 2006). One reason for seeing this could be due to disturbed habitats having improved leaf quality (Ganzhorn, 1995), meaning individuals and troops want to maximise their nutritional intake (Norscia *et al.,* 2006), at a time when food availability is low, and infants are present and nursing. This follows the energy frugality hypothesis, which states in response to habitat disturbance lemurs will adopt strategies of energy optimisation (Wright, 1999). Interestingly, McGoogan (2011) found no significant differences between the activity budgets between troops of *P. coquereli* observed in disturbed forests and pristine forest. However, groups did show differences in spatial patterns of behaviour.

Here the activity budgets of *P. coquereli* were explored during the dry season in one area, Mahamavo. However, past studies have shown the behaviour and activity budgets of species in the *Propithecus* genus to differ on an annual and seasonal basis (Arrigo-Nelson, 2006). Additionally, other factors including overall food availability and group demography, such as infant presence will drive the activity budgets (Irwin, 2006). These are all aspects that need to be considered and explored when making conclusions on how species are responding behaviourally to disturbance.

4.4 Limitations

Throughout the process of data collection and write up for this study a variety of limitations were highlighted. Including:

A) A total of 80 observations, for both species, were made across the study period. A number that was almost halved to n=44 for data on canopy cover, tree height and lemur height. This small sample size seen across the whole data set made statistical analysis difficult and meant some results were not statistically sound. However, this is an issue seen frequently in wild animal research and small sample sizes are beyond the researcher's control (Nc3rs.org.uk, 2018)

B) Small sample sizes again were a major issue for data on *E. fulvus*, with a size of n=19 and only n=8 for canopy cover, tree and lemur height. Despite this lack of data being key in terms of species abundance in the area, it made statistically analysis on habitat use an issue.

C) The inability to successfully distinguish between troops of *P. coquereli* and *E. fulvus* during search routes meant some troops may have been repeatedly sampled, making data less reliable.

D) Search routes were predetermined by Opwall, and only covered a small percentage of the Mariarano forest fragment compared to Matsedroy. This meant a proportion

of troops of both species in the Mariarano fragment could have been missed during the data collection period.

E) Due to *P. coquereli* troops being semi-habituated, it was decided that 10-minute continuous focal samples would be conducted. (Altman, 1974). However, upon completion of these it could be seen that 10 minutes was not a sufficient enough time to collect data on activity budgets. As this would only gather data from a small moment in time and often troops would flee or only show vigilance behaviours.

F) Due to time constraints this study took place in the dry season only. Meaning conclusions made are only for the dry season. It has already been highlighted that species can change the way they use their habitat depending on season and food availability (Arrigo- Nelson, 2006).

G) When identifying tree species, a large proportion (n=23) were unable to be identified. This is a large amount which could have impacted the results found.

4.5 Conservation Implications

Across their ranges, both *P. coquereli* and *E. fulvus* are facing serious threats from habitat loss, degradation and fragmentation, as well as exploitation through unsustainable hunting pressures (Andriaholinirina *et al.,* 201a). With a restricted range, *P. coquereli* are facing more severe declines and are at a higher risk of extinction currently, compared with *E. fulvus*.

Despite this however, results from this study indicates the Mahamavo region to be a 'haven' for *P. coquereli*, as indicated by their high abundance and population densities. Unlike in other areas of their range (McGoogan, 2011), P. *coquereli* in this region appear to be responding more positively to the increased levels of human disturbance seen across these fragments. Various factors could be contributing to this response. It may be due to cultural beliefs within the area, which place taboos on the hunting and consumption of *P. coquereli*, which is keeping their numbers stable. In addition, it could be that *P. coquereli* as a species are just responding and adapting better, both behaviourally and ecologically, to the changes in habitat, because of

their folivorous diet. However, increasing human movement and activity into the area could see this change, placing new pressures on the species, such as hunting. As the area appears to harbour high numbers of the species, which is now listed as critically endangered, the protection and conservation of the troops seen across these two fragments is vital and a high priority to ensure the survival of the species into the future.

