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Trees for the Primates: A Community-Based Assessment of Crowned Lemur (Eulemur coronatus) Habitat Preferences and Conservation in Northern Madagascar

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Abstract

As a result of the continuous loss of forest habitats in Madagascar, forest fragments that exhibit a high degree of degradation and are strongly embedded on the livelihood needs of rural Malagasy people are increasingly being considered as the focus of conservation management operations. This new type of protected areas, based on the IUCN’s Category V management model for conservation action, promises a social-ecologically balanced method of environmental intervention that seeks to protect ecological communities while promoting sustainable socioeconomic systems. However, due to the poor ecological quality and immense level of anthropogenic influence in the type of forests that serves as the background to this conservation system, the benefit that this model can provide to lemur conservation remains unclear. In this thesis, I address these uncertainties exploring how the habitat conditions and current conservation initiatives of a small Category V new protected area in northern Madagascar influence the present and long-term viability pattern of a resident crowned lemur population. Using ecological niche models (ENMs) and occupancy assessments, my research shows that at Oronjia Conservation Park, crowned lemurs navigate high levels of anthropogenic disturbance and poor habitat quality by maximizing their use of the few forest sections capable of supporting the population. Furthermore, my research shows that community-based conservation initiatives are creating a social landscape where the continued risk of habitat loss and deterioration can be properly managed.

Keywords:
Primatology, conservation biology, spatial ecology, ethnoprimatology, ecological anthropology, habitat loss, environmental niche model, Category V management, crowned lemur, northern Madagascar.
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Chapter 1

1 INTRODUCTION:

This chapter has three goals: Section 1.1 introduces the problem that is to be addressed. In Section 1.2, the research objectives are outlined. Lastly, Section 1.3 provides a brief review of crowned lemur ecology.

1.1 Statement of the Problem:

The cumulative effects of human activities in Madagascar have had a thorough and significant negative impact on the quality and extent of the island’s original vegetation cover. Nowhere has this impact been more pronounced than along the forests and woodlands that comprise the natural habitats of over 90% of the island’s endemic fauna (Green and Sussman, 1990; Harper et al., 2007; Peacock, 2009; Carret, 2013; Schwitzer et al., 2013; Reuter, 2015). Regarding the remaining percentage of forest cover, it is estimated that its quality continues to be significantly deteriorated by the processes of fragmentation and habitat loss that result from the continuation of improperly managed or illegal economic activities targeting forest-bound, natural resources (Irwin et al., 2005; Carret, 2013; Volampeno et al., 2013).

Today, it is estimated that less than 10% of the original forest habitats of Madagascar remain in existence, and an even smaller percentage appears to bear the necessary conditions and resources to properly sustain the island’s endemic wildlife. While the exact amount of habitat that has been eroded as a result of anthropogenic disturbance is hotly debated (Dufils, 2003; McConnell & Kull, 2014), the fact remains that Madagascar faces a dire environmental situation that demands comprehensive conservation action. This fact is reflected by the designation of the island as a global biodiversity hotspot and one of the IUCN’s (International Union for Conservation of Nature) top conservation priorities (Myers et al., 2000; Harper et al., 2007; Aymoz et al., 2013; Carret, 2013; Schwitzer et al., 2013).

While the risk of habitat loss has been shown to be detrimental for a large portion of the island’s endemic fauna and flora, the risk it poses to extant lemur species is, as worded by the latest IUCN conservation action plan – at time of this publication –, the single greatest primate conservation priority in the world (Schwitzer et al., 2013). According to the IUCN’s
Red List, over 94% of all lemur taxa are classified as being under threat of extinction. Recent assessments show that out of 99 species for which there is sufficient information, 24 are classified as Critically Endangered, 49 as Endangered, 20 as Vulnerable, 3 as Near Threatened, and only 3 are classified as showing Least Concern (Schwitzer et al., 2013; Estrada et al., 2017). As such, it is clear that further fragmentation and loss of the remaining forest habitats in Madagascar can cause the extinction of over half of all present-day species. This could result either from a lack of availability of habitats that meet the necessary characteristics to sustain them on a long-term basis, or because the ongoing loss of forests brings them in direct contact with other forms of anthropogenic disturbance detrimental to their survival – i.e., bushmeat hunting or ethnobotanical exploitation of resources (Colquhoun, 2005; Golden, 2009). Such a prospect would not only be detrimental to primate biodiversity (Schwitzer et al., 2013), but would also have a dire backlash on the remaining forest habitat of Madagascar due to the important roles that many lemur species play as seed dispersers and pollinators to many endemic plant species (Birkinshaw & Colquhoun, 1998; Chen et al., 2015).

1.1.1 Overview of the Protected Area Network:

Efforts to impede the continuous loss of habitat have firmly depended on the island’s extensive protected area (PAs) network (Randrianandianina et al., 2003; Kull, 2014). Often boasted as one of the world’s oldest system of PAs, the first set of forest reserve were established in 1927, covering an approximate area of 5,601.81 km² (Randrianandianina et al., 2003). Today, the PA network in Madagascar extends across an area nearing 47,000 km², and represents over 8% of the island’s total vegetation cover (Schwitzer et al., 2013). Overall management of the total PA network is under the supervision of the Ministry of Environment and Forestry, but gives day-to-day responsibility of individual reserves to actors such as the Madagascar National Parks service (formerly known as l’Association Nationale pour la Gestion des Aires Protégées, ANGAP), NGOs (non-governmental organizations), or other private actors (Kull, 2014).

During the inception of the PA system, all areas were classified according to three different types of reserves, and management of each type was done according to the specific criteria of the IUCN’s protected area management categories. The three main types of PAs included: the Strict Natural Reserve (Réserve Naturelle Inégrale, RNI) – based on the
Category 1a, is used to protect fauna and flora within a boundary by limiting all-non scientific forms of anthropogenic presence; National Parks (Parc National, PN) – based on Category II areas, it is used to protect an exceptional national or cultural patrimony and promote recreational or educational use only; and Special Reserves (Réserve Spéciale, RS) – based on Category IV areas, it is used to protect a unique ecosystem or a specific animal or plant species (Randrianandianina et al., 2003; Dudley, 2008; Peacock, 2011). While the means by which each of these different types of PAs approach their goal of conservation is slightly different, they all share the same characteristic that seeks to control human action within their boundaries, excluding all types of livelihood activities and providing strict guidelines of what is permitted. This system, however, left forest areas outside of the protected area network particularly susceptible to anthropogenic disturbance, partially as a result of their limited coverage of the island, as well as their inability to address social drivers of conservation issues (See section 1.1.2; Nicoll, 2003).

Following the 2003 World Park Congress in Durban, SA, the original reserve classification system was expanded as part of an effort to triple the total coverage of the PAs network employed at the time. The New Protected Areas (NPAs) were based around the Categories V (protected landscape/seascape) and VI (managed resource protected area) of the IUCN’s management systems. Unlike the previous categories, these new management models centred their objective around the interaction between people and their environments to promote sustainable anthropogenic land use patterns that protect biodiversity and habitat structure (Dudley, 2008; Kull, 2014). The Category V system, in particular, became an especially useful framework to use as the basis of protected areas situated along human-dominated landscapes that boast plant or wildlife species of conservation priority – note: landscapes here are defined as habitats wherein ecological and anthropogenic factors play an equally active role in structuring the characteristics of that area of habitat (Phillips, 2002; Raharimampionona, 2015). Unlike the other PAs classification models, the NPAs based on the Category V management system permit a type of conservation action that promotes community-based approaches – a bottom-up system of conservation where local communities take an active role in the management process – to protect endangered species along forests where the impact of human action cannot be dissipated (Colquhoun, 2015; Gould & Andrianomena, 2015).
While the Category V NPAs model promises clear conservation benefits over the traditional PAs classifications (Phillips, 2002; Gould & Andrianomena, 2015; Missouri Botanical Gardens, 2015), there has been little effort to verify how well this system can deliver on these goals. Specifically, it is unclear whether human-dominated forest habitats managed under the Category V model possess the necessary conditions and resources to sustain lemur populations. Similarly, it is unknown whether the social-ecological management system employed by this model addresses the values and livelihood needs of local stakeholders in such a way, that threatened species can be sustainably protected over the long-term (Shafer, 2015).

1.1.2 Social Drivers of Natural Resource Exploitation in Madagascar:

As mentioned above, the conservation crises in Madagascar are primarily driven by the unsustainable, and sometimes illegal, exploitation of natural resources across the island. This situation, in part, owes its origins to improper social-ecological management of the environment during the country’s colonial era. Since then, over the past two decades, the conservation issues observed across the island have continued to worsen as a result of the state of poverty afflicting the majority of rural families – over 90% of the population lives on less than $2.00 USD a day – combined with their inherent socioeconomic dependency on natural resource based livelihoods. This, for many individuals or families, is the only form of economy that allows them to meet their basic economic and social needs (Aymoz et al., 2013; Gardner, 2014; Scales, 2014a; Osborne et al., 2016). Indeed, both the major and minor patterns of habitat loss documented in Madagascar are known to be the direct or indirect results of natural resource-based activities, such as logging and mining operations, charcoal production, as well as shifting agriculture, and to services that support these activities, like road-building or – under certain circumstances – the establishment of work camps for Malagasy migrant workers in search of job opportunities (Walsh, 2012; Carret, 2013; Schwitzer et al., 2013; Gardner, 2014; Reuter, 2015).

Based on the inherent dependency of Malagasy people upon the declining forests habitats of the island, then, it is clear that undertaking conservation programs in Madagascar is not easy. The majority of human-dominated landscapes, where the last forest extents found outside of the three primary categories of protected areas – RNI, PN, RS – are located, exhibit high degrees of fragmentation or severe deterioration produced by the continuous
extraction of specific resources (Nicoll, 2003). Furthermore, based on the need that people exhibit for these habitats, it is clear that their conservation cannot strive to simply mitigate their influence. Instead, it is necessary to consider how anthropogenic action plays an active role on the structure of these habitats to develop sustainable strategies that sustain conservation while providing for human agency (McConnell, 2009; Hoffman & O’Riain, 2012). As such, these types of habitats require that careful consideration of both the anthropogenic and ecological dimensions of the habitat are taken into consideration when developing conservation programs or studying the ecologies of resident species. Conservation in Madagascar, then, requires approaches based on ensuring that people establish, improve, or maintain good relationships with nature, not ones that seek to disconnect people from their surroundings to achieve some theoretical concept of a pristine environment (Ingold, 2000b; Sandbrook, 2015).

1.2 Research Objectives:

New protected areas of forest habitats, established within human-dominated landscapes, have become an important component of the conservation plan for Madagascar. These PAs seek to manage the conservation pressures affecting plant and wildlife communities while finding alternative pathways that promote sustainable livelihood styles for the human populations residing in their vicinity (Phillips, 2002; Schwitzer et al., 2013; Colquhoun, 2015). On paper, this new type of PAs appears to promote a system of conservation that better integrates the social drivers at the heart of the environmental and biodiversity problems it seeks to address. It is still necessary, however, to understand whether this conservation model targets landscapes that contain the essential qualities needed to sustain the habitat needs or realized niche characteristics of endangered lemur species (Hutchinson, 1957; Schickhoff, 2011; Shafer, 2015). Here, habitat is defined as any area of space offering the necessary resources and conditions (i.e., food, cover, shelter, etc.) to promote the occupancy of a specific species based on their unique niche requirements (Huggett, 1998; Schickhoff, 2011). Similarly, “niche” refers to the abstract multidimensional distribution of resources and conditions available to and used by a species, which defines their occurrence in a specific area (Hutchinson, 1957). Understanding a species’ occupancy patterns in relation to the total availability of the background conditions that correlate to their presence, then, provides a basis for measuring the overall quality and fit
of that habitat for the species viability (Bracebridge et al., 2013; Hoffman & O’Riain, 2012; Mugume et al., 2015; Kamilar & Tecot, 2016).

Furthermore, it is necessary to explore whether the social-cultural approach employed by this conservation model can produce sustainable relationships between local stakeholders and the environment that help protect the structural characteristics influencing the occurrence of lemur species within this landscape (Gardner et al., 2009; McConnell, 2009; Reuter, 2015). In order to properly consider how people’s social values and socio-economic concerns influence the effectiveness of conservation measures and the niche of species, I utilize an ethnoprimatological approach that permits the exploration of the interface between human and non-human primate populations to understand how social circumstance directly or indirectly contextualize ecological problems (Sponsel, 1997; Colquhoun, 2005; Remis & Hardin, 2009; Fuentes, 2012; Malone et al., 2014). Ethnoprimatological theory provides a flexible framework to conceptualize how human action plays an active role stimulating the adaptive niche expressions of lemur species within a landscape of interest. More important, however, analysis of the human and non-human primate interface permits the description of synergistic relationships beyond the limiting lens of competition, to ascribe opportunities for sustainable relationships or at least comment on the nature of roadblocks preventing the fulfillment this goal.

To evaluate these concerns, the present study has two main research objectives: (1) to explore the influence that ecological and anthropogenic factors have on the habitat preference patterns of a small population of endangered crowned lemurs, *Eulemur coronatus*, [Gray, 1842] inhabiting the protected area of Oronjia Conservation Park (Figure 1.1; see Section 2.1 for a full description of the ecological and anthropogenic context of the site and its immediate vicinity); and, (2) to evaluate the impact that current conservation initiatives can potentially have on the viability of this lemur population, based on the effectiveness of these initiatives to protect the current quality of the forest from the influence of the human-dominated landscape that surrounds it. As such, this thesis presents a case study to assess how well the Category V management model of NPAs protects extant lemur species from anthropogenic disturbance and habitat loss.
FIGURE 1.1 – Protected area of the Oronjia Conservation Park in northern Madagascar.

I meet these objectives by addressing the following key research questions using multiple methodologies (See Chapter 3):

1) How does the interaction between background ecological and anthropogenic conditions that structure the habitat characteristics of the Oronjia landscape affect the realized niche patterns of crowned lemurs within the protected area?
2) What is the total availability of habitat sections bearing the effective characteristics for crowned lemur occupancy in comparison to the total coverage of the protected area?
3) How do the livelihood patterns of local Malagasy stakeholders influence the habitat structure of the protected area?
4) To what extent do the socio-economic concerns of local Malagasy stakeholders drive their value-judgement of the importance of conservation activities in this landscape?
By addressing these concerns, I will formulate a conceptual model that describes the social-ecological interface between the local Malagasy and crowned lemur communities found within the protected area and the surrounding human-dominated spaces, that provides some level of insight on the success of the conservation model employed at Oronjia. As such, this study aims to contribute to the continuous developing of the Category V management model of NPAs, by highlighting current strengths and weaknesses on its ability to deliver its ultimate goals.

This chapter has defined the problems and objectives of the thesis. Chapter 2 provides a thorough overview of the social and environmental contexts of the study site, a summary of the history and goals of conservation at Oronjia Park, and outlines the major findings of previous studies of the local crowned lemur population. Chapter 3 provides a rationale and outline for the methodology and analytical framework used in this study to assess both the distribution patterns of crowned lemur in relation to background landscape characteristics as well as the livelihood dynamics and socio-economic values of local stakeholders. Chapter 4 presents results from the crowned lemur occurrence and distribution models, as well as an overview of livelihood dynamics in the vicinity of the protected area. Finally, in Chapter 5 I discuss trends of crowned lemur occurrence across the protected area in relation to background characteristics and what they mean for the conservation of the population, while also discussing how socio-economic necessities from local stakeholders can potentially support or limit the future viability of the population. Chapter 5 also provides a summary of major conclusions for this study and highlights future directions of research.

1.3 Ecology of the Crowned Lemur:

The crowned lemur is a medium-sized lemur that belongs to the genus *Eulemur* – also known as the “true lemurs” (Tattersall & Sussman, 1998) – and is commonly recognised by the orange V-shaped pattern found on their foreheads. The species shows notable signs of sexual dichromatism, as males exhibit more vibrant colouration than their female counterparts (Figure 1.2 – A & B). Furthermore, the species has been shown to exhibit a *cathemeral* activity pattern, meaning it is active during both the day- and night-time cycles, though it exhibits a bias for the diurnal portion of the day cycle (Wilson et al., 1989; Garbutt, 2007). In terms of their diet, crowned lemurs appear to show preference for a frugivorous dietary pattern, though at times of resource scarcity, it is known to supplement its diet with
young leaves, pollen, insects, and soil (Wilson et al., 1989; Freed, 1996). Previous studies in Ankarana and Montagne des Français show that mating usually occurs in late May and June, and births taking place from mid-September through October (Wilson et al., 1989; Freed, 1996; Garbutt, 2007). In captive settings, females are known to give births after 125 days of gestation to one or two young (Kappeler, 1987). Group size fluctuates drastically, ranging between groups of two to four individuals, and reaching a maximum of 15 during the more resource-scarce periods of the year (Freed, 1996).

**FIGURE 1.2** – Female (left) and male (right) crowned lemurs; their marked differences in colouration are clearly visible.

In terms of its geographic patterns, the species is endemic to the northern-most portion of Madagascar, where it can be primarily found in semi-deciduous dry lowland and mid-altitude forests. However, it has also been recorded across high-altitude tropical forests, woodland savannahs, and agricultural areas, showing a high degree of behavioural flexibility (Wilson et al., 1989; Freed, 1996; Garbutt, 2007; Andriaholinirina et al., 2014a; Rakotondraparany and Andriambeloson, 2015). Indeed, Wilson et al. (1989), and more recently Sato et al. (2016), have reported that this species, similar to many of the other members of the genus, is able to thrive in highly heterogeneous habitats by employing a power-feeding strategy by which it increases energy expenditure to make use of particular resources with scattered, patchy distribution across disturbed areas. This shows a type of resilience to disturbance, or behavioural flexibility, by adapting their behaviour to make the best out of existing conditions (Wilson et al., 1989; Freed, 1996; Sato et al., 2016; Tattersall and Sussman, 2016).
Chapter 2

2 RESEARCH CONTEXT:

This chapter has three major aims: Section 2.1 outlines the background contexts that define the social and environmental characteristics of Oronjia Conservation Park. Section 2.2 summarizes the goals and history of the ongoing conservation work by MBG and KODINA in the region. Finally, Section 2.3 outlines the major findings from previous projects studying the ecology and distribution of the crowned lemur populations inhabiting Oronjia and Montagne des Français.

2.1 Description of the Research Site:

Oronjia Conservation Park (also known as Amoronjia-Orangéa, Anoronjia, Cap D’Orangéa, Orongéa) is a New Protected Area (NPA), classified as an IUCN Category V Protected Area, located in the rural municipality of Ramena, District of Antsiranana II, DIANA region of northern Madagascar (Figure 2.1; Dudley, 2008). The park is situated 14 km east of the city of Antsiranana (also known as Diego-Suarez; hereby referred to as Diego), across the Andovobazaha Bay, in the Oronjia peninsula, and 8 km north of La Montagne des Français (The French Mountain) conservation area, located at the base of the peninsula (Appendix 1 – Figure A1-1). The site covers an area of 16.42 km², situated between 12°14”00.8” and 12°18”48.1” south longitude and 49°22”44.8” and 49°23”34.0” east longitude (Appendix 1 – Figure A1-2). It is bounded in the northwest and southwest by the Villages of Ramena and Ankorikahely respectively. Management and conservation activities of the park are handled by the Missouri Botanical Gardens (MBG) and their community partners, KODINA (Komitin’ny Dina – Committee for the monitoring of local, natural resource rules). The exact details of these two organisations will be further explained in Section 2.1.3. In addition, administration of the site is under the purview of the Ministère de la Défense Nationale (Ministry of National Defence), represented in the region by the military base in the north of the peninsula, “Military Field D’Orangéa Ankoriky” TFN 5228 BK, which houses the CEOS (Régiment d’Artillerie Anti Aérien – Regiment of Anti-Air Artillery) (Missouri Botanical Gardens, 2015).
FIGURE 2.1 – Map of Oronjia Conservation Park and the rural municipality of Ramena, District of Antsiranana II, DIANA region of northern Madagascar. Boundaries of Oronjia park are classified based on the three-primary management sub-sections.

At a management level, Oronjia is made up of three sub-sections, each of which provides a specific level of conservation protection in pursuit of a specific end-goal. These are the community area located on the west of the park, the protected area on the centre-east, and the restoration zone along the eastern shore and middle of protected area (Figure 2.1). The community area is set-up to stimulate the development of sustainable resource exploitation practices, following natural resource regulations established by MBG and local stakeholders. The protected area serves the priority conservation zone for the park, where strict regulations prohibit all forms of natural resource extraction. This area is primarily structured to support continued monitoring of habitat conditions and conservation of the existing biodiversity, as well as to generate opportunities for conservation and ecological research. Finally, the restoration area is subject to management regulations seeking to assist with the regrowth of clear cut areas across the protected areas and promote the establishment
of a forest corridor along the eastern shore to act as a buffer to soil erosion (Missouri Botanical Gardens, 2015). A more detailed account of the management organization of Oronjia is covered in section 2.1.3.

2.1.1 Description of Ecological and Environmental Characteristics of the NPA Oronjia:

![Figure 2.2](image.png)

**FIGURE 2.2 – Map of northern Madagascar showing the distribution of major habitat types.** Original data obtained from the Madagascar Vegetation Mapping Project (Kew, 2006).

The vegetation patterns across Oronjia Conservation Park are primarily classified as a combination of a fragmented mosaic of western dry deciduous forest, interlaced with a mixture of dense shrubs and wooded savannah sections that make up the main forest fragment that stretches across the totality of the protected area. There is also a plateau of wooded and grassland savannah that extends from the western edge of the forest fragment, occupying most of the community area, towards the townships of Ramena and Ankorikahely. In addition to these two major areas, the site is also bordered on its eastern shore by a thinly elongated fragment of littoral forest that covers the perimeter of the restoration area, and by
patches of mangrove vegetation located along the southern portions of the coastline (Figure 2.2; Wells, 2003; Moat & Smith, 2007; Ileiry Geospatial Services, 2014; 2015; Missouri Botanical Gardens, 2015).

The fragmented forest mosaic covers an area of approximately 8.5 km$^2$. The vertical structure of tree cover along the fragment is not highly stratified, it rarely reaches a maximum height of approximately 8 m, and the maximum leaf concentration is found at a level between 0.2 to 2 m from the soil. In addition, the continuous structure of vegetation cover within the fragment is highly heterogenous. This is primarily attributed to disturbance due to past natural resource exploitation in the area—including charcoal production, shifting cultivations, and small-scale tree harvesting. Because of these past activities, the continuity of the forest matrix has been severely disrupted, leaving behind grassy clearings bordered by small shrubs and soft-wood trees not selected for extraction (Andriambololonera et al., 2015; Missouri Botanical Gardens, 2015; Rakotondraparany & Andriambeloson, 2015). As reported by MBG (2015), regeneration of these clearings has been slow, and has created the opportunity for competition between native and invasive species seeking to recolonize these areas.

As mentioned above, tree cover across the site is primarily dominated by soft-wooded species or drought-adapted species, not valued for resource exploitation due to their poor quality for those specific tasks (Personal observation; Missouri Botanical Gardens, 2015). Some of the more common soft-wooded tree species occurring in the fragment include *Delonix regia* (Fabaceae), *Slerocarya birrea* (Anacardiaceae), and *Broussonetia greveana* (Moraceae). These species are primarily located across the more canopy-dense sections of the site, in the northern, southern, and central core areas. Similarly, some of the more common drought-adapted species include *Andansonia madagascariensis* (Bombacaceae) and *Pachypodium rutembergianum* (Apocynaceae). These species are located across the more arid areas of the site, near the edge of the forest fragment in the southern and central-west section (Schatz, 2005; Andriambololonera et al., 2015; Missouri Botanical Gardens, 2015; Rakotondraparany & Andriambeloson, 2015). In addition to these, the site also hosts some tree species introduced by people for horticulture, the most abundant of which is the grove of cultivars of mango trees (*Mangifera indica*) that dominates the southern subsection of the site surrounding Mamelon Vert.
While Oronjia park boasts a high diversity of large tree species that noticeably dominate the vertical structure of the forest fragment, the presence of these are considerably less abundant than the number of large shrubs and mid-sized trees that make up the main continuity of the forest fragment (Personal observation; Ileiry Geospatial Services, 2014 & 2015). The forest fragment at Oronjia is quite heterogenous in vertical height and density because of the aggregation of the large trees to specific sections of the sites and the broad dispersal of the mid-size vegetation, coupled with the grassy clearing distributed across the site. This means that some forest sections can be quite dense, displaying some structural complexity made up by vegetation of various sizes, whereas other sections can be quite open, bearing mid-sized vegetation with little connectivity or vertical complexity (Figure 2.3). The result of this is a forest with highly varying local conditions that do not provide spatially equal resource exploitation opportunities to its occupants.

**FIGURE 2.3** – Examples of the variation in vegetation structure along the protected area of Oronjia Park. Includes examples of: (A) Mixed forest with tall canopy and sparse vegetation profile, (B) Dry brush thicket with intermittently distributed trees, and (C) open grassy fields with small- to mid-level vegetation.

Oronjia Park is located at an elevation that ranges between sea level to 85 m (Appendix 6 – Figure A6-1; Missouri Botanical Gardens, 2015). The lowest elevation point of the park is recorded along the eastern shore and the ravine along the south-western slope of Mamelon Vert. In addition, the locations of the highest elevation points are in Mamelon Vert and the area of Cote-44 (Appendix 1 – Figure A1-2). Drainage of the park is rather poor; the local water system is maintained by two seasonal water bodies located on the boundary of the southern and northern parts of the protected area, which act as the exclusive sources of fresh water for both the human and non-human populations living in the area (Figure 2.4 – A & B respectively; Missouri Botanical Garden, 2015). The amount of water available in these two bodies varies throughout the year as a function of the decrease in
precipitation that occurs between the wet and dry season (Wells, 2003). During their highest extent, the two waterbodies cover a total coupled area of 17,000 m², and gradually decrease until they reach their lowest range of their area and depth between the months of August and October (Appendix 1 – Figure A1-1). Furthermore, during the wettest months, the southern water body is drained by the riverine water course running through the small valley on the south-eastern slope of Mamelon Vert (Missouri Botanical Garden, 2015).
FIGURE 2.4 – Location of (A) northern and (B) southern seasonal waterbodies (satellite scenes obtained from WorldView-3, 2015).

The geology of the park is primarily shaped by a bedrock of Mesozoic limestone covered by a layer of consolidated sandstone running along the eastern section of the site. Sandstone is limited to the eastern section, with exposures of the limestone layer, due to continuous past erosion along the western section resulting from the site’s sharp topography (Besairie; 1964; Du Puy & Moat, 2003; Missouri Botanical Gardens, 2015). In addition, soil deposits along the surface of the park are characterized by a layer of unconsolidated sands that vary in constitution throughout the site (Missouri Botanical Gardens, 2015). The degree of constitution ranges from loose and fine-grained in sections with sparse vegetation, to compacted and humid in sections with high vegetation density.

Average precipitation records in the broader geographic region range between 320 mm of rainfall during the month of January, to a minimum of 11 mm during the month of September (Figure 2.5). This broad variation in precipitation marks two distinct climatic seasons in the region, corresponding to a wet season that typically runs from October to
April, and a dry season that runs from May to September (Figure 2.5; Freed, 1996; Colquhoun, 1997; Missouri Botanical Gardens, 2015). Past studies by the MBG and students from the Département de Biologie Animale in the Faculté de Sciences, Université d’Antananarivo have reported that the seasonal transition has noticeable effects on the quality of the forest structure, producing a drastic reduction in the extent of canopy density, the availability of fresh flower blooms, and the presence of ripe fruits. Similarly, the seasonal transition affects the amount of moisture present in the soils across the park and the extent of the two waterbodies (Andriambololonera et al., 2015; Missouri Botanical Gardens, 2015; Raherilalao & Rasoazanakolona, 2015; Rakotondraparany & Andriambeloson, 2015).

**FIGURE 2.5** – Monthly precipitation (mm) totals for the Antsiranana II region (data obtained from CLIMATE-DATA.ORG, 2017).

In contrast to the marked seasonal precipitation patterns, annual variation of monthly average temperature is less marked. As Figure 2.6-A shows, during the past ten years, annual daytime temperatures at Oronjia Park have ranged between 23 to 35 degrees Celsius. Temperatures appear to be at their lowest range from the end of the wet season, through the
dry season, from January to August. From the late dry season, temperatures steadily increase, reaching their maximum peak during the months of October and November. Similarly, as seen in Figure 2.6-B, annual daytime temperatures for the last ten years have also shown no substantial variation, ranging from 19 to 24 degrees Celsius. The lowest temperature trend was recorded from the months of June to August, while the highest night-time temperatures are generally seen between March and October, with December and January dipping again. Overall, night-time trends appear to be more stable than the day-time temperature variation. It is noteworthy that the seasonal period during which this study was conducted consistently exhibits some of the lowest temperatures during the year (Figure 2.5; 2.6 – A & B). According to Wells (2003), the low temperatures recorded during this period are controlled by strong prevailing winds that run northwest across the island and are able to reach farther north this time of the year, carrying moist air from the Indian Ocean that cools the surface of the site.
For its relatively small size and relatively isolated location on a small peninsula adjacent to Montagne des Français, Oronjia Park boasts a high diversity of flora and fauna. Its floristic inventory contains over 149 different species, belonging to 58 families—two families of which, Physenaceae and Sphaerosepalaceae, are endemic to Madagascar. Over 80% of these species are endemic to Madagascar, among which, 21% are endemic to the greater region and 4% are endemic to the site. These locally endemic species are each restricted to a single population that can only be found within the protected area (Schatz, 2005; Andriambololonera et al., 2015; Missouri Botanical Gardens, 2015).

In addition to the floristic composition seen at Oronjia, past inventories have shown that the forest fragment hosts a broad diversity of wildlife, with 117 species that have been identified thus far. These include: 2 species of amphibians, 40 species of reptiles, 63 species of birds, and 12 species of mammals (Missouri Botanical Gardens, 2015). Of the 12 species of mammals found in the site, there are two lemur species, the endangered crowned lemur (*Eulemur coronatus*, Gray, 1842; Andriaholinirina et al., 2014a) and the vulnerable northern
rufous mouse lemur (*Microcebus tavaratra*, Rasoloarison et al., 2000; Andriaholinirina et al., 2014b). Of the species found here, 88% of the herpetofauna, 32% of all birds, and 50% of observed mammals, including the two lemur species, are endemic to Madagascar. The highest levels of diversity are found within the area of the forest fragment and the two seasonal waterbodies located on the northern and southern edges, as well as within the mangrove fragments that surround the periphery of the peninsula. However, the exact distribution patterns of these various species have not been thoroughly surveyed (Missouri Botanical Gardens, 2015; Raherilalao & Rasoazanakolona, 2015; Rakotondraparanany & Andriambeloson, 2015). For example, it is not well understood how abundant each of these populations are, or how they fluctuate seasonally and annually due to expected mortality, birthing, and migration events. Furthermore, there is no clear sense of whether any of these populations are locally isolated within the Oronjia fragment, or if they are more broadly connected to other populations in adjacent areas. As such, further work is still needed to properly understand the stability and viability of the wildlife communities that Oronjia hosts. A more detailed account of the two lemur populations, for which more research has been conducted, will be summarized in Section 2.3.

### 2.1.2 Description of Social and Economic Characteristics of the NPA Oronjia:

As described above in section 2.1.1, Oronjia Park is bordered on its northwest and southwest edges by the villages of Ramena and Ankorikahely (Figure 2.1). These villages are two of the five villages that constitute what is known as the rural municipality of Ramena (hereby referred to as Ramena), which extends through the Oronjia peninsula south past Montagne des Français. Furthermore, the boundary of Oronjia is lined by an additional number of smaller human occupations and individual households/farms that fall under the purview of one of the two villages. These include the households in Ambararata, the farms surrounding Mamelon Vert, and the lodges and households in Baie de Sakalava and Bozy Antsivoragnana that border the southern edge of the park all constitute parts of Ankorikahely. Also included are the farm near the Grotte, as well as the lodges along Baie de Dunes and Baie de Pigeon bordering the northern edge represent parts of Ramena (Figure 2.1; Appendix 1 – Figure A1-2). In addition, the military base Orangea is located on the northern tip of the peninsula, next to Ramena, and controls access to the park along the northern road. Similarly,
the field offices of MBG for the park are located in Ankorikahely, and control access to the southern portion of the park (Figure 2.1; Bradt, 2011).

The park plays an important part in the lives of the residents of Ramena and Ankorikahely. This is because of both, the close proximity of these communities to the park boundaries as well as the livelihood opportunities that the park provides to nearby residents (Harper, 2002; Missouri Botanical Gardens, 2015). Due to these relationships, both villages have and will continue to play important roles in the organisation and management of the conservation strategies taking place across the park. For example, the basis of planning for the specific management sections that make up the park was done in close consultations with local stakeholders from these villages. These consultations and negotiations were the basis for establishing the boundaries between areas of biodiversity priorities and the socioeconomic needs of people. Similarly, it is the continuing goal of MBG that management of conservation priorities in the park progresses with a clear path that also provides direct benefits to the lives of the people living in the area (Missouri Botanical Gardens, 2015). To this end, then, it is necessary that in our consideration of the landscape context of Oronjia for the current study we also understand some of the characteristics of the people that live and work in the areas surrounding the park.

Census records from 2006, 2008, 2010, and 2011 for the villages of Ramena and Ankorikahely in the Ramena commune are summarized in Table 2.1. As of 2011, these census data indicate that the villages of Ramena and Ankorikahely share a population of about 3,157 individuals (Table 2.1). Nearly 98% of the local Malagasy population that occupy the two villages (n = 3,091) are identified as permanent residents. This refers to members of the population that occupy a household and possibly work in the commune for a major portion of the year. The remaining 2% (n = 66) were classified as temporary residents, referring to people who live in the community for short periods of time in temporary residences. The population, as seen today, is primarily composed of the descendants of the local Antankarana people of the north of Madagascar, as well as individuals from past and current migration events to the area. Prime among these migrations was movement of the Sakalava, people who originally came to the region in search of natural conditions more favourable for their livelihood activities. These migration events were then followed by a myriad of similar ones from other sections of the island, most notably by the Antandroy from the extreme south of the island. Today, the dominant ethnicity across the two villages are the
Sakalava and Antankarana, followed by the Antandroy and other minor groups (Personal conversations; Allen & Covell, 2005; Scales, 2014b; Missouri Botanical Gardens, 2015). In addition, the composition of the population sees high seasonal variation due to the seasonal patterns of certain livelihood activities at different times of the year. This is specifically marked by a period of migration, from December to April, of individuals of Malagasy descent from Diego and other rural communities adjacent to Ramena, who come to fish. The period of May to September also sees French migrants and Malagasy young adults from Diego move to the area to manage and support the tourist business (Nawrotzki et al., 2012).


<table>
<thead>
<tr>
<th>Village Name</th>
<th>Year</th>
<th>Sex Ratio</th>
<th>Age Structure</th>
<th>Number of Permanent Residents</th>
<th>Number of Temporary Residents</th>
<th>Total Number of Residents</th>
</tr>
</thead>
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<tr>
<td><strong>Ramena</strong></td>
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<td></td>
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</tr>
<tr>
<td></td>
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<td>848</td>
<td>12</td>
<td>1549</td>
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<tr>
<td></td>
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<td>N/A</td>
<td>220</td>
<td>144</td>
<td>1931</td>
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<td></td>
<td></td>
<td></td>
<td>1549</td>
<td>18</td>
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<tr>
<td></td>
<td>2010</td>
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<td>219</td>
<td>547</td>
<td>2416</td>
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<td></td>
<td></td>
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<td>1635</td>
<td>15</td>
<td>2450</td>
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<tr>
<td></td>
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<td>N/A</td>
<td>239</td>
<td>547</td>
<td>2458</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>1652</td>
<td>20</td>
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<tr>
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<td>198</td>
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<td>220</td>
<td>19</td>
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<tr>
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</table>

Both Ramena and Ankorikahely share the demographic profile of populations that are predominantly local. That is, the majority of the people that live and/or work in the two villages of the commune consider it to be, and depend on it, as their primary residence. The age breakdown of the resident population is quite disproportionate between the two villages.
In the case of Ramena, the population seems to exhibit a slightly left-skewed normally distributed age structure. The largest age-category, adults [18 -59], makes up 67% (n = 1652) of the total population. This is followed by the juvenile [6-17] age-category, which represents close to 22% (n = 547) of the total. The age-groups at the edge of the distribution, infant [0-5] and senior [60+] represent less than 11% (n = 259) (Table 2.1), though it is important to mention that this category summarizes a larger age-group than the other three (41 years of variation, as opposed to 11 years in the second largest category for this village). When compared to the age distribution of Ankorikahely, the differences between the two villages are remarkably apparent. Keeping in mind the larger size of the adult age-group, Ankorikahely appears to exhibit a left-skewed age distribution that is more akin to the national age distribution of Madagascar (Table 2.1; Central Intelligence Agency, 2013), with the adult [18 -59] group making up 43% (n = 275) of the total population. When grouped, the infant [0-5] and juvenile [6-17] age-categories account for nearly 53% of the total population (Table 2.1).

The larger proportion of infants and juveniles to adults in Ankorikahely, in contrast to the broader adult population in Ramena, suggests that Ankorikahely exhibits a higher birth rate per household. In their 2015 report, MBG attributed the possible sources of this disparity to a number of interrelated factors that mark the different social contexts between the two villages. These include the possibility of different social landscapes of family values in each village, a higher need for large family size to sustain home economics in Ankorikahely than in Ramena, or unequal access to family planning resources like health-care units or education centres.

This last explanation is possible due to the small size and more-peripheral significance of Ankorikahely to the administration of the commune. The socio-political context of Ankorikahely contrasts to the relatively larger size and the status of Ramena as the commune’s administrative centre. Residents of either village could have unequal access to family planning resources. This is best represented by the fact that the only health clinic in the commune is found in Ramena. Similarly, while both villages have basic schooling institutions, the only secondary-level school is located in the vicinity of Ramena. As such, it is clear that the two villages do not offer the same access to family planning amenities for their residents (Missouri Botanical Gardens, 2015). While a person in Ramena can have immediate access to basic health care and higher education, a person in Ankorikahely would
have to travel to Ramena to have the same resources. Research on family planning has shown that the degree of access that an individual has to communal resources that promote health-care and family education/counselling can have significant impact on how old they are when they marry and/or have their first child, how they value contraceptive methods, and in certain circumstance the number of children they have (i.e., Mwaikambo et al., 2011; Noonan, 2012; Harper et al., 2015; Mohan et al., 2015).

While Ramena and Ankorikahely exhibit marked differences that are due to their demographic profiles and the resources individuals have available to them; it is difficult to conclude as to whether these differences are influential enough to significantly deviate the ways in which residents value their environments and their surrounding fauna, as well as the opportunities that individuals have access to in each village. Specially since the two villages belong to the same communes and share similar rural contexts, are well connected through extended kin networks and common livelihood activities, and share a great deal of access to the general amenities available throughout the commune. Based on this, it can be surmised that the two communities are mainly inhabited by people under similar, yet not identical conditions, residing under a shared cultural landscape of family values that support the socio-economic interests of their rural lives (Keller, 2008; Kull, 2014; Pollini et al, 2014).

However, a conclusion based on slight demographic and spatial differences is rather shallow, since it does little to explain how these differences are born in the first place. Rather, then, it is more likely to assume that the marked demographic differences between the two villages are an expression of the two broad characteristics that best describe the social setting of Oranjia. That is, it represents a centralized commune favoured by migrants of neighbouring regions for the economic opportunities it hosts.

The demographic differences, then, reflect the relatively biased access to opportunities that residents have when they live in Ramena in contrast to Ankorikahely. Because of these opportunities, the appeal of the two villages can be valued differently by incoming residents, migrating to the community in search of employment opportunities (Hardin & Remis, 2006). This pattern shows that in comparison to Ankorikahely, Ramena can best be viewed as the host residence of a larger portion of recent migrants who choose to reside there because the immediate access of amenities and employment opportunities (Nawrotzki et al., 2012; Mazza & Punzo, 2016). The demographic quality of Ramena, then, reflects the characteristics of the people migrating into the area to participate in the local
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economy. Ethnographic research concentrating on similar localities that exhibit booming tourist and resource-based industries in northern Madagascar have shown that such economies as those seen in Oronjia are mainly occupied by young adults who migrate alone to these areas – leaving their families back in their home towns – in search of financial opportunities (Gezon, 2006; Walsh, 2012; Gezon, 2014; Scales, 2014b; Borgerson et al., 2016). This means that the adult to infant ratio in Ramena is inflated by the realities of the people who move to the area. While the local infant population is not as large as would be expected, it is likely that many adults, whether local or not, identify themselves with the financial burden of primary provider for their families.

While there is no concrete answer as to the causes influencing the larger ratio of children to adults in Ankorikahely in contrast to Ramena, the two scenarios discussed here promote insights into the lives of the residents of Oronjia. For example, the centralized organisation of the Ramena commune means that management operations in the peninsula need to consider the fact that residents in different sections of the commune may not share similar concerns and necessities. Furthermore, the seemingly significant proportion of adult residents who migrated into the commune without their families, in search for employment opportunities, suggests that conservation action in the peninsula needs to maintain a clear path for the population to continue to have access to local opportunities that support livelihood activities.

The second point discussed above is of important consideration with regards to the context of this study. Indeed, proper understanding of the socio-economic links in the context of conservation action between the local residents of the Ramena commune and the physical landscape of Oronjia park, demands the recognition of the necessity for regular access to employment opportunities that fulfill livelihood demands (Harper, 2002; Phillips, 2002; Gezon, 2006; Dudley, 2008; Schwitzer, 2013; Gardner, 2014; Gezon, 2014; Scales, 2014b; Reuter, 2015). This is certainly true for the case of the Oronjia peninsula, because the local economies of the Ramena commune are heavily dependent on the quality and availability of the physical resources and characteristics that are readily available. This means that the opportunities for people to work are attached to the available access natural resources, for reasons that may relate to either their exploitation or simply their admiration. The socioeconomic work in Oronjia is, thusly, a complex landscape to navigate. In certain circumstances, it may necessitate free-roaming access to the physical environment for the
intended purpose of extracting resources from it. This represents a scenario that can run against regular conservation priorities. In other circumstances, however, the values of possible livelihood opportunities may depend on their engagement with the physical environment that relies on aesthetic and recreational appreciation (Gezon & Freed, 1999).

Due to the large number of ways in which people working in Oronjia may engage with the physical environment, it is necessary to briefly explore the various industries that maintain the local economy. Nevertheless, before starting with that, it is important to reiterate that the one value unifying the various industries in Oronjia is a necessity to navigate the land. The local goal for conservation management, then, demands a focus on sustainable mediation (Harper, 2002; Kull, 2014).

The local economy of Oronjia is sustained by a combination of wage-based and subsistence-based work that belong to the various industries present in the peninsula. Here, wage-based work is defined as any livelihood activity in which individuals are either employed by a company or another individual, or work independently in marketable production. Similarly, subsistence-based work refers to any livelihood activity that primarily produces for personal use (Gardner, 2014; Pollini, 2014). The primary industries in the peninsula that provide opportunities for wage-based employment include tourism, traditional fishing, sand mining operations, charcoal production, and craft-making. In addition to these, the local economy is supplemented by small-scale activities that include shifting agriculture, free-ranging livestock farming, and resource gathering (Missouri Botanical Gardens, 2015).

The tourism industry in Oronjia is one of the most active attractions in the north of Madagascar, with far-reaching national and international attraction. The importance of this site is mostly due to the combined product of the close proximity of the peninsula to Diego, the natural beauty of the numerous beaches spread across the coastline of the peninsula (including Baie de Sakalava, Baie de Dune, Baie de Pigeons, Orongéa Beach, and Ramena Beach), as well as the cultural significance of the site for national memory due to the historic remains of a French military base from World War II. Because of these touristic attractions, in addition to the presence of the park, the local tourism industry has many opportunities to offer to local residents of the commune as well as residents of Diego. The main employment chances are organized through the numerous tourist lodges and shore-front restaurants found across the peninsula; these establishments, on top of hotel-restaurant roles, also provide employment for kite-surfing and ATV instruction to visiting tourists, as well as guided tours.
across the main park landmarks. In addition to this, local groups may also set up their own small business ventures to provide cultural entertainment to tourists. An example of this includes the women’s unions, which organise the independent work of masseuse, make-up artists, and hair-stylists (Personal observation; Missouri Botanical Gardens, 2015).

As mentioned above, the traditional fishing industry is also of high importance to the local economy of Ramena. Reports by MBG (2015) show that fishing makes up 90% of the local economy for resident households. The significance of this activity is related to the location of the peninsula at the merging point of the Indian Ocean and Baie Andovobazaha. This location makes the peninsula a good access point to access multiple zones of ocean wildlife without having to venture too far from land. Furthermore, Oronjia forest is home to the tree species traditionally used in the fabrication of the ‘hazon-drangola’ fishing canoes. These are produced from mature Delonix velutina, an endangered species of hardwood that grows across the main forest fragment in the site. As such, Oronjia is not only an important point for the launching of fishing activities, it is, in addition, a significant locale for the manufacturing of traditional fishing instruments. Fishing in Oronjia is performed for the purpose of subsistence as well as for providing a revenue source for commerce in the neighbouring markets. Local fishermen are organized through an unified association that regulates the industry to be more sustainable given the reliance on an endangered hardwood species, and also allow communications with other local organisations, like the local conservation body (Personal observation; Missouri Botanical Gardens, 2015).

The history of charcoal production in Oronjia is very complex. It is traditionally produced by a process that involves the slow, anaerobic burning of hardwoods within pits enclosed in layers of coarse leaf litter, and regularly reshuffled to ensure constant burning (Minten et al., 2013; Gardner, 2014). The charcoal industry used to be one of the more common activities in which people would take part on the peninsula to supplement their livelihood needs, perhaps second in importance after traditional fishing. Indeed, charcoal production was favoured by residents of Oronjia who, according to MBG, did not have the time nor the required expertise for fishing. However, the environmental footprint of charcoal production was highly detrimental to the survival of hardwood species in Oronjia. Occurrence of the activity today has been significantly reduced thanks to conservation action in the region, specially within the boundaries of the park. Nevertheless, charcoal production remains an important source of revenue for many local households. Practiced outside of the
park, it relies on trees from the areas of the forest fragment that extend south of the boundaries of the protected area. Charcoal production is now restricted to the periphery of private properties like local farms and enclosed residence lots. Most of the charcoal produced in Oronjia is sold to households in Diego, with the remaining stock kept for local use (Missouri Botanical Gardens, 2015).

Sand mining operations in Oronjia are located in close proximity to the village of Ankorikahely, along the main road entrance to the peninsula (Appendix 1 – Figure A1-2, the sand quarry is identified by the white body on the southwest section of the scene). Because mining operations are not in direct proximity to the park boundaries, the industry does not pose immediate concern to the primary conservation goals of the region. Nevertheless, it is still an example of how the local economy is primarily driven by a strong dependency on the availability of natural resources, which in this case are non-renewable and put high stress on the distribution of local plant populations. The industry primarily employs local residents from the local and neighbouring villages of the Ramena commune as well as Diego (Personal observation; Missouri Botanical Gardens, 2015).

Traditional craft-making is another means by which local residents supply their livelihood needs. Some of the most common products of Oronjia include baskets and other containers made out of vegetable fibre collected from the forest and savannah, custom embroidery of traditional clothing, as well as sculpture and ornaments that are crafted from local resources like drift wood and empty seashells. While artisans operate year-round, the industry shows a high degree of seasonality in accordance with the influx of tourists during the tourist season who are the primary source of revenue. Artisan shops are primarily located on the side of the main road, near all the major lodge, and the marketplace in the village of Ramena (Missouri Botanical Gardens, 2015).

Agricultural activities and resource gathering in Oronjia are exclusively taking place for the purpose of subsistence. With regards to agriculture, farming is generally a family venture, practiced at a small-scale by a limited portion of the population. The usual crops grown in the region include corn and sweet potatoes, which help supplement their diet during times of necessity. Likewise, livestock breeding and raising are practiced by families in small-scale contexts that supplement wage-based livelihood activities like fishing or charcoal production. The common type of livestock in the region includes zebu cattle, poultry, and goats. While poultry and goats help to supply household resources, zebu are primarily a good
of prestige used for social rituals and a form of long-term investing. While the livestock industry has small participation within the resident population, its footprint on the local environment is disproportionately high because the livestock roams freely across the park, grazing in the protected area.

During times of financial necessity, the local residents of Ramena are aware of the resources that the forest and grasslands have to offer. This is best represented by the prevalent collection of wild yams (*Dioscorea orangeana*, known locally as “Angona”) that takes place during the dry season, when fishing is not possible due to the strong seasonal winds. While the exploitation of wild yams within the park is illegal under the local “Dinas” (community-based legal arrangements), the tubers are still regularly collected by locals, who dig them out of the ground to supplement their livelihoods during times of financial need. In most cases, the tubers are consumed by local households that cannot afford other food staples like rice. Sometimes, however, the tubers are sold in Diego to generate some small profit for other needs (Wilkin et al, 2009). Another example of people’s reliance on natural resources is the small-scale collection of wood products and other related resources (i.e., cutting-down branches, logging of single trees) from the forest. While there is no large-scale logging at Oronjia, residents sometimes illegally participate in small-scale tree extraction, to collect wood that may be used to repair their households in situations of need, or to collect honey that can be sold at the market (Andriambololonera, 2015; Missouri Botanical gardens, 2015).

As shown here, then, it is clear that the livelihood activities of the resident population of Oronjia strongly depend on access to natural resources. If these activities are not carefully managed in such a way that they strive to achieve a balance between environmental and financial sustainability, the consequences to the people of Oronjia and the park can be detrimental (Hardin, 1968). As it is, from an ecological standpoint, the local population of the two villages has a strong influence over the environment of Oronjia, taking into account the 568 households occupied by the permanent resident population, plus the various tourist lodges and restaurants, business and government buildings, farms and grazing pastures, as well as the road and trail networks that link the various settlements to each other and other communes/cities. The population uses an irregular area of over 1,509,791 m², which cover both the periphery of the park and certain internal areas (Figure 2.1; Appendix 1 – Figure A1-2). Indeed, while the majority of the population is restricted to the main area of the Ramena and Ankorikahely villages, a notable percentage lives in one of the smaller
communities that surround the protected area. Furthermore, the road and trail network is very extensive through the park, specially within the protected area. For example, the main southern road cuts right between the Mamelon Vert section and the extend of dry forest that gives way to Cote-44, before it turns north at the entrance of Baie de Sakalava, and splits the eastern section of the protected area, near the boundary with the restoration buffer.

2.2 **The Goal of Conservation Management at Oronjia Park:**

Conservation activities in the forest of Oronjia were started by MBG in 2007, as part of their nation-wide community-based conservation project that sought to identify priority areas for plant conservation in Madagascar. Oronjia was selected as one of 12 Priority Areas for Plant Conservation (PAPCs) that were deemed of necessary importance and under significant threat to require conservation intervention. The broader goals of MBG in Madagascar are to understand the influence that human activities have on the vegetation profile of these forests in order to design conservation strategies that support their sustainable use and directly benefit the lives of people in their peripheral zones by taking into account their knowledge and traditional practices. Each of the PAPC units is managed by following the same five underlying principles. These are: (1) analytics that support information-based decision-making, (2) conservation by the people and for the people, (3) a project roadmap that is inclusive and driven by consensus, (4) respect for local traditions, and (5) ensuring that from conception to implementation the project takes on a bottom-up grassroots approach (Missouri Botanical Gardens, 2015; Raharimampionona, 2015).

Oronjia Conservation park was formally established as a New Protected area, under a Category V Protected Landscape/Seascape classification in 2015. This was done following extensive monitoring of the site’s ecological significance to Madagascar’s plant and wildlife biodiversity. This involved close negotiations with local stakeholders, including government bodies that have direct authority over the use of the site, as well as the local residents that lived in the area prior to the arrival of MBG and depend on the access to natural resources to sustain their livelihood needs (Missouri Botanical Gardens, 2015). The IUCN Category V designation used by MBG in the management of Oronjia refers to the international classification system by which the design of conservation protection is specified as it pertains to the management of human action within areas of conservation concern. From Category I to Category VI, the IUCN protected areas categories propose broad-stroke guidelines that
recognise the variety of scenarios to which conservation management may be applied. This covers circumstances from where protection may require the complete ban of human activities within conservation areas, to circumstances where the appropriate course of action is to influence the sustainable expression of human action with their natural environment (For a more detailed overview of the IUCN management categories, see Dudley, 2008). At the core of the Category V system lies in the core idea that in circumstances where the interaction between people and nature are deeply entangled, the maintenance and management of protected areas requires the proper integration of environmental and cultural values. As such, Category V systems do not propose the strict conservation of nature, rather they seek to guide human action towards more sustainable ends. It primarily recognises that in many systems, human action cannot be considered as a separate entity from nature (Phillips, 2002; Dudley, 2008). Due to its emphasis on the interaction between people and nature, the Category V system has seen much adoption in the developing nations like Madagascar because they seek to provide opportunity for sustainable livelihood styles that do not affect environmental health and biodiversity (Phillips, 2002; Kull, 2014).

Governance and administration of Oronjia Park is shared between MBG – who oversee the planning of conservation activities, management of research interests, and coordination with the local community; the RM7 Military Base in Ramena – who hold tenure of the land and grant permission of entrance; and the local population – in charge of the developments of Dina and their implementation. In the day to day management of Oronjia, the local population is represented by KODINA, which is made up of local residents of the Ramena commune elected for service consisting of a two-year period. In addition to representing local community interests, the members of KODINA are also in charge of patrolling the park, policing resource use, and applying the DINA in case of a discovered infraction in the protected area. In addition to these three partners, coordination of the park is also supervised by other governmental and international bodies (Pollini et al., 2014Missouri Botanical gardens, 2015). These include, the Ministère de l’Environnement, de l’Écologie, et des Forêts (Ministry of Environment, Ecology, and Forests) – which ensures that national conservation laws are adhered to, Le Ministère de l’Agriculture (Ministry of Agriculture) – which oversees agricultural and fishery activities in the area, Ministère de l’Énergie et des Mines (Ministry of Energy and Mine Services) – which provides energy and topographical
services, and the Madagascar Biodiversity Fund – which coordinates international funding for the park with MBG (Missouri Botanical Gardens, 2015).

**FIGURE 2.7** – Example of forest clearings within the protected area of Oronjia Park (satellite scenes obtained from WorldView-3, 2015).

Prior to the launch of conservation management operations in the area by MBG, the quality of the local forest had been severely exhausted by the local Malagasy residents, whose unchecked exploitation of natural resources led to the severe fragmentation of the internal vegetation structure of the forest fragment that is still observed today (at the time of this study). Discussions with local residents and MBG staff indicated that anthropogenic disturbance was primarily produced by the charcoal industry, agricultural activities, and small-scale instances of resource gathering. Following our interviews, as well as past observations by MBG, there appears to be no indication that disturbance factors commonly observed across Madagascar, like the hunting of lemurs or slash-and-burn agriculture procedures are taking place at Oronjia (Missouri Botanical Gardens, 2015). The effects of the
charcoal industry had perhaps the most significant influence on the present structure of the forest fragment. Indeed, historic charcoal production, coupled with the selective extraction of hard-wooded tree species that are the target of this activity, led to the clearance of forest sections that produced the clear-cut scars that can be prominently observed today within the fragment, (Figure 2.7; Figure 2.8 - A).

The effect of agricultural activities, while less dramatic than that of the charcoal industry, were just as problematic. Shifting agriculture led to the loss of forest habitat along the northern and southern edge sections of the fragment that are in close proximity to each the two seasonal waterbodies (Figure 2.4). Likewise, the constant grazing of livestock raised by local herders led to the disturbance of the forest understory. This affected the availability of floor-level leaf-coverage for native species whose diet might be based around them, as well as hindered the ability of native, slow-growing plant species to regenerate in the habitat sections lost to other anthropogenic activities. Finally, while some forms of resource gathering in Oronjia have always been highly opportunistic and not very intrusive – for example, logging for non-charcoal purposes has been very limited and selective – the collection of yams has left a large footprint on the forest (Figure 2.8 – B & C). The process of yam extraction is highly intrusive as it leaves behind holes across the landscape that are not backfilled; the intrusiveness of this activity has the potential to affect the growth of ground-level vegetation and moisture levels of the soil – a problematic fact considering how dry the site is and that vegetation in many sections is currently regenerating from past human activities (Hartmann & Messier, 2011; Kurek et al., 2014). Furthermore, yam extraction, in addition to other forms of resource gathering, possess a threat to the structural continuity of vegetation across the site as people carve new trails for continued access to these resources.

\textit{FIGURE 2.8} – Examples of anthropogenic disturbance within the protected area of Oronjia Park. This includes: (A) illegally logged tree, (B) unfilled yam-hole, and (C) old charcoal-pit.
Thanks to the intervention of MBG and the enforcement of local Dinas by KODINA at Oronjia, through their extensive community work and conservation planning (as discussed at the beginning of this section), charcoal production and the expansion of shifting agriculture within the forest fragment have virtually come to a halt. Today, the residual effects of these activities are all that remain of immediate concern within the protected areas. Nevertheless, other aspects of human activity continue to pose a threat to the park’s environment and biodiversity. The economic situation under which many local residents live perpetuates the problematic reliance they have on natural resources. Indeed, my observations at Oronjia and reports by MBG (2015) show that illegal resource gathering within the park’s boundaries – specifically the collection of wild yams – in addition to the intrusive grazing of livestock, continue to be a threat to the recovery of the park’s disturbed vegetation (Andriaholinirina et al., 2015; Rakotondraparany & Andriambeloson, 2015).

To manage these activities within the park, MBG established park operations with the parallel goals of: (1) restoring the forest’s health while providing protection to its native inhabitants; and (2) supporting the sustainable use of the local environment by local residents. To achieve this, in partnership with their community and governmental counterparts, MBG has established programs to monitor use of the park while educating local residents on the importance of environmental sustainability. These efforts are supported by their outreach work to aid in the establishment of tourism programs that benefit all demographic sections of the local resident population. The most recent of such programs involves the partnered efforts between MBG, SAGE (Service d’Appui à la Gestion de l’Environnement – Support Services for Environmental Management), and Conservation International to establish the Ramena Complex. Under this project, the three conservation bodies seek to coordinate conservation management and tourism activities between the three, recently established New Protected Areas that are located in this region – NPA Oronjia Park, NPA Montagne des Français, and NPA Ambodivahibe (Sabel et al., 2009; Randriamahefa, 2016). The ultimate end goal of MBG at Oronjia is, in accordance with their Category V classification, to establish a management system that transfers the reliance of people on natural resources located within the park to sustainable industries like tourism and traditional activities that serve local Dinas (Phillips, 2002; Pollini et al., 2014; Missouri Botanical Gardens, 2015).
2.3 Description of Local and Neighbouring E. corona tus Populations:

The population of crowned lemurs inhabiting Oronjia Park has never been the focus of any sort of long-term study or monitoring protocol that could provide a rigorously backed figure of their size, distribution, and/or demographic breakdown. Nevertheless, I was able to compile a rough timeline of the population, thanks to a number of short-term studies that have taken place in Oronjia forest (Oronjia forest here refers to the forest fragment located in the peninsula, and not to the protected area since two of the studies took place prior to the establishment of the park), as well as some assessments of the neighbouring crowned lemur population located at Montagne des Français (Table 2.2). Previous surveys on the Oronjia population include short-term site-assessments conducted during the pilot season of two different graduate research projects (Arbelot-Tracqui, 1983; Freed, 1996). There was also a year-long population survey consisting of monthly observations conducted by MBG, and a short-term, three-week survey conducted by students from the Université d’Antananarivo (Missouri Botanical Gardens, 2015; Rakotondraparany & Andriambeloson, 2015). In addition, I also report the findings of surveys focused on the crowned lemur population at Montagne des Français in order to establish a comparative baseline that can help to corroborate the findings of the Oronjia reports.

**TABLE 2.2** – Summary of previous crowned lemur studies conducted within the new protected areas (NPA) found along the Ramena complex, including Oronjia Conservation Park and Montagne des Français. Population size in all instances is reported as the number of observed individuals.

<table>
<thead>
<tr>
<th>Year of Survey</th>
<th>Author / Publication Date</th>
<th>Population Count</th>
<th>Count Methodology</th>
<th>Length of Study</th>
<th>Survey Boundaries</th>
</tr>
</thead>
<tbody>
<tr>
<td>1983</td>
<td>Arbelot-Tracqui / 1983 (Available in Freed, 1996)</td>
<td>Average group size of 9 individuals / group, n = 3 groups **</td>
<td>Average counts following observations along survey paths</td>
<td>N/A</td>
<td>Forest fragment adjacent to Baie de Sakalava</td>
</tr>
<tr>
<td>1989</td>
<td>Freed / 1996</td>
<td>Average group size of ~ 3.25 individuals /</td>
<td>Average counts following observations</td>
<td>3+ Days to a Month *</td>
<td>Northern section of Forest Fragment (Cote 44)</td>
</tr>
<tr>
<td>Year</td>
<td>Location</td>
<td>Methodology</td>
<td>Population Estimation</td>
<td>Results</td>
<td></td>
</tr>
<tr>
<td>-------</td>
<td>-------------------------------</td>
<td>------------------------------------------------------------------------------</td>
<td>-------------------------------------------------------------</td>
<td>-------------------------------------------------------------------------</td>
<td></td>
</tr>
<tr>
<td>2012</td>
<td>Missouri Botanical Gardens / 2015</td>
<td>2 groups, 149 individuals along survey paths. Total count following monthly observation session along survey transects.</td>
<td>Monthly observations for a one year, each lasting 1 or 2 days.</td>
<td>Protected Area of Park.</td>
<td></td>
</tr>
<tr>
<td>1989</td>
<td>Freed / 1996</td>
<td>~ 3.25 individuals / group, n = 15 groups. Average counts following observations along survey paths.</td>
<td>3+ Days to a Month *</td>
<td>N/A</td>
<td></td>
</tr>
</tbody>
</table>

* No specific description of time spent at each site beyond a note stating surveys were conducted for a minimum of three days.
** Average population count derived from observations across fragments in the Ramena complex.

The oldest available report of the Oronjia population was completed as part of the graduate thesis by Arbelot-Tracqui (1983), which compared the reproduction ecologies of crowned lemurs and Sanford’s brown lemurs throughout their range to explain mechanisms of speciation. While I was not able to obtain access to the original thesis – which means that I am not fully aware of the specific characteristics of the survey techniques used in the study or any commentary on distribution patterns that the main author may have had – the summary...
available in Freed’s (1989) thesis provides some valuable insight on the population’s size and demography at that time. As seen in Table 2.2, the Oronjia population observed around the Sakalava area is quite small, only three groups were observed, each composed by an average of nine individuals. Group structure could be defined as multi-male multi-female; generally composed of 3 to 4 adult females, 2 to 3 adult males, and 3 to 4 sub adults. This group patterning possibly indicates that membership to the observed groups was not limited to the nuclear family, but was rather characterised by the inclusion of a combination of various adult pairs and their offspring. In addition to the observation of crowned lemurs in the forests near the Sakalava region, which corresponds to the tall forest strips near Mamelon Vert, Arbelot-Tracqui reports that crowned lemurs were also seen in the northern sections of the Oronjia forest and south of the site along the forest fragments located between Oronjia and Montagne des Français.

Similar to Arbelot-Tracqui (1983), Freed’s (1996) research included a short-term assessment of the crowned lemur population that inhabited the cluster of forest fragments that more-or-less make up what is today known as the Ramena Complex. The specific purpose of Freed’s survey was to aid in the selection of a suitable site for his dissertation research on the co-occurrence of crowned lemurs and Sanford’s brown lemurs. While the broad characteristics of the Ramena complex, including Oronjia, did not merit further research on the local crowned lemur population, the results of his initial assessment do provide some valuable insight on the stability of the population in comparison to the earlier research by Arbelot-Tracqui. As seen in Table 2.2, two crowned lemur groups, hosting between 3 to 4 individuals on average, were observed along Cote 44 and the forests adjacent to Baie de Sakalava. Based on the population figure reported by Freed, is it possible to surmise that the size of the crowned lemur group at Oronjia declined in the years that separate the two studies. Nevertheless, since there is no clear record of when the Arbelot-Tracqui study took place, its duration, or the survey techniques that were employed, no direct comparison between the two population counts can be made. It is clear from these two early studies, however, that the historic size of the Oronjia population was relatively small, and its range seemed to be most prevalent along the forest sections that today correspond to northern and southern sections of the park’s protected area.

In comparison to the small size of the Oronjia population, Freed (1996) reported that 15 groups, with a similar membership count of 3 to 4 individuals on average, were observed
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in Montagne des Français and the forest fragments that surround the massif. Furthermore, while Freed’s demographic inventory does not separate the Oronjia population from the rest of Montagne des Français, the aggregated summary for the entire population present in the Ramena Complex indicates that on average group membership was made up by 1 to 2 female adults and 1 to 2 male adults, as well as the occasional inclusion of one nonadult offspring. Freed further reported that the presence of the Oronjia and other local crowned lemur populations was not restricted to sections of forest where the canopy was continuous and relatively undisturbed. Instead, their presence did not seem to be affected by the state of degradation of the forest structure. Finally, he also noticed that the population showed a strong intolerance to the presence of humans, as most groups would flee within five minutes of contact with people.

The first study to survey the state of the population since the establishment of the park and conservation activities in the area was carried out by the Missouri Botanical Gardens (2015). As Table 2.2 indicates, this study was also the first and only long-term survey of the Oronjia population, consisting of two-day population inventories, repeated on a monthly basis for one year. In this study, MBG reports that in 2012 the Oronjia population consisted of 149 individuals, a figure that is strikingly higher than those reported by Freed (1996) and Arbelot-Tracqui (1983) before the turn of the century. Nevertheless, it is necessary to understand that this statistic reflects the total count of observed individuals after the one year period, and it is not an accurate estimate of the population size since it does not take the necessary approach to avoid taking the same individuals into account multiple times. For example, simple solutions like reporting an average count of individuals per survey unit (i.e., day or transect) as seen in the previous two studies, which helps to limit the possibility of overcounting individuals, or reporting more comprehensive estimates that are produced by modelling the population density through direct or indirect methods like distance sampling or capture-mark-recapture (Ross & Reeve, 2011) were not executed. Since no attempts were made to deal with this issue, then, it is likely that this statistic is over representing the Oronjia population.

Nonetheless, the MBG (2015) study does inform us about important population parameters that were not available through previous studies due to their temporal resolution. The main insight is that the crowned lemur population at Oronjia is present at the site throughout the entirety of the year, meaning that this site is not a seasonal refuge for
neighbouring populations along the Ramena Complex. This reinforces the necessity to understand the possible mechanism by which crowned lemurs are able to persist in this site given how deteriorated the forest fragment is, and how persistent human disturbance is. However, it is still not clear if the population density fluctuates across the year, as adult individuals migrate between neighbouring forests as they become independent from their parents; and if it does, how significant this is for the relative abundance of the population. In addition, the MBG study supports previous findings that show that the distribution of the Oronjia population is most prevalent along the forest sections in the vicinity of Baie de Sakalava, specifically in around Mamelon Vert, as well as the northern sections of the site, specifically the Grotte and Cote 44. The unchanging distribution patterns suggest that these specific areas possess important resources and habitat conditions that have yet to disappear.

The final and most recent study conducted on the Oronjia population consisted of a short-term survey carried out by students from the Université d’Antananarivo in partnership with MBG, to report on several aspects of the park’s vegetation and wildlife (Rakotondraparany & Andriambeloson, 2015; See also: Andriambololonera et al., 2015; Raherilalao & Rasozanakolona, 2015). The study by Rakotondraparany & Andriambeloson reports that in 2015 three different multi-male multi-female groups were observed along the protected area. The first two groups were observed during the day in the southern portion of the site, along the dense forests that surrounds Mamelon Vert and the littoral-like forest strip immediately adjacent to Baie de Sakalava. The first group was composed of seven individuals, while the second group only included 4. While Rakotondraparany & Andriambeloson report these two groups independently, they note the possibility that the second smaller group may be an offshoot of bigger one since they were in close proximity to each other. This is possible considering that group membership for crowned lemur troops is very flexible (Wilson, 1989; Freed, 1996). The third group, composed of four individuals, was located in the northern section of the site. The group could often be heard during the early hours of the morning near the Grotte, or seen traveling along the canopy in Cote 44. This group was composed of one adult-male, one adult-female, one sub-adult, and one unidentified individual.

While the crowned lemur groups were primarily observed within the perimeter of the forest fragment, Rakotondraparany & Andriambeloson (2015) also report that some of the groups were often observed along settlements in close proximity to the protected area.
Indeed, they remark that the second group of lemurs with four individuals was sometimes seen resting and foraging on the trees located adjacent to some of the lodges near Baie de Sakalava. Similarly, they reported that in some rare occasions crowned lemurs had been seen coming into close proximity with people in touristic areas to get access to food from tourists that enjoy feeding them. It is worth mentioning, however, that these events were not very common, and in general lemurs would not get close to people. Nevertheless, this information contrasts with Freed’s observations that the crowned lemur groups showed little tolerance towards human presence. While the implications of this will be furthered considered in line with my own observations of the population in Chapter 4, it is at least possible to say that the relationship between humans and crowned lemurs at Oronjia is more complex than might initially appear; and may be subject to continued change as a result of increasing tourist activities and shifts on the importance of natural resource exploitations.

Unlike the reports previously presented in this section, the study by Sabel et al. (2009) only considers the population densities of the flora and fauna species that are present in the NPA Montagne des Français. Their study consisted of four independent, short-term sampling periods, starting on the summer of 2015 and finishing in the spring of 2016, along three independent line-transect plots covering a subsection area of the protected area. As such, while the population counts reported in this study only reflect a limited sample of the complete crowned lemur population at Montagne des Français, the results allow us to consider the relative density of this population. Based on the counts obtained through the four sample periods, average population size in the subset sample area at Montagne des Français includes an average of 21 individuals. By roughly comparing the results of this study with the latest population density estimate at Oronjia (Rakotondraparany & Andriambeloson, 2015), while controlling for the size differences of each study region; it is apparent that in contrast to Oronjia, the population at Montagne des Français appears to display a higher density relative to the sample area explored in their survey. Indeed, these figures suggest that close to two individuals (15 E. coronatus / 8 km² = 1.875 lemurs per km²) may be present for every square kilometer available in the protected area of Oronjia park. In contrast, Montagne des Français holds close to four individuals for every square kilometre (21 E. coronatus / 6 km² = 3.5 lemurs per km²).

These population density estimates are, of course, very simplistic. For one, the observations of Oronjia are based on the entire forest fragment, while the observations for
Montagne des Français are based on a limited portion of the entire site. As all of the previous reports have suggested, the crowned lemur population at Oronjia does not seem to display an even preference for all sections of the forest fragment. Instead, they appear to favour certain sections of the site where they were commonly sighted, while seemingly overlooking neighbouring sections were sightings were either rare or non-existent (Freed, 1996; Missouri Botanical Gardens, 2015; Rakotondraparany & Andriambeloson, 2015). In contrast, because the Sabel et al. (2009) study is based on a specific subset of the available forest habitat at Montagne des Français, it is not possible to determine if it accurately represents the availability of suitable habitat throughout the site. Because of such coverage contrasts between the two studies, it is difficult to determine if there is indeed such a difference in population density between Oronjia and Montagne des Français. Nevertheless, given Freed’s (1996) earlier population surveys across the Ramena Fragment, there is some support to the idea that the population at Montagne des Français is present at that site at a higher density than is the case at Oronjia.

The pattern of population density discussed here, of course, makes sense when it is considered that Montagne des Français contain larger expanses of forest that exhibit more structural complexity than what is seen at Oronjia, in part due to the site’s topography that has provided some relative degree of protection in comparison to surrounding forests (Green et al., 2007; Sabel et al., 2009). This helps to put into perspective the quality of conditions that make up the forest habitat at Oronjia. At Montagne des Français troops of crowned lemur are often seen occupying overlapping home ranges with only a small degree of separation. The realisation of home ranges at Oronjia seems to not resemble this pattern, as the two main discernible groups appears to not overlap; and instead occupy distant locations within the northern- and southern-most sections of the site (Green et al., 2007; Rakotondraparany & Andriambeloson, 2015). This dissimilarity becomes most striking when it is considered that the life-history processes of the crowned lemur population across the Ramena Complex are likely highly connected, forming a metapopulation that is maintained by the degree of connectivity available between the forest fragments. After all, as Freed (1996) and Rakotondraparany & Andriambeloson (2015) report, the local crowned lemur groups are able to move with ease along forest sections with semi-continuous canopy structure. The fact that the populations likely exhibit some degree of connectivity along the Ramena Complex means that their density within the forest fragments can be sustained near
carrying capacity by common metapopulation processes (i.e., birth and death rates within fragments, as well as migration between fragments), as long as the demographic profiles of each population subset matches the resource conditions of each fragment (Wiens, 1997; Abrams, 2002; With, 2004). This supports the idea that the quality of the forest fragment at Oronjia is not suitable to sustain a large population of crowned lemurs, owning to the stability of the small population that has been observed at the site for a long time. Instead, only a limited portion of the site appears to hold the resources and conditions necessary to support the behavioural and physiological needs of the population on a stable basis (Hutchinson, 1957; Turner et al., 2001). However, questions still remain: what defines these areas, how are they distributed, and how do they ensure that crowned lemurs are able to persist in this site? These questions will be addressed as part of the analysis of this project.
Chapter 3

3 METHODOLOGICAL FRAMEWORK:

This chapter has two major goals: Section 3.1 describes the sampling protocol used to: (1) measure landscape covariates that describe the habitat structure and anthropogenic influence across the protected area, (2) estimate the influence that landscape conditions play on the habitat use patterns of crowned lemurs, and (3) conduct interviews on the livelihoods and socioeconomic needs of Malagasy stakeholders. Finally, Section 3.2 discusses the analytical framework used to model the habitat preferences of crowned lemurs, and explores how human and non-human interactions influence conservation action in the vicinity of the park.

3.1 Data Collection Protocols:

The following sections detail the methods used in this study to assess the influence that landscape conditions and conservation initiatives have on the habitat use patterns of crowned lemurs at Oronjia Park. Data collection protocol consisted of a field and a remote sensing component. Collection of field data took place in the summer of 2016, between June 06, 2016 and August 15, 2016. Additionally, collection and preparation of remote sensing data took place between November 2016 and January 2017.

3.1.1 Summary of Field Observation Methods:

All field observations were recorded by FM Mercado Malabet (FMMM) with the assistance of two local Malagasy guides who had past work-experience at the site. In addition, our research was supported by members of the MBG – Oronjia team and Dr. Alex TOTOMAROVARIO from the Université d’Antsiranana, who provided logistic or advisory support whenever necessary. Preliminary data were gathered during a five-day pilot-study, which consisted of three days of random walks along the park’s protected area, as well as two days of consultation with members of the MBG – Oronjia team and local residents of the Ramena complex who belong to the KODINA organisation. Observations along the protected area served two purposes: First, with the help of the previous reports, narrowing down the location of crowned lemur hotspots and daily activity patterns to predict both their spatial and
temporal distribution patterns across the site. This was done to determine the time of day during which the likelihood of observation is highest and to update population size estimates to ascertain the minimum survey effort necessary to accurately study them. Second, these observations facilitated determination of the optimal location and characteristics for the placement of survey strips by exploring the site’s topography and vegetation patterns. Similarly, consultation efforts with conservation agents and local stakeholders from MBG – Oronjia and KODINA served to localize the design of our survey protocols so as to better match the conditions of the site. These talks involved a mixture of discussions regarding the appropriate covariates necessary to representatively summarize the range of conditions making up the Oronjia landscape. These discussions also allowed for a review of the questions included in the questionnaires for interviews to understand the socio-economic needs and opinions of local stakeholders, so as to accurately communicate the meaning and intentions of the questionnaire with possible participants.
FIGURE 3.1 – Summary of observational field protocols carried out in the protected area of Oronjia Conservation Park. This includes locations of landscape observation points and transect trails, as well as communities included in the scope of interviews with Malagasy stakeholders.

Following the conclusion of the pilot study, all appropriate sections of the main field survey were modified as necessary. In order to address the main objectives of this study, the survey was designed to include three parallel and interrelated research components. These included: (1) a geospatial survey of the protected area and immediate periphery to measure the continuous distribution of chosen landscape covariates; (2) a set of transect surveys along key crowned lemur hotspots and areas lacking observations of their presence to measure how landscape conditions affect their presence within the protected area; and lastly (3), a series of short interviews with Malagasy stakeholders living in the periphery of the park’s boundaries. The details of these procedures will be further discussed in the following sub-sections. A summary of the survey efforts along the site can be observed in Figure 3.1.

3.1.1.1 Geospatial Survey:

I used a non-standardized point sampling to collect GPS (Geographic Positioning System) observations on landscape conditions, including anthropogenic disturbance and ecological characteristics, along the protected area of Oronjia Park and the surrounding zone in its direct periphery (Cochran, 1977; Ross & Reeve, 2011). I chose a non-standardized sampling design because of the heterogenous spatial characteristics of the Oronjia landscape, namely the fragmented quality of the vegetation cover which disproportionately affects the accessibility to certain areas of the site in contrast to others due to the thick density of tree and tall shrub stands. Since the carving of new trails is not permitted in the park, the randomized design permitted the next-best scenario by providing the flexibility to collect observations wherever possible. To account with the issue that this design introduces, which is biased in favour of the observation of habitat sections with open vegetation patterns that permit the ease of human movement, the sampling effort was constrained to favour a higher density of observation in the perimeter surrounding areas of low accessibility in comparison to more open habitat sections.

I assessed landscape conditions across the protected area of Oronjia Park and its immediate periphery by collecting a series of ‘snap-shot’ observations along the target area.
With each observation point, I recorded a description of the ecological characteristics and patterns of anthropogenic influence relevant to the niche qualities of wild crowned lemur populations. Selection of appropriate covariates was based on the findings of previous studies of crowned lemur ecology and biogeography, as well as those of closely related taxa living in similar environmental conditions (Wilson et al., 1989; Freed, 1996; Colquhoun, 1997; Tattersall & Sussman, 1998; Sabel et al., 2009; Peacock, 2011; Chen et al., 2015; Colquhoun, 2015; Donati et al., 2016; Kamilar & Tecot, 2016). Note that while previous studies – i.e., Peacock (2011) as well as Kamilar & Tecot (2016) – have also stressed the importance of taking into account climate correlates in model of habitat preferences, the small size of the study area in addition to the short length of the project made taking into account such variables redundant as no meaningful spatial or temporal variation was observed to occur. Furthermore, due to the logistic complexity of directly measuring certain landscape conditions like habitat structure and anthropogenic impact, qualitative measurement scales adapted to the characteristics of the Oronjia landscape were used when appropriate (Turner et al. 2001a; Lehman et al., 2006b).

In total, 125 observations were collected along the target zone, during a period of 27-days (Appendix 2 – Table A2-1). At each point of observation, the research team recorded the geographic coordinates and other identifiable metadata – such as the date of observation and the specific Observation-ID. Furthermore, at every location, we also recorded the following four covariates: elevation (m) from sea level, the classification of habitat structure, the intensity of anthropogenic influence, and the vertical degree of canopy cover. We measured all appropriate covariates within an area of 15 m² from the central point, following the specific protocols specified below. The maximum area of observation considered at each point was truncated to prevent the possibility of reporting the same landscape features in different points which could occur between points that were in close proximity and provided unimpeded visibility to each other (Buckland et al., 2015).

Geographic coordinates and elevation measures for all observations were recorded using a Garmin eTrex 20x GPS (Location = ± 3.7 m error range; Elevation = ± 3 m error range). All coordinate points were collected along existing paths and traversable forest sections so as to not damage the existing vegetation cover. Additionally, points were regularly separated by a minimum distance of 25 m to its nearest neighbour so as to not record observations within the sensor’s error range. However, it should be noted that the
meaning of “separation” fluctuated in accordance to landscape factors such as the site’s topography and/or the degree of continuity between habitat sections (i.e., continuity of vegetation patterns). To ensure that observed variation between measured covariates did not result from independent temporal processes (i.e., variation in light conditions across the day), all observations took place during the same day-time period, running from 10:00 am to 4:00 pm (Ross & Reeve, 2011). Similarly, due to the inherent subjectivity of some of the classification measures employed in this survey protocol (as seen below), all qualitative observations were done by F.M. Mercado Malabet so as to avoid inter-observer bias (Bajorquez-Tapia et al., 2003; Lehman et al., 2006b). Finally, whenever lemurs were observed, we followed the procedure specified in Subsection 3.1.1.3.

We estimated habitat structure by employing a pseudo-continuous, 5-point classification scale that serves to summarize the variation of habitat types within the area of study. The classification scale was developed following consultation with conservation agents from the MBG – Oronjia Team and the most up-to-date maps displaying vegetation patterns across the region (Moat & Smith, 2007; Ileiry Geospatial Services, 2014; Ileiry Geospatial Services, 2015). As seen in Appendix 3 – Table A3-1, the habitat classification-key summarizes the observed variation in habitat structure by linearly scaling in a logical sequence that is informed by the degree of vertical complexity (i.e., the maximum height of the most common type of vegetation at every observation point). This criterion informs the first four levels of the classification key – (1) Bare rock/soil, (2) wooded grassland/brush thicket, (3) degraded forest, and (4) intact forest; however, the fifth class – (5) Anthropogenic habitat – breaks from the main logical form of the scale, but it is nevertheless included due to the prevalent influence of people in certain sections of the area of study (See Appendix 3 – Table A3-1, for a description of the qualities of each category).

Similarly, we estimated the intensity of anthropogenic influence across the area of interest using a pseudo-continuous, 5-point classification scale (Appendix 3 – Table A3-2). The classification scheme used here was taken from Lehman et al. (2006b), and adapted to better suit the specific manner of ways in which the Malagasy people of Oronjia engage with their local landscape as they seek to fulfill their livelihood needs. To accomplish this, I modified the descriptive qualities of the original four classification points developed by Lehman et al. – (1) None, (2) light, (3) moderate, and (4) heavy – to describe the suite of disturbance patterns observed at Oronjia; and included a fifth – (5) Dominated – category,
that describes habitat sections where human settlements are present. The last category was included in this study because of the presence of small settlements and agricultural fields along the border of the protected area, which represent a continuous mode of human and non-human interactions unlike those described in the four previous categories (Ingold, 2000a; Bogaert et al., 2014; Gardner, 2014; See Appendix 3 – Table A3-2, for a description of the qualities of each category).

Finally, we estimated the relationship between vertical forest structure and the degree of canopy cover (hereinafter referred to as vertical canopy cover) by recording the density of illumination (200,000 LUX range) at ground level. Here vertical canopy cover is defined as the interaction between tree height and the percentage of canopy thickness. Measurements of the variation in the total amount of illumination provide a quick and indirect way to measure the relationship between vegetation height and canopy thickness since it allows a comparison of how the amount of light reaching the forest floor varies as a product of these two factors. However, it should be noted that under certain circumstances, the accuracy of this method can be heavily skewed. This bias can be attributed to the daily and day-to-day variation of the sun’s position and the amount of cloud coverage on the sky (de Souza et al., 2010). To limit some of the confounding influences that these factors can have on the chosen metric, observations were limited to days when cloud coverage was minimal; and as mentioned before, survey walks were scheduled during peak sun hours. Luminance records were collected by using a PYLE-METERS PLMT15 Handheld LUX Photometer (Accuracy = ± 3%; Sampling Rate = 2 samples/sec). Operation of the photometer was done following the best practice guidelines indicated by the manufacturer – this included the following steps: (1) Facing the photo sensor directly towards the target light source, (2) waiting 5 seconds for the sensor to warm up before recording a reading, and (3) ensuring all readings were done at the same standard height (150 cm from ground) and sensor range (200,000 LUX) so as to not introduce noise variation into the dataset. Furthermore, to validate the accuracy of the photo sensor at each point, observation readings were repeated three times in each instance; when noticeable differences between readings were observed, they were averaged so as to avoid the possibility of random sensor error.

Mapping of the continuous distribution of these four landscape variables across the length of the protected area was performed by FMM using the Empirical Bayesian Kriging (EBK) interpolation tool from the geostatistical analyst extension in ArcGIS Desktop v10.3.1
Kriging is a commonly used interpolation method that predicts the continuous probability distribution of a process of interest – i.e., elevation. Kriging estimates the distribution of the data by fitting a density function known as a semivariogram. This function is used to quantify the amount of spatial autocorrelation and variation observed between sample points, to predict characteristics of the process of interest along unknown locations. As such, the predictive power of kriging depends on how well the semivariogram function explains the sample data.

EBK is a type of kriging method that, unlike other methods, takes into account the error introduced from the defining process of the semivariogram function to develop a more accurate model. This is done by replicating the estimation procedure of the semivariogram through $n$ number of simulations, to develop a grouped function from all the simulated replicates, that provides the best fit for the data with the lowest possible degree of error (Krivoruchko, 2012; ESRI, 2017). For the EBK models of our four landscape covariates, we defined the replication interval of the semivariogram at 1000 simulations to ensure that the resulting curve could properly fit the wide range of variation observed across the site.

EBK in ArcGIS is capable of supporting a total of six different classes of semivariogram functions: in order of their computational and predictive complexity, these include the power, linear, thin plate spline, exponential, Whittle, and K-Bessel distributions. The major difference between all of these semivariograms relates to how each distribution assumes that similarity diminishes over distance – which is a common way of measuring spatial autocorrelation and variation. While the first three distributions listed above assume that autocorrelation diminishes quickly, the following three assume that autocorrelation diminishes slowly. The choice of semivariogram model, then, depends on the nature of the process of interest. I used the K-Bessel distribution in all four of our EBK models, since this type of semivariogram reported the lowest standard error in each case (Krivoruchko, 2012; ESRI, 2017). I validated the accuracy of each interpolation output by plotting the distribution of predicted and measured values to ensure that the relationship between the two did not deviate drastically from a 1:1 ratio (ESRI, 2017). Finally, I recorded each interpolation output as a raster dataset with a 1.24 m resolution and a geographic extent bounded by the boundaries of the protected area. The size of the resolution used here was determined to permit direct comparison with the satellite data presented in Section 3.1.2.1, which has a native resolution of 1.24 m.
3.1.1.2 Transect Survey:

I established five line-transects (T01 – T05) of equal length (500 m) across the protected area to measure how landscape conditions vary across sections of the forest fragment where crowned lemurs were and were not observed (Figure 3.1). Transect observations were collected to estimate whether or not the spatial variation in habitat structure and anthropogenic disturbance across the site influences the previously observed differential use of habitat subsections exhibited by the local population of crowned lemurs. However, because the small size of the crowned lemur population at Oronjia impeded constant observations of individual’s or group presence, the survey method employed here was modified from regular line-transect protocols that measure population distribution through presence/absence sightings to incorporate elements of occupancy surveys (Baker et al., 2011; Plumptre et al., 2013; Buckland et al. 2001; Buckland et al., 2015). Occupancy surveys use presence/absence observation to estimate the proportion of the landscape occupied by a species. This method relies on the detection of a species from repeated observations to survey units to estimate the probability that they will be occupied. A key advantage to occupancy surveys is that they do not depend on direct detection, and may also work on methods of non-visual detection like sound, signs, and local knowledge (Karanth et al., 2010; Baker et al., 2011; Plumptre et al., 2013). This aspect of the technique was specifically useful because of the small size of the Oronjia crowned lemur population.

The key assumptions of occupancy surveys are as follows: (1) sampling plots are closed to changes in occupancy; (2) heterogeneity in occupancy across plots is accounted for by model covariates; (3) any heterogeneity in the probability of detection across survey units is accounted for by covariates; and (4) detections within each plot are independent (MacKenzie et al., 2006:104). As assumptions 2 and 3 show, occupancy survey helps to test whether a species’ differential use of their habitat can be explained by the variation of landscape covariates across the sample units. Based on this framework, then, occupancy surveys are suitable to examine whether the set of landscape covariates used in my geospatial survey properly explains the observed variation of crowned lemur presence and absence at Oronjia.

Since the goal of my survey was to measure how the variation of independent covariates along each individual transect corresponded to lemur presence, rather than to
estimate the size and distribution of the population across the site, I adapted the framework of occupancy survey so as to specifically test the 2nd and 3rd assumptions of the technique. Based on this, then, I placed the set of line-transects along subsections of the protected area where crowned lemurs were either regularly observed or absent during the length of our study. Once transect placement was confirmed, I measured the spatial variation of the chosen set of landscape covariates along the length of each independent transect. In order to estimate whether landscape conditions varied in accordance to crowned lemur presence / absence, each independent transect was coded to define one of these two modes of detection. To be exact, each transect was assigned a value of 1 (present) or 0 (absent) to identify whether it corresponded to subsection of the protected area where crowned lemurs were or were not detected. Transects surveys were carried out for a period of 29 days, ensuring that repeated observations along each line-transect were completed following the protocol highlighted below. In total, each line-transect was visited a minimum of three times – Transects T01 and T02 were replicated four times each, while transects T03, T04, and T05 were each replicated three times. I chose to employ a transect design over the sample quadrats used in regular occupancy surveys, due to the difficulty of movement within certain sections of the site. In addition, transects posed the added benefit of permitting the continuous survey of landscape conditions along the survey unit that better helps to frame how they vary spatially.

Given the significance given to the location of line-transects, thorough consideration was given to the protocol employed to select these areas so they could properly communicate the covariates influencing detections and non-detection. As such, transect placement was decided following a validation method that involved my consultations with site patrollers and conservation managers from the MBG – Oronjia team, as well as reviewing the locations where previous site reports had indicated crowned lemur hotspots are located within the park. Using this information, I developed a series of candidate target zones to be monitored for signs of lemur presence during my pilot walks and geospatial survey. Proofing of presence zones involved both direct sighting of crowned lemurs within the target area, as well as non-visual methods, like identifying crowned lemur calls in close proximity to the survey strip or sighting fresh foot-prints that could indicate their recent presence. Once a sighting was confirmed, the candidate zone was put into consideration for a presence qualification. In contrast, candidate zones where no direct or indirect detection took place were assigned a qualification of absence. While this protocol does not rule out the possibility that areas
qualified absent of crowned lemur presence may in fact be utilized by the species during time slots when no survey activity took place, or may be utilized at such a smaller rate that confirming presence would require a more intensive survey protocol (Baker et al., 2011; Peacock, 2011; Ross & Reeve, 2011). The observed spatial variation in the detection of the species during the length of my surveys nevertheless suggests that the areas where utilization was confirmed are, in comparative terms, further preferred over the other areas, since lemur groups continued to consistently revisit them (Chapman, 1987; Lammertink et al., 2003).