The *Eulemur* genus and *E. fulvus* themselves are known for their high degree of ecological flexibility and ability to adapt and inhabit a variety of habitat types. However, as frugivores they are also known to respond negatively to habitat disturbance. Some frugivorous primates have been seen to disappear completely from forests fragments (Estrada and Coates-Estrada 1996; Tutin e*t al.,* 1997) due to their inability to adapt to restricted home ranges and food availability as a result of disturbance. With the low numbers of *E. fulvus* observed across these two fragments, and their negative response to human disturbance, it could be that *E. fulvus* are to beginning to disappear completely from this area. Despite their near threatened conservation status, this highlights the need to prioritise the species as a conservation concern. Particularly in the Mahamavo area, wherein the species are not protected by local taboos or fady preventing their hunting. This additional risk factor would pose another pressure to the species, in addition to existing anthropogenic pressures associated with increased human activity and human induced habitat disturbance. The consequence of this cumulative pressure would almost definitely have negative effects for *E. fulvus,* further stressing the conditions that they live in and their ability to sustain their populations in the region.

4.6 Recommendations for Future Studies

Despite the informative and key results that have emerged from this study, further work can be done to gather an even better understanding of how both species are responding.

Firstly, it is recommended that the completion of this study or a similar one of its kind is to occur during the wet season. This would enable us to see whether the responses seen here are

seasonal and change as resource availability, habitat structure and human disturbance levels alter. This will allow stronger and more reliable conclusions to be made.

In terms of the assessment of behavioural responses and activity budgets, it is recommended that future studies undertake behavioural observations on troops of *E. fulvus* within the Mahamavo area, as well as *P. coquereli*. Being able to collect this behavioural data will allow for a better understanding of how *Eulemur* species are using their habitats, i.e. feeding or resting. Additionally, to gather more reliable data from the behaviour focal, it is recommended that day follows of troops of both species occur. It is recommended that a maximum of two troops from each habitat type, marginal and reserve, for each species are chosen and habituated to human presence using the techniques set by Williamson and Feistner, (2003). These troops will act as study troops and will allow for more reliable data to be gathered and compared across the disturbed and undisturbed habitats. It will also prevent the occurrence of repeat sampling of troops.

Due to the low numbers of *E. fulvus* observed across the two fragments it is recommended that future research is to focus strongly on this species. This will allow for detailed analysis and assessment into why the species are responding so negatively, and how these populations may differ from others of the same species in different areas.

Finally, the conclusions of this study show the responses of these two species to be strongly linked to their dietary requirements. Therefore, it is strongly recommended that future studies explore the feeding ecology of each species across the two fragments, similar to that done by Arrigo-Nelson, (2006).

Chapter 5: Conclusion

Few studies have been conducted looking into the responses of lemur species to increased levels of human disturbances and the impact it is having on their habitat (Irwin *et al.,* 2010a). With 95% of lemur species now facing extinction (Schwitzer *et al.,* 2014), and human populations rising across the island this research is of high importance if the conservation of these species is to be successful. Here the responses of two lemur species, the Coquerel's sifaka (*P. coquereli*) and the Common Brown lemur (*E. fulvus*), were explored across two dry forest fragments in Northwest Madagascar.

Overall, this study achieved its aims. Finding that *P. coquereli* were observed in higher numbers across both fragments and appear to be responding more positively to human activity and the habitat change associated with human disturbance, compared with *E. fulvus.* The *Eulemur* genus is known for their ecological flexibility and their ability to adapt to various habitat types. However, as frugivores they are also known to respond negatively to human disturbance. This is thought to be due to several reasons, one being their inability to adapt to the restricted home ranges associated with habitat disturbance and fragmentation. Another reason being that folivores are better adapted to disturbed habitats than frugivores, due to the improved leaf quality associated with such habitats.

Regardless of the reason for the responses seen, it is important to remember that these responses have only been studied here in the short term and a lag time is known to exist between disturbance and change in long-lived primates, such as lemurs (Worman and Chapman, 2006). Additionally, ecological and behavioural responses have been shown to change on an annual and seasonal basis, due to resource availability, habitat structure and troop demography. For these reasons, further research is highly recommended on both species to fully assess and understand the responses to increased human disturbance and activity, and what affect they have on the long-term survival of the species in the area.

Although there were some limitations to this study, including small sample sizes and lack of behavioural data on *E. fulvus*, the data collected is valuable, acting as a reliable baseline data source for future studies on lemurs in the Mahamavo area. The study also clearly highlighted areas for future research, including the completion of a similar study in the wet season, to compare seasonal responses. Results from this study also indicate the despite the near threatened conservation status of *E. fulvus* across their range, within this specific area the species appear in low numbers and require conservation action before they are fully lost from these fragments. It was also found that this area appears to act as a stronghold for *P. coquereli,* which were observed in high numbers across both fragments. Due to the critically endangered status of the species its protection and conservation in this area is a high priority, to ensure the survival of the species into the future.