Following this validation procedure, I selected the following types of habitat sections for the placement of transects: (1) two zones in the southern section of the site surrounding Mamelon Vert, where lemurs were commonly observed; (2) two zones, respectively located south of Cote 44 and southwest of the Grotte in the northern section of the park, where no direct indication of lemur presence was found; and (3) one zone along Cote 44, where lemur groups were sometimes seen traveling. Transects T01 and T02 were located on the first two zones, where lemurs were regularly observed. As seen in Figure 3.1, Transect 1 is located across the southern road, which is located to the north of Mamelon Vert, while transect T02 is found next to the southwestern slope of Mamelon Vert, along the southernmost edge of the protected area. Furthermore, the eastern sections of both transects are located in close proximity to human settlements. I assigned transect T03 to the third zone-group, where lemurs were occasionally observed traversing the canopy. This transect is located along Cote 44, and it is at the highest elevation point in comparison to the other transects. Finally, transects T04 and T05 were assigned to the second zone-type discussed above, where lemur groups were never directly observed. Transect T04 is located directly south from the Grotte, running along the edge of the protected area. My study confirmed earlier site reports that stated that at least one group of crowned lemurs was regularly seen in this area, as one group was indirectly spotted northeast of this location, along the cliffs that surround the Grotte – no group was spotted along this strip. Similarly, transect T05 is located south of Cote 44, in close proximity to the eastern road and along a regularly traveled trail.

I decided on standardizing transect length (500m) to ensure that all habitat subsections considered in our survey received an equal weight of effort. Longer trails could not be established because of the influence of the site’s topography, variation in altitude, and thickness of the vegetation cover in certain areas of the site. Similarly, the direction of the transects along the survey area could not be standardized to ensure their parallel placement.
from each other due to the reasons highlighted above. As such, to ensure all observations within a transect were independent of each other, I separated the trails at a length sufficient to prevent observation of the same features from different sampling units (Solomon, 2009; Baker et al., 2011; Buckland et al., 2015). To limit the confounding effects that temporal variation could introduce in some of the selected covariates, I limited survey effort to cover one transect per day during the diurnal period of highest lemur activity (1:00 – 4:00 pm). Furthermore, I ensured that transects in close proximity to each other were not visited in sequential days so as to introduce some degree of temporal randomization into our survey protocol. Finally, to maximize the range of variation observed along each individual line-transect, I took the following steps to randomize the observation protocol for each transect replication. First, I switched the starting and finishing points of the survey walks for each repeated visit. Secondly, I semi-randomized the observation interval to collect points every 25 to 30m. This allowed me to shift the number and locations of observations collected during each visit, so that each transect replicate is not an exact copy of the previous visit.

In total, the survey team collected 354 observations that summarized the landscape characteristics along each of our five line-transects (Appendix 2 – Table A2-2). Similar to the geospatial survey, at each point along the transect I recorded the geographic coordinate and other identifiable metadata – such as the date of observation, a specific Observation-ID and Transect-ID, a transect number to highlight replicates, and an observation number to identify individual observations within a replicate. Furthermore, at each and every location I recorded the same covariates used in the geospatial survey using the methods outlined in the previous section (3.1.1.1): elevation (m) from sea level, the classification of habitat structure, the intensity of anthropogenic influence, and the vertical degree of canopy cover. Whenever I identified the presence of crowned lemurs, I followed the procedure outlined in Section 3.1.1.3. Due to the difficulty of the terrain, no night-time surveys were completed. Similarly, no observations were collected in conditions of rainfall or heavy cloud cover.

3.1.1.3 Protocol for Observations of Crowned Lemur presence:

To maximize the number of detection records, points of crowned lemur presence were collected throughout both the transect- and geospatial-survey components of the study, using non-intrusive observation methods to estimate their location. I estimated the point-of-presence coordinates of crowned lemurs by recording the point-of-observation coordinates,
as well as the perpendicular sighting distance and the relative degree to their cardinal direction from their point-of-observation. Group location was defined in one of two ways depending on the length of separation between members: (1) one central location defined by the first observed individual for groups whose members are closely clustered together; or, (2) defining a central location every 10m if group-members are separated over 20m (Lehman, 2006b; Solomon, 2009; Buckland et al. 2001; Buckland et al., 2010). This method permitted me to collect detection coordinates of lemurs in the relative area of their initial sighting location without needing to be in close proximity to their groups. Observer to group distance was measured using an Eyoyo Range-Finder – AF1000L 1000 (Distance = ~ 1m error range), and group’s cardinal direction from observer was recorded using our Garmin eTrex 20x GPS. To ensure that detection coordinates reflect habitat preferences of crowned lemurs, I did not consider locations where groups/individuals were only observed traveling and did not engage with the habitat in any other behaviourally meaningful way – i.e., foraging, resting, playing. This was done to ensure that habitat qualities at each location reflect ecological and evolutionary variables that may directly influence behavioural processes. Furthermore, traveling locations were not included because it could not be clear if these locations reflect suitable habitat sections or if their presence there was owed to them traveling between preferred locations. In total, I identified 12 occurrence records of crowned lemur presence across the protected area (Table 4.1). In addition to the covariates listed above, whenever a group or individual was identified, I also recorded the number of individuals in the group, the sex-ratio (if identifiable), and the initial method of detection – visual or sound.

3.1.1.4 Interviews with Local Stakeholders:

I conducted 16 structured interviews, completed via a short (~1 hour long) four-part questionnaire, with Malagasy stakeholders residing in the villages and smaller settlements that surround Oronjia Park. My aims were to understand: (1) how much the livelihood activities of local residents today depend on their ability to access natural resources available in the peninsula, in contrast to seven years ago, before the formal establishment of conservation activities by MBG; and, (2) to formulate a sense of how conservation and ecotourist activities in the area have impacted the opinions and values that local stakeholders place on their access to the forest, the presence of lemurs and other animals, the rules that conservation activities imposes on their lives, and the opportunities – or lack thereof – that
ecotourist economies present. The questionnaire consisted of a mixture of closed-ended questions – i.e., yes or no questions and ‘choose from the following’ questions, as well as short answer questions that allowed participants to briefly elaborate on their opinion regarding some of the subjects highlighted above (Appendix 4).

Participants for the interviews were selected using a mixture of targeted and opportunistic sampling (Newing, 2010). Targeted sampling was utilized to identify potential participants from communities neighbouring Oronjia Park. This was done to obtain a range of participants that could appropriately represent the variation of livelihood profiles and local experiences. Additionally, opportunistic sampling was employed to identify potential participants among residents working for ecotourist businesses or participating in conservation activities held by MBG and KODINA. Potential participants were only considered eligible if they were: (1) permanent residents of the target communities, (2) financially independent or a primary financial provider for their family, (3) a Malagasy national, and (4) 18-years or older and capable of consent.

Access to participants was made possible by the support of MBG and KOIDNA, who facilitated initial introductions to residents of the various Oronjia community and explained to them the purpose of the project prior to the start of the interviews. After this, the research team approached potential participants to inquire about their interest in the project. Participation was voluntary and confidential to everyone but members of the research team. Questionnaires were delivered in either French or Sakalava – Malagasy (depending on the participant’s language preferences) by the Malagasy members of the research team, under direct supervision of FM Mercado Malabet. The location and time of interviews were chosen by each participant to suit their own convenience. To ensure confidentiality, questionnaires were completed anonymously by participants, and no directly identifiable information was collected.

The first section of the questionnaire collected basic socio-demographic information about the participant. This included information about their age, the ethnic group that they identify with, the name of their place of residence, and the number of years that they have lived in the Oronjia community for. To maintain a suitable degree of anonymity, answers to these questions were defined through broad categories, rather than specific information that could identify participants. Answers to this section of the questionnaire were necessary to get an idea of the demographic profile of people who participated in the survey, and so as to not
generalize responses on to other social categories that are either poorly represented in our sample or completely absent.

The second section of the questionnaire explores the distribution of people’s involvement in the various livelihood activities available in peninsula. The goal was to understand the relative importance that each activity plays for people’s capacity to supply their household’s income/resources, and to explore if this profile has changed since the start of conservation activities by MBG. The framework of this questionnaire section was adapted from Gardner’s (2014) study on charcoal production, which sought to explore the socio-economic drivers influencing the increased practice of charcoal production in Madagascar. Based on Gardner’s original questionnaire, I provided participants with a list of livelihood activities commonly practiced by stakeholders during the progress of a year (as discussed in Section 2.1.2), and asked them to rate their relative importance following a three-point ordinary scale as follows: (1) indicates that the activity is of no considerable importance / is never carried out; (2) indicates an activity of minor or secondary importance / is carried out infrequently or for parts of a season as a fallback to other activities; (3) an activity of major and continuous importance / carried out often throughout the year as the main livelihood activity. Participants were asked to complete the list for both the current year, and seven years prior.

The third and fourth sections of the questionnaire involved semi-open questions that provided opportunities for participants to briefly elaborate on their opinions towards a number of issues related to sustainability and land accessibility needs. The third section was concerned with exploring the range of views and values that individuals hold towards the presence of conservation and ecotourism activities in the peninsula. To address this, I first asked participants to reflect on the impact that the actions of MBG have had on the quality of the forest and the land since the start of their operations in 2007. Related to this, I also asked whether they support or question the need for conservation activities, and what motivates their opinion. Furthermore, I asked them whether or not they think that the conservation efforts have been successful in including local stakeholder needs into their operation. Finally, I asked participants to judge the effect that the ecotourism industry has had in their lives, and whether they feel they have personally benefitted or been ignored.

The fourth and last section considered how local stakeholders value the presence of lemurs in the forest, as well as the importance the presence of the forest plays in their lives.
Specifically, I was interested in understanding how aware people are of the species present at Oronjia. This included whether or not they are able to identify the number and characteristics of species present in the park, as well as the conservation issues they are facing. Moreover, I asked people to reflect on the number of ways in which they interact with the forest – i.e., subsistence, recreation, cultural traditions, movement between settlements – and the value they place on the health and continuous presence of the forest. My goal with the last two sections of the questionnaire was to establish a framework of how the concerns and values of the local Malagasy stakeholders align with conservation incentives.

3.1.2 Summary of Remote Sensing Methods:

In addition to the four covariates identified in previous sections, nine landscape covariates were derived from satellite data and other publicly available datasets. These additional variables were obtained to supplement field observations in order to generate a more comprehensive description of the habitat structure and anthropogenic disturbance patterns observed across the Oronjia forest fragment. Similar to the four original covariates, this additional set of landscape conditions will be used to assess which factors influence the distribution of crowned lemurs across the protected area. As such, they are included in both the geospatial and transect datasets.

The supplemental variables measured here include: (1) variation of net primary productivity, (2) variation of vegetation moisture, (3) distribution of cleared-cut sections across the vegetation mosaic, (4) distribution of human-made features across the fragment, (5) distance to standing bodies of water, (6) distance to human settlements, (7) distance to secondary roads, (8) distance to forest trails, and (9) percentage of canopy cover. The first eight covariates were calculated using satellite data from the WorldView-3 multispectral and panchromatic sensors (DigitalGlobe, 2015). The last covariate was obtained from Global Forest Change 2000 – 2014, using their open source dataset of global canopy cover patterns (Hansen et al., 2013). These variables were selected because of any of the following reasons: They represent conditions or resources that previous studies have confirmed have an influential effect on the distribution of crowned lemur or closely related taxa (Wilson et al; 1989; Freed, 1996; Solomon, 2009; Kamilar & Tecot, 2016); they quantify the presence of anthropogenic features and their influence on the spatial structure of the protected area; and finally, they exhibited some degree of heterogeneity within the protected area. The covariates
were modelled using ArcGIS for Desktop and the Spatial Analyst toolbox (ESRI, 2017). I added the remote sensing data to the presence-absence dataset by centering the GPS locations of observation points along each transect and then interpolated the information of each variable at each respective location using the Extract Values to Points tool in the Spatial Analyst extension. Furthermore, I included the remote sensing covariates in the geospatial dataset by clipping the extent of each raster using the boundaries of the protected area as a mask so as to only include data limited to the target area (ESRI, 2017).

### 3.1.2.1 Satellite Image Processing:

I used visual to near-infrared (NIR) multispectral data (8-band, 1.24m spatial resolution at nadir) to calculate Normalized Difference Index (NDI) ratios capable of modelling the first four covariates described above (Pettorelli et al., 2005; Wolf, 2010). NDI refers to a family of satellite indexes commonly used to derive the spatial distribution of an ecological or physical features of interest. NDIs are applied by exploiting the difference between the strongest and weakest spectral responses correlated to the presence of a specific feature. The most common example is the Normalized Difference Vegetation Index (NDVI), which derives an estimate of net primary productivity from the reflectance ratio between the RED and NIR spectral wavelengths, highlighting the fact that chlorophyll is absorbed by RED radiation while the mesophyll structure of a leaf reflects NIR radiation (Pettorelli et al, 2005; Deng et al., 2015). Based on the reflectance ratio of the bands, NDI values range from -1 to +1, where negative values correspond to an absence of the feature of interest (Pettorelli et al, 2005; Deng et al., 2015). In this study, I utilized four commonly used NDIs; these included the NDVI, NDWI (Normalized Difference Water Index), NDSI (Normalized Difference Soil Index), and the NDBuI (Normalized Difference Built-Up Index). A description of each specific index and its respective purpose is presented in Table 3.1. Since the accuracy of NDIs can be easily reduced by random sensor or atmospheric error, which can skew the reflectance values of the multispectral data; the satellite data were orthorectified and corrected for colour imbalance as well as atmospheric distortion by the data providers. Furthermore, I used “top of atmosphere” reflectance values for all calculations (Ingram & Dawson, 2006; Wegmann et al., 2016). All four NDIs were computed using the Raster Calculator tool in ArcGIS Desktop.
**TABLE 3.1** – Description of NDIs used in the project; formulas fitting the spectral resolution of WorldView-3 adapted from Wolf (2010).

<table>
<thead>
<tr>
<th>Index Ratio</th>
<th>Formula</th>
<th>Purpose</th>
<th>Background</th>
</tr>
</thead>
<tbody>
<tr>
<td>NDVI</td>
<td>$\sum \frac{(NIR2 - Red)}{(NIR2 + Red)}$</td>
<td>Used to identify the amount of aboveground primary productivity, to infer vegetation quality. Values close to 1 indicate high vegetation quality.</td>
<td>Pettorelli et al., 2005</td>
</tr>
<tr>
<td>NDWI</td>
<td>$\sum \frac{(Coastal - NIR2)}{(Coastal + NIR2)}$</td>
<td>Used to identify bodies of standing water as well as to calculate the vegetation water content. Values close to -1 indicate strong water content.</td>
<td>Li et al., 2013</td>
</tr>
<tr>
<td>NDSI</td>
<td>$\sum \frac{(Yellow - Green)}{(Yellow + Green)}$</td>
<td>Identify areas where soil is the dominant cover type, such as vegetation clearings, trails, dirt roads, etc. Values close to 1 indicated the presence of exposed soils.</td>
<td>Deng et al., 2015</td>
</tr>
<tr>
<td>NDBuI</td>
<td>$\sum \frac{(Coastal - Red Edge)}{(Coastal + Red Edge)}$</td>
<td>Used to identify areas with a sharp contrast in relation to its surrounding background, indicative of man-made features. Values close to 1 indicate the presence of human features.</td>
<td>Xu, 2007</td>
</tr>
</tbody>
</table>
Next, I calculated the four distance variables listed above -- distance to standing bodies of water, distance to human settlements, distance to secondary roads, and distance to forest trails -- using a pan-sharpened, true-colour-composite (TCC) of the Oronjia peninsula, with a spatial resolution of 0.30m at nadir, from which I could digitize all target features. TCC refers to multi-spectral image consisting of the combination of Red, Green, and Blue bands to define a scene with a coloration gamut similar to what can be observed by the human eyes. This type of multi-spectral composite is commonly used as the base layer of object digitization since features of interest are easily identifiable as long as the resolution and image quality are adequate (Wegmann et al., 2016). As indicated above, I utilized the pan-sharpening tool in ArcGIS desktop, using the ESRI method – which refers to a process by which a higher-resolution panchromatic image is used to sharpen the resolution of lower-resolution multi-spectral images – to increase the resolution of the base TTC so as to better identify the presence and shape of all features of interests. This process permitted me to define the presence of features like small trails, single houses, and the contour of farms, which were not visible at higher resolutions. Once all features had been digitized, I used the Euclidean Distance function in the Spatial Analyst toolbox (ESRI, 2017) to create distance rasters that convey the closeness of any of the indicated features from any point in the protected area.

3.1.2.2 Third Party Dataset Preparation:

Percentage of canopy cover estimates for the protected area were derived from raster datasets available in the Global Forest Change 2000 – 2014 database (Hansen et al., 2013). The original datasets used in our analysis included two 8-bit GeoTIFF files with a spatial resolution of 1 arc-second per pixel (~ 30m resolution at nadir). The first of the two datasets contained estimates of the percentage of tree canopy cover for the year 2000. Here, canopy cover was defined as the canopy closure for all vegetation taller than 5m in height. To reflect this, the raster was encoded so that each pixel represents a percentage of the output, in the range of 0 to 100 where 0 reflects complete openness or no canopy and 100 reflects full closure. The second dataset contained estimates of global forest cover loss between the years 2000 and 2014. Forest loss was defined as forest-stand areas where, during the 14-year interval, a change was observed from a forest to a non-forest state. As such, this dataset reflects the occurrence of habitat loss or clearings since the original 2000 estimate, but does
not communicate about other factors such as the thinning of canopy. To reflect this, the dataset was encoded so that each pixel represents an area of loss (1) or no loss (0).

\[
\text{Percentage of Canopy Cover 2014} = \text{condition} (\text{loss} == 0, \text{loss}, \text{PrcntlCover2000})
\]

**Formula 3.1** – SQL conditional statement used for the reclassification of ‘Percentage of Canopy Cover 2000 (PrcntlCover2000)’ dataset to reflect estimates of forest cover loss between the years 2000 and 2014 (loss).

To obtain the most up-to-date estimates of the percentage of canopy cover available from the Hansen et al (2013) dataset, I updated the percentage of canopy cover estimates from the year 2000 using the binary 14-year interval loss dataset. To accomplish this, I used the raster calculator tool to develop a conditional SQL (Structured Query Language) argument that would allow us to reclassify pixel clusters where loss (0) occurred during the 14-year interval in the percentage of canopy cover 2000 raster layer, as highlighted by the binary raster (Formula 2.1). Based on this SQL argument, then, the resulting dataset containing estimates of the percentage of canopy cover in the year 2014 displays all loss pixels identified by the binary dataset with a value of 0% canopy cover. While this method conveys a simplistic representation of how habitat loss and fragmentation affect the canopy structure of forests – for example, the canopy structured near newly cleared areas may lose density due to the higher exposure to strong winds – it is nevertheless useful to represent a baseline of the influence that this covariate can have on the habitat choice process of crowned lemurs.

### 3.2 Protocol for Data Analysis:

This section provides details of the analytical protocol employed to summarize and examine the various datasets utilized in this project: Section 3.2.1 lists a summary of all of the explanatory covariates selected for the study, as well as a short rationale for their inclusion. Section 3.2.2 details the statistical methods used to estimate the influence that each landscape covariate has on the on the presence of crowned lemurs observed during the transect survey. Section 3.2.3 lists the methods for the construction of our environmental niche model (ENM) used to project the distribution of crowned lemurs across the protected area based on our geospatial survey. Finally, section 3.2.4 lists the analytical framework used to summarize the results of our interviews with local stakeholders.
3.2.1 **Review of Chosen Explanatory covariates:**

As explained above, I measured a total of thirteen explanatory covariates to characterize the landscape conditions of the protected area at Oronjia Park. My selection of covariates included: (1) Elevation from sea level (m), (2) classification of habitat structure, (3) classification of the intensity of anthropogenic disturbance, (4) density of illumination at ground level (200,000 LUX range), (5) NDVI, (6) NWI, (7) NDSI, (8) NDBuI, (9) distance from standing bodies of water (km), (10) distance from edge of human settlements (km), (11) distance to secondary roads, (12) distance to forest trails, and (13) percentage of canopy cover. The thirteen variables listed here were selected because they describe some aspects of three broad conditions known to affect the distribution of crowned lemur and other *Eulemur* species. These three conditions include: the structure of the forest – described by covariates 2, 4, 6, and 13 (Wilson et al., 1989; Freed, 1996; Solomon, 2009; Sato et al., 2016); the topography of the site – described by covariates 1, 6, 7, and 9 (Johnson et al., 2011; Johnson et al., 2016); and the presence of anthropogenic influences – described by covariates 3, 8, 10, 11, and 12 (Solomon, 2009; Ament & Cumming, 2016; Kamilar & Tecot, 2016).

3.2.2 **Presence-Absence Models:**

Simple logistic regression models were developed to estimate the influence that spatial variation of habitat structure and anthropogenic disturbance across the protected area have on the observed presence of crowned lemur (Zuur et al., 2009; Quinn and Keough, 2012). Logistic regression, a non-linear model commonly recognised by its sigmoidal shape, is a type of Generalized Linear Model (GLM) used to explain the observed variation of response variables that are binary in nature, such as presence/absence data, based on independent predictors that can be continuously or categorically distributed. In simple logistic regression, the variation of response variables is explained by estimating the change in probability of an event occurring \( P = \pi_i \) – i.e., presence – or not occurring \( P = 1 - \pi_i \) – i.e., absence – based on the variation along a given independent predictor. To model the change in probability that produces either a presence or absence outcome, logistic regression fits the data along the binomial distribution, which describes the likelihood of an event occurring as defined by \( N \) independent trials with an equal probability of occurrence. Since the response variable and error terms along a binomial distribution are non-linear, regression estimates for logistic regression are fitted using maximum likelihood procedures instead of
the Ordinary Least Square procedures used in linear regression (Zuur et al., 2009; Quinn and Keough, 2012; Buckley et al., 2015).

Finally, to define the relationship between the dependent response variable and the independent predictor covariates, logistic regression uses a link function that maps the independent values of \( n \) to the presence/absence events. Commonly used link functions include the log-link, prob-link, and logit-link. Here, I use the logit-link since it provides the most flexible curve and the most commonly used function (Zuur et al., 2009). The logit-link works by modelling the log-odds \([\log (O_i)]\) of an event occurring along a linear function of the explanatory covariate (Zuur et al., 2009; Quinn and Keough, 2012; Buckley et al., 2015).

The entire logistic GLM can be defined as follows (Formula 2.2)

\[
\begin{align*}
\text{Binomial error distribution:} & \quad Y_i \sim B(1, \pi_i) \\
\text{Expected mean and variance of } Y_i: & \quad E(Y_i) = \pi_i \quad \text{AND} \quad \text{var}(Y_i) = \pi_i \times (1 - \pi_i) \\
\text{Logit-link function:} & \quad \pi_i = \frac{e^{\beta_0 + \beta_1}}{1 + e^{\beta_0 + \beta_1}} 
\end{align*}
\]

**Formula 3.2** – Logistic GLM with a binomial density function and logit-link function. Note: \( \beta_0 \) and \( \beta_1 \) refer to the intersect and regression estimates necessary to fit the function.

As explained in Section 3.1.1.2, detection of crowned lemur presence was hindered by the small size and grouped distribution of the population. Because of this, the direct proportion of presence and absence records available in the dataset presented certain problematic violation to the assumptions of the logistic GLM highlighted above. This was due to the small pool of occurrence events and the uneven distribution between the two detection modes. To take consideration of this issue, the definition of the dependent binary variable was modified to focus on the comparison between transects where detection occurred and did not occur, rather on the comparison of the observations within the transect. While this procedure artificially inflates the records of presence in the dataset, creating an artificial distribution of positive occurrences, it prevents any possible abuse of results by limiting the review of the models to discuss the nature of the relationships they project to the specific context of Oronjia, without making any sort of broad generalization or projection. Based on this, then, to examine the influence that my chosen set of landscape covariates has on the occurrence of crowned lemurs across the protected area, I test the null hypothesis \((H_0)\) that there is no significant difference in the habitat structure and patterns of anthropogenic
disturbance observed along sections of lemur presence and absence. If landscape context influences the differential use of the forest fragment exhibited by the local crowned lemur population, then I predict that the analysis will show significant contextual differences between the sample areas.

I used the R Language and Environment for Statistical Computing v3.3.3, with the nlme package (Pinheiro et al., 2017; R Core Team, 2017) to build all the simple logistic regression models. In total, I model the influence of twelve of the thirteen landscape covariates selected for this study. As a result of the ~30 m spatial resolution of the Percent of Canopy Cover variable, data from this dataset could not be properly included with the transect observation due to the ~25 m observation interval. Inclusion would have resulted in different observations sharing the same pixel value even if on ground conditions were not similar. To ensure that the accuracy of the models was not inflated by spatial autocorrelation, I tested the relationship between my presence dataset and each variable using Global Moran’s I. No autocorrelation was observed with any of the candidate variables. To assess the predictive power of each simple GLM, we compared the difference between the residual and null deviance reported by each model (Note: null deviance is a measure of goodness-of-fit that indicates how well the response variable is predicted by a model that only includes the intercept, it is used to assess the gain in predictive power obtained by including an independent covariate). To assess the degree of variation occurring between presence and absence transects, I plotted the distribution of each independent landscape covariate using boxplots (See Appendix 5). Furthermore, I ran diagnostic plots to visually assess all models for possible issues of outlier effect, perfect separation, or appropriateness of the chosen logit function (Buckley et al., 2015). Finally, I plotted each model using graphical scripts from the ggplo2 package (Wickham, 2009).

3.2.3 Environmental Niche Model:

I developed an environmental niche model (ENMs) using MaxEnt v3.3.3k (Phillips et al., 2006) to estimate the influence that habitat structure and patterns of anthropogenic disturbance (See Appendix 6 for maps displaying each of the covariates used in these models) have on the probabilistic distribution of crowned lemurs across the protected area. MaxEnt is a type of species distribution modelling software (SDMs) commonly used to estimate the relationship between species and their environment (Phillips et al., 2006;
Peacock, 2011). It uses the principles of machine learning, a form of artificial intelligence algorithm, to make predictions on a species’ distribution and probability of occurrence from presence-only records and associated landscape covariates (Phillips et al., 2006; Thorn et al., 2009; Elith et al., 2011; Peacock, 2011; Merow et al., 2013; Johnson et al., 2016; Kamilar & Tecot, 2016). This is done by using the principles of maximum entropy – i.e., measure of dispersedness over geographic space – to define the probability distribution of a species that exhibits the highest possible degree of dispersal and/or uniformity. This ideal or ‘raw’ distribution is then constrained by the mean values of independent landscape covariates used as the model’s explanatory background, along the points where the species’ presence is known. The resulting output is the likely distribution of a species based on the habitat subsection where its behavioural and physiological needs can be met (Elith et al., 2011; Peacock, 2011; Johnson et al., 2016). Although MaxEnt relies on incomplete, presence-only data, which commonly presents a number of limitations, past studies have supported the accuracy of this SDM method, by performing as well or better than other, SDM models (Elith et al., 2011; Kamilar & Tecot, 2016).

MaxEnt is well suited to estimate the probabilistic distribution of the crowned lemur population at Oronjia because, unlike other SDMs, it performs relatively well with very small samples. This is a result of the regularization procedure present in the model, which compensates for overfitting by smoothing the predicted distribution at the cost of model fit and complexity. Indeed, the number of presence records can be as low as five or more records. However, it is recommended that at least 30 observations are used to generate an estimate of occurrence that cannot be easily compromised by sampling bias and outlier observations (Phillips et al., 2006; Baldwin, 2009; Peacock, 2011; Merow et al., 2013). Furthermore, regularization presents MaxEnt with some degree of robustness against autocorrelation – as long as any form of autocorrelation is not nested on a sampling procedure introducing observer bias. This means that variable reduction procedures are not necessary when various independent covariates are being considered (Elith et al., 2011; Peacock, 2011; Merow et al., 2013).

I trained and tested the MaxEnt model using the bootstrapping replication procedure recommended when fewer than 25 occurrence observations are used (Phillips et al., 2006; Elith et al., 2011; Peacock, 2011). Bootstrapping works by replicating the training and testing procedure on the model $n$ times, where $n$ refers to the number of available occurrence
records. During each replicate, then, the model is trained on \( n-1 \) points and tested on the remaining point. Based on this procedure, the probabilistic distribution for the species of interest is generated by averaging the output of each replication run. Since my dataset included a total of 12 observation records, I set the bootstrapping procedure for that number of replicates (Merow et al., 2013). The result of this training and testing process is the continuous logistic output that estimates the relative probability of a species’ occurrence at any point given the background environmental conditions. The logistic output expresses the habitat suitability potential of any location along the target zone by identifying it with a value between 1 and 0, where values close to zero indicate a lack of suitability, while values closer to 1 indicate that the location meets conditions that favours the species’ occurrence. It is important to note, however, that since MaxEnt uses presence-only data, this is not a true estimation of a logistic probability of occurrence. Instead, it is a post-transformation of the MaxEnt ‘raw’ occurrence probability estimate based on areas that fail to show the estimated suitability characteristics of the species (Elith et al., 2011). As long as the independent predictors are free of detrimental observation bias, and reflect realistic landscape conditions, the logistic output is expected to reflect a relatively accurate picture of the probabilistic distribution for the target species.

To predict the influence that landscape conditions have on the habitat use patterns of crowned lemurs at Oronjia, I developed two complementary ENMs. The first model was constructed using the thirteen landscape covariates listed in Section 3.2.1. Since MaxEnt requires that all background layers share the same spatial resolution, I downscaled the 1.24 m native resolution of the 12 covariates obtained from the field-observations and WorldView-3 satellite data to a spatial resolution of 15 m. Similarly, I upscaled the 30 m resolution of the canopy cover (\%) variable to 15 m (Phillips et al., 2006; Johnson et al., 2016). I chose this resolution because the upscaling process of the canopy cover data would not necessitate a comprehensive resampling process that could affect the accuracy of the data. The second model was constructed as a high-resolution version of the first model, using the first 12 variables listed in section 3.2.1, which exhibit a native 1.24 m resolution – Note: percentage of canopy cover was not included because upscaling its resolution from 30 m to 1.24 m severely affected the quality of the patterns present in the original dataset. I developed the high-resolution model because the high-level of detail present in the background datasets presented the opportunity to better visualize the influence that small-patterns defining the
landscape structure of the protected area have on the probability distribution of crowned lemur occurrence.

I identified the distribution of habitat suitability hotspots across the protected area by defining a threshold for the selection of presence/absence locations along the logistic probability distribution of the MaxEnt output. Here I used the 10-percentile logistic threshold (10PLT), which uses up to 90% of occurrence records and background information to define the occurrence suitable habitat sections. The 10PLT is particularly useful for datasets likely to have some degree of error (such as the one being used here) because it assumes a reasonable reflection of a species’ occurrence, by balancing the unequal degrees of underrepresentation in certain areas of the target zone with the overrepresentation from other target zones (Phillips et al., 2006; Peacock, 2011; Kamilar & Tecot, 2016). The 10PLT was applied to both the complete and high-resolution models, from which I developed presence/absence maps that highlight priority zones of high probability of crowned lemur occurrence. The predicted distribution for each MaxEnt model was visually validated by referencing how well it matches to accounts of crowned lemur distribution given by conservation agents from the MBG - Oronjia team and previous site reports.

I used three different approaches to assess the influence that habitat structure and patterns of anthropogenic disturbance have on the relative probability of crowned lemur occurrence across the protected area. This first approach involves the probabilistic distribution output from MaxEnt, to explore partial response curves that show how the logistic prediction of the multivariate ENMs change as a product of the observed variation in each independent landscape predictor, while keeping all other covariates at their average sample value. In other words, these curves show the marginal effect that changing the value of exactly one variable has on the overall model. For the second approach, I explored single-variable response curves – similar to our simple logistic models – that represent a MaxEnt model created using one landscape covariate. These curves help us understand the predicted suitability estimate depends on the selected variable, as well as the dependency induced by the interaction between the selected model and other independent covariates (Phillips et al., 2006; Merow et al., 2013).

The third approach is an analysis of the relative importance of each predictor in relation to the overall accuracy of the MaxEnt model. Here I used the jackknife test of regularized training gain to explore the predictive and permutational importance for each of
the thirteen landscape covariates. The estimate of regularized gain is a measure that reflects
the influence that a single variable has on the computational accuracy of the complete model.
The jackknife statistic assesses variable importance by taking into consideration the
following: (1) how much useful information each variable provides to the discriminative
power of the full model based on the gain a single variable shows when it is used in isolation;
and (2) how much the overall predictive power of the model decreases when the variable is
removed from the model (Phillips et al., 2006; Thorn et al., 2009; Peacock, 2011).

I judged model performance using receiver-operating characteristic (ROC) curves
from data predicted by the average of the replicate runs, and used the area under the curve
(AUC) value to compare model performance. The ROC curves, plot locations of predicted
presence (sensitivity) and absences (1 - specificity) to report model accuracy. The AUC,
then, is a test-statistic that measures the ability of a model to discriminate between areas
where the occurrence of a species is confirmed and where it was not confirmed. As such,
AUC permits confirmation of the model’s ability to recognise areas of importance (See
Figures 1 & 2 in Appendix 7 for ROC plots of our MaxEnt models). AUC values range from
0 to 1, where 1 suggests perfect discrimination, 0.5 suggest discrimination is not better than
random, and < 0.5 suggests discrimination worse than random. Here I use the interpretation
by Hosmer and Lemeshow (2000; also, used by Kamilar & Tecot, 2016; Johnson et al. 2016),
where an AUC value of 0.7 – 0.8 is acceptable, 0.8 – 0.9 is excellent, and > 0.9 is
exceptional.

3.2.4 Summary and Analysis of Interview Data:

Responses of Sections 1 and 2 were tabulated and plotted using graphical scripts from
ggplot2 package in R (Wickham, 2009; R Core Team, 2017) to: (1) summarize the
sociodemographic characteristics of survey participants; and (2) explore how livelihood
dynamics for local stakeholders have changed since the formal start of park operation and
conservation activities by MBG. Responses to open-ended short question in sections 3 and 4
were used as a point of context to explore community-based opportunities for conservation
action that may help sustain present habitat use patterns of crowned lemurs along Oronjia
Forest – as they were highlighted by simple logistic GLMs and the probabilistic distribution
from MaxEnt ENMs, as well as possible socio-economic issue, that if not properly addressed,
may affect the efficacy of conservation measures.
Chapter 4

4 RESULTS:

This chapter presents explanatory patterns of crowned lemur distribution highlighted by the presence/absence and environmental-niche models. It also reviews the influence that community-based conservation operations at Oronjia have had on the livelihood dynamics of local stakeholders. Section 4.1 outlines the distribution and group-size counts for crowned lemur occurrence records obtained during the field season. Section 4.2 reviews results of the simple logistic GLMs, to determine how well the degree of spatial-variation in each of the landscape conditions included in this study explains the observed occurrence patterns of crowned lemurs across the study’s sample strips. Section 4.3 reviews the probability distribution outputs of the ENMs, to examine the influence that variation in the landscape structure and resource availability across the protected area have on the habitat choices of crowned lemurs. Section 4.4 presents a summary of the socio-demographic patterns of interview participants, as well as a review of temporal shifts in their livelihood dynamics since the start of park operations at Oronjia.

4.1 Occurrence Patterns of Crowned lemurs:

Occurrence patterns of crowned lemur presence across the protected area of Oronjia Park were visually assessed using a Voronoi map. Voronoi maps are an exploratory method of spatial data analysis used to denote an area or cell containing every location within a target zone closest to an observation record, as well as its immediate neighbours. Voronoi Maps have a number of functions, including the ability to calculate local statistics such as local cluster analysis (used here). This type of statistic identifies each cell into one category of a five-class interval, and compares if the class identity of each cell is different from its neighbours. Furthermore, Voronoi maps help to identify the weight of observation that represents every relative subsection of a study area. The smaller each cell is, the better that specific subsection is represented by the higher number of observation points available.

The Voronoi map shows that the distribution of crowned lemur is highly clustered on the southern portion of the site, across the forest sections surrounding Mamellon Vert and Baie de Sakalava (Figure 4.1). Comparatively, occurrence records in the central and northern
portions of the site, corresponding to the locations of Cote 44 and the Grotte, were observed at a much lower proportion (Figure 4.1). This pattern suggests that crowned lemurs at Oronjia do not favour the use of every forest section across the protected area equally, and may instead seek out specific habitat sections across the total extent of the forest fragment that meet specific background requirements (See Section 1.2; see also, for example, Chapman, 1987; Lammertink et al., 2003). Based on this, then, the southern extent of the protected area may represent a type of ‘ecological island’ present within the total extent of the forest fragment, with certain characteristics and resources that make it readily different from neighbouring habitat sections.

**FIGURE 4.1** – Voronoi map of crowned lemur occurrence and group density records across the protected area of Oronjia Pak.

The density counts for each of the observation records help to better define the uneven distribution that the local crowned lemur population seems to exhibit. Similar to the occurrence locations, the density counts highlight the importance of the southern section.
given the constant occurrence of groups consisting of 3 to 15 individuals. Indeed, the two largest group records were observed foraging along the higher canopy levels of the forest surrounding the south-eastern slope of Mamellon Vert (Figure 4.1; Table 4.1). The first and largest group record (CLP06) consisted of 15 individuals in total, made up by 6 adult females, 5 adult males, and 4 unidentified individuals. Similarly, the second group record (CLP08) consisted of 10 individuals, made up by 4 adult females and 6 adult males.

Interestingly, the third largest group record (CLP11) was observed on the northern section of the site, along the small cliff that marks the entrance of the Grotte (Table 4.1). This group included 6 unidentified individuals. It is important to note, however, that even though only one occurrence record was obtained for the northern section of the site, presence of the population in this area was not uncommon, just difficult to confirm. Interviews with local residents that live near the entrance of the Grotte confirmed that at least one group would frequent the area during the late night and early morning. Nevertheless, since this study was limited to daytime observation periods, direct confirmation of the group was constantly missed. Based on the constant presence of a moderately-sized group in this location, then, it is likely that similar to the southern section of the protected area, the northern section may also represent an ecological island with the necessary conditions to promote the occurrence of the species.

**TABLE 4.1 – Summary of occurrence records locations and observation of group structure.**

<table>
<thead>
<tr>
<th>Occurrence ID</th>
<th>Group Size</th>
<th>Sex Ratio</th>
<th>Relative Location*</th>
</tr>
</thead>
<tbody>
<tr>
<td>CLP01</td>
<td>2</td>
<td>1 Female / 1 Male / 0 Unidentified</td>
<td>South-Central Sectors</td>
</tr>
<tr>
<td>CLP02</td>
<td>2</td>
<td>1 Female / 1 Male / 0 Unidentified</td>
<td>Southern Sector</td>
</tr>
<tr>
<td>CLP03</td>
<td>3</td>
<td>2 Female / 1 Male / 0 Unidentified</td>
<td>Southern Sector</td>
</tr>
<tr>
<td>CLP04</td>
<td>2</td>
<td>2 Female / 0 Male / 0 Unidentified</td>
<td>Southern Sector</td>
</tr>
<tr>
<td>CLP05</td>
<td>2</td>
<td>1 Female / 1 Male / 0 Unidentified</td>
<td>Southern Sector</td>
</tr>
<tr>
<td>CLP06</td>
<td>15</td>
<td>6 Female / 5 Male / 4 Unidentified</td>
<td>Southern Sector</td>
</tr>
<tr>
<td>CLP07</td>
<td>5</td>
<td>2 Female / 3 Male / 0 Unidentified</td>
<td>Southern Sector</td>
</tr>
<tr>
<td>CLP08</td>
<td>10</td>
<td>4 Female / 6 Male / 0 Unidentified</td>
<td>Southern Sector</td>
</tr>
<tr>
<td>CLP09</td>
<td>3</td>
<td>2 Female / 1 Male / 0 Unidentified</td>
<td>South-Central Sectors</td>
</tr>
<tr>
<td>CLP10</td>
<td>1</td>
<td>1 Female / 0 Male / 0 Unidentified</td>
<td>Central Sector</td>
</tr>
<tr>
<td>CLP11</td>
<td>6</td>
<td>0 Female / 0 Male / 6 Unidentified</td>
<td>Northern Sector</td>
</tr>
<tr>
<td>CLP12</td>
<td>3</td>
<td>1 Female / 2 Male / 0 Unidentified</td>
<td>Southern Sector</td>
</tr>
</tbody>
</table>

* Coordinates of occurrence are omitted to anonymize the dataset. Instead, only the relative location of the population as indicated by Voronoi map is included here.
4.1.1 Inferences of Population Structure:

While the quality of the available occurrence dataset prevents an accurate modelling of the size and demographic structure of the crowned lemur population (See Buckland et al., 2010 for more information), I present the maximum population count – CLP06: 15 individuals – obtained from a single occurrence record, to present a cautious inference of the population size for the Oronjia population. This is based on the fact that whenever a group of 5+ individuals was observed, no other occurrences would be observed for the given day. Furthermore, the only instance during which two different occurrence records were obtained in the same day included small group counts with 3 and 2 individuals (CLP03 and CLP02 respectively). Based on this, then, I was only able to differentiate between the 15 individuals observed in the south of the protected area, and it is not known with any certainty whether or not the other occurrence records represent new individuals or a reoccurrence of the same individual with a different group organization.

The observed range of variation of group sizes in the occurrence dataset is also of interest since it reflects a pattern of flexible group-membership structure that shows elements of fission-fusion dynamics. Along certain locations, occurrence records indicate small single-male, single-female groups, that sometimes include a third individual of either sex. Similarly, I also observed groups made-up exclusively of adult females where no male was identified. On other instances, however, I observed multi-male, multi-female groups, with a group membership of 5 to 15 individuals, traveling and foraging together. Since it was not possible to differentiate individuals observed between different occurrence records, it is possible that that the variation seen here indicates the presence of one main, large group, whose individuals transition into subgroups during specific circumstances. It is noteworthy that occurrence records with 6+ group members were only located in the extreme north and south of the site, whereas group membership in occurrence records was observed to decline towards the centre section of the protected area.

4.2 Review of simple, presence-absence GLMs:

The simple logistic GLM analysis shows that 10 of the 12 background landscape conditions measured along the presence and absence transects exhibit a significant range of variation that explain some of the observed bias of crowned lemur occurrence across the protected area. These included: elevation from sea level (m), classification of habitat
structure, intensity of disturbance, luminance density (LUX), index of net primary productivity (NDVI), index of vegetation moisture (NDWI), distance from standing bodies of water (km), distance from edge of settlement (km), distance from secondary roads (km), and distance from trails (km). In contrast, the logistic models failed to show any significant level influence from the indexes of habitat clearing distribution (NDSI) and human-made features (NDBuI). Below, I review the outputs of each of the models showing a significant degree of influence, and review their accuracy.

**FIGURE 4.2 – Logistic regression displaying the relationship between elevation (m) and crowned lemur occurrence between sample transects.** Observations are classified by transect of origin to display the range of background variation measured within each specific transect. Furthermore, I plotted the variation of the residual deviance by placing error bands along the regression line.

My first model demonstrates that the degree of variation in elevation (m) present between sample habitat sections has a significant negative influence on the occurrence of crowned lemur (Figure 4.2). According to the model, for every 1m increase in elevation observed along each of the sample transects, the odds ratio of occurrence decreases by a
factor of ~ 6% (Odds Ratio = 0.9410; 95% CI = 0.9267 – 0.9542; Std. Error: 0.00744; z-value: -8.18; p-value = 2.9e-16). This pattern suggests that the likelihood of crowned lemur occurrence is higher along habitat sections present in the lower elevation ranges of the protected area, between ~15 to 50 m above sea level. In contrast, observation along higher elevations is much more unlikely. While the present model supports the importance of this covariate for the habitat choice process of crowned lemurs at Oronjia, it is important to note that the model is only able to explain a moderate portion of the observed variation in crowned lemur occurrence (Residual deviance = 327.55 on 304 df; Null deviance = 424.15 on 305 df).

**FIGURE 4.3** -- Logistic regression displaying the relationship between habitat classification and crowned lemur occurrence between sample transects. To plot the distribution of observation points, I used a jitter function to introduce some aesthetic random variance to their horizontal position that would allow us to observe them.

Similar to the first model, variation in the classification of habitat structure between sample habitat sections exhibits a significant negative influence on the likelihood of crowned
lemur occurrence (Figure 4.3). Based on the regression estimate, increasing the classification of the habitat section by one ordinal unit reduces the odds of occurrence by a factor of 59% (Odds Ratio = 0.4137; 95% CI = 0.2692 – 0.6253; Std. Error: 0.2146; z-value: -4.112; p-value = 3.92e-05; Residual deviance = 406.03 on 304 df; Null deviance = 424.15 on 305 df). Based on this, it appears that habitat sections where crowned lemur occurrence was confirmed are more likely to contain mixed forest and highly disturbed, wooded grassland habitat. However, it should be noted that relatively intact forests patches were still common along these tracks. This pattern suggests that the habitat segments occupied by crowned lemurs display a higher range of structural variation than those where no occurrence could be confirmed.

**FIGURE 4.4** – Logistic regression displaying the relationship between the intensity of anthropogenic disturbance and crowned lemur occurrence between sample transects.

Variation in the intensity of anthropogenic disturbance shows a significant positive influence on the occurrence of crowned lemurs between sample sections (Figure 4.4). As shown by the odds ratio estimate, sample sections where crowned lemur presence was
confirmed are 80% more likely to exhibit higher levels of disturbance intensity than the habitat segments where no presence could be confirmed (Odds Ratio = 1.8037; 95% CI = 1.4103 – 2.3339; Std. Error: 0.1282; z-value: 4.601; p-value = 4.20e-06; Residual deviance = 401.08 on 304 df; Null deviance = 424.15 on 305 df). Nevertheless, both presence and absence sections reflect a mosaic of low to high intensities of disturbance, which suggest that the degree of disturbance is highly heterogeneous to the point where lemurs are not able to completely avoid habitat sections exhibiting strong levels of disturbance.

![Logistic regression displaying the relationship between luminance density (LUX) and crowned lemur occurrence between sample transects.](image)

**FIGURE 4.5** – Logistic regression displaying the relationship between luminance density (LUX) and crowned lemur occurrence between sample transects.

The luminance density (LUX) model reflects a small degree of significant negative influence on the occurrence of crowned lemurs between the sample sections (Figure 4.5). According to the model, the odds of occurrence slowly decrease by a factor of ~0.16% for every unit increase in the density of luminance at the forest floor level (Odds ratio = 0.9984; 95% CI = 0.9975 – 0.9993; Std. Error: 0.0004; z-value: -3.452; p-value = 0.000557; Residual deviance = 411.68 on 304 df; Null deviance = 424.15 on 305 df). This suggests that canopy
structure in areas of crowned lemur occurrence provides a greater deal of coverage, and that the overall structure of the vegetation was much taller in comparison to transects where no occurrence could be confirmed. The results of this model are interesting when compared to the habitat classification model, which suggests that occupied habitat sections exhibited a higher degree of poor quality conditions.

**FIGURE 4.6** – Logistic regression displaying the relationship between net primary productivity (NDVI) and crowned lemur occurrence between sample transects.

The observed variation of primary productivity (NDVI) between sample sections exhibits a significant positive influence on the occurrence of crowned lemurs across the protected area (Figure 4.6). Based on this model, it appears that the odds of crowned lemur occurrence increase by a factor of 7.279% after observing a 0.1 growth on the value of NDVI along each habitat segment (Odds Ratio = 72.7917; 95% CI = 14.6607 – 405.7330; Std. Error: 0.8447, z-value: 5.076, p-value = 3.86e^-07). Such a large estimate, however, is a sign of issues with the model, relating to its ability to properly converge on a logit estimate. Indeed, the width of the 95% confidence interval, paired with the uneven distribution of deviance
residuals (Figure 4.6), shows that the model is overestimating the strength of the relationship between NDVI and crowned lemur occurrence. Based on this, then, I am unable to elaborate on the implications the model output present with regards to the relationship between crowned lemur occurrence and vegetation quality.

**FIGURE 4.7** – Logistic regression displaying the relationship between net vegetation moisture (NDWI) and crowned lemur occurrence between sample transects.

The vegetation moisture model shows that variation of NDWI has a significant negative influence on the occurrence of crowned lemurs between sample habitat sections (Figure 4.7). According to the odds ratio estimate, a 0.1 increase on the value of NDWI sharply reduces the likelihood of crowned lemur occurrence along confirmed segments by a factor of 99.85% (Odds ratio = 0.0015; 95% CI = 5.6845e-05 – 0.0336; Std. Error: 1.624, z-value: -4.009, p-value = 6.1e-05; Residual deviance = 406.84 on 304 df; Null deviance = 424.15 on 305 df). This suggests that the availability of moisture content across the protected area has a strong influence on the confirmed occurrence of crowned lemurs. This pattern makes sense when the predominant dryness of vegetation patterns and the small availability
of water resources across the protected area are considered (For reference, see: Figures 2.3 B & C; Figures 2.4 A & B; Appendix 6 – Figure A6-9). Lemurs, of course, would be attracted to stay in close proximity to areas of higher moisture to sustain their physiological needs. Furthermore, the results of this model are interesting when we compare them to the output of the elevation model, which shows that lemur occurrence is more likely at lower elevations; since higher moisture content can be accumulated in these areas by a product of gravity influencing the flow of water.

**FIGURE 4.8** – Logistic regression displaying the relationship between the distance (km) from the edge of water bodies and crowned lemur occurrence between sample transects.

Variation of the distance (km) from edges of water bodies between each sample segment exhibits a significant negative influence on the likelihood of crowned lemur occurrence (Figure 4.8). Based on the regression estimate, for every 1 km increase in the separation between a location and the edge of a water body, the likelihood of lemur occurrence is slightly reduced by a factor of ~ 0.11% (Odds ratio = 0.9989; 95% CI = 0.9986
Similar to the NDW model, the water distance model suggests that crowned lemur occurrence is related to the proximity of water resources across the protected area. Based on this, then, it is clear that the availability of water resources and moisture may act as factors that strongly influence the distribution of crowned lemurs within the Oronjia fragment.

**FIGURE 4.9** – Logistic regression displaying the relationship between the distance (km) from the edge of human settlements and crowned lemur occurrence between sample transects.

The next model demonstrates that variation of the distance (km) from edges of human settlements between sample segments has a significant negative influence on the occurrence of crowned lemurs within the protected area (Figure 4.9). As the odds ratio estimate shows, for every 1 km increase in the distance from the edge of human settlements, the likelihood of crowned lemur occurrence along sample segments exhibits a minor decline by a factor of ~0.18% (Odds ratio = 0.9982; 95% CI = 0.9977 – 0.9987; Std. Error: 0.0003; z-value: -7.046;
The settlement distance model suggests that the likelihood of crowned lemur occurrence is higher near the edge of the villages and farms that surround the protected area Oronjia park. Interestingly, these results support the earlier output from the anthropogenic intensity model, showing that crowned lemur presence at Oronjia seems to favour anthropogenically dominated landscapes. The results of these two models, however, seem to directly contradict the negative responses that crowned lemur groups displayed upon encounter with the research group. These involved the individuals who first noticed our presence emitting alarm calls to warn other group members, followed by a flight response to escape the area. As such, when discussing the implications of these models (see chapter 5), it is necessary to more carefully consider what these two models tell us about the relationship between crowned lemur presence and anthropogenic land-use patterns, by more closely considering the social-ecological context of Oronjia.

**FIGURE 4.10** – Logistic regression displaying the relationship between the distance (km) from secondary roads and crowned lemur occurrence between sample transects.
The distance (km) from secondary roads model reflects a small degree of significant positive influence on the occurrence of crowned lemurs between sample sections (Figure 4.10). According to the model, the odds of lemur occurrence between sample segments are reduced by a factor of ~ 0.29% for every 1 km increase in their distance from secondary roads (Odds ratio = 1.0029; 95% CI = 1.0014 – 1.0046; Std. Error: 0.0008; z-value: 3.688; p-value = 0.0001; Residual deviance = 409.82 on 304 df; Null deviance = 424.15 on 305 df). The output of this model suggests that the likelihood of crowned lemur presence within the protected area of Oronjia is negatively affected by the location of the secondary roads that cut through it. Based on this, it is possible that roads can act as hurdles to the distribution of the species, if not carefully managed.

**FIGURE 4.11** – Logistic regression displaying the relationship between the distance (km) from walking trails and crowned lemur occurrence between sample transects.

The final model demonstrates that the variation of distance (km) from walking trails between habitat sections has a significant positive influence on the occurrence of crowned lemurs (Figure 4.11). According to the odds ratio estimate of this model, the odds of crowned
lemur occurrence between sample segments are reduced by a factor of ~ 0.31% for every 1 km increase in their distance from walking trails (Odds ratio = 1.0031; 95% CI = 1.0023 – 1.0040; Std. Error: 0.0004; z-value: 7.031; p-value = 2.05e^{-12}; Residual deviance = 362.28 on 304 df; Null deviance = 424.15 on 305 df). Similar to the distance from secondary roads model, the present model shows that the occurrence of the species is negatively affected by the presence of walking trails within the protected area.

With the exception of the NDVI GLM, none of the models seem to exhibit a problematic degree of bias that could skew their predictive power. The relatively even distribution of residuals observed in the elevation (m), distance (km) to water bodies, distance (km) to settlements, and distance (km) to walking trails GLMs show that the four covariates explain a significant amount of the observed variation in crowned lemur occurrence. This suggests that these four variables may have an important influence on the realisation of crowned lemur distribution patterns, possibly limiting their occurrence in areas where these resources and conditions are expressed in poor quality. Nevertheless, further work is necessary to properly explain how these habitat mechanisms control their behavioural processes. With regards to the remaining covariates, while the residual distribution of the habitat classification, disturbance intensity, luminance (LUX), NDWI, and distance (km) to secondary roads GLMs exhibit some small degree of unevenness, the absence of problematic outliers and the low standard error report for the regression estimate means that is in not necessary to call these results into question.

On a final note, it is important to consider that while the simple GLM analysis shows that most of the chosen landscape covariates are correlated in some form with the occurrence of crowned lemur, each of these models is only able to explain a small to moderate amount of the total residual variation. This means that no single resource or condition included here has a dominant form of influence upon the overall distribution process of crowned lemur, but most likely it is the interaction of these various covariates that has the most significant effect. This is reflected by the parallel patterns that the various models showed, complementing each other to better illustrate the social-ecological context of the output. In this regard, then, the MaxEnt ENMs, which are capable of modelling the interactions of the various conditions and resources included in this study to define the multidimensional niche expression of the species, will help to better define the reasons for the differential habitat use that the local crowned lemur population exhibits.
4.3 **Review of ENMs Probability Distribution Patterns:**

The low- and high-resolution MaxEnt models showed