Overall, this study and others of its kind that explore the responses of threatened primate species to human disturbance are vital and should be of a high priority. They contribute to the current understanding of how primate species are responding and adapting their behaviour and ecology to allow them to live in an increasingly human dominated landscape. While also provided crucial insights into ways to better target conservation strategies and efforts in the future to ensure species survival.

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Appendices

Appendix 1: Data Collection Sheets

Appendix 1.1: Data Collection Sheet

Date	Number of observers:
Camp:	Weather:

Group ID	Time (24hr)	Species	Number of Individuals	GPS Waypoint	Elevation (m)	Sex Ratio (M:F:U)	Infant present (Y/N)	Tree Height and Category	Lemur Height and Category	Canopy Photo Number	Habitat Type (D/M/R)	General Notes

Appendix 1.2: Behaviour Data Collection Sheet

Behaviour Data Collection Sheet		
Date:	Camp:	Weather:	Perpendicular distance:
Time:	Route:	GPS:	Number of people on route:
Group size:	Group ID:	Individual ID:	Sex of individual:

Time Point	Behaviour Code	Time Point	Behaviour Code	Time Point	Behaviour Code

Appendix 2: Results from Shapiro-Wilks Test for Normality

Appendix 2.1: Distance Data

Results for the Shapiro Wilks test for normality. Values that shows normal distribution are highlighted in yellow.

		Both Species (n=80) P=	P. coquereli (n=61) P=	E. fulvus (n=19) P=
Distance Data (m)	Distance From Camps	0.046	0.04	0.40
	Distance From Roads	<0.01	<0.01	<0.01
	Distance From Village Centre	<0.01	<0.01	0.01

Appendix 2.2: Canopy Cover Data

	Both Species (n=44) P=	P. coquereli (n=36) P=	E. fulvus (n=8) P=
Canopy Cover	<0.01	<0.01	0.5

Appendix 2.3: Tree Height Data

	Both Species (n=44) P=	P. coquereli (n=36) P=	E. fulvus (n=8) P=
Tree Height	0.01	0.04	0.05

Appendix 2.4: Lemur Height Data

	Both Species (n=44) P=	P. coquereli (n=36) P=	E. fulvus (n=8) P=
Lemur Height	0.01	0.05	0.18

Appendix 2.5: State Behaviour Data

Results for the Shapiro Wilks test for normality on the state behaviour variables (n=51).

		P. coquereli (n=51) P =
State Behaviours (min/hr)	Resting	<0.01
	Vigilance	0.02
	Vigilance Towards Humans	<0.01
	Vigilance Towards Animal	<0.01
	Vigilance Towards Conspecific	<0.01
	Locomotion	<0.01
	Locomotion Across Ground	<0.01
	Feeding	<0.01
	Allo-Grooming	<0.01
	Self-Groom	<0.01
	Groom Infant	<0.01
	Groom Other	<0.01
	Groom By Other	<0.01
	Play	<0.01
	Scenting	<0.01
	Suckling	<0.01
	Out Of Sight	<0.01

Appendix 3:State Behaviour Mean Results

Appendix 3.1 : Mean state behaviours for P. coquereli (n=51) across both forest fragments. To 2 decimal places.

		P. coquereli (n=51) Mean ± S.E.
State Behaviours (min/hr)	Resting	7.89 ± 1.52
	Vigilance	12.88 ± 1.32
	Vigilance Towards Humans	13.20 ± 1.71
	Vigilance Towards Animal	0.27 ± 0.10
	Vigilance Towards Conspecific	0.44 ± 0.11
	Locomotion	1.38 ± 0.23
	Locomotion Across Ground	0.01 ± 0.01
	Feeding	3.14 ± 0.85
	Allo-Grooming	0.11 ± 0.07
	Self-Groom	0.83 ± 0.26
	Groom Infant	0.22 ± 0.15
	Groom Other	0.20 ± 0.12
	Groom By Other	0.03 ± 0.02
	Play	0.02 ± 0.02
	Scenting	0.05 ± 0.03
	Suckling	0.04 ± 0.04
	Out Of Sight	19.32 ± 3.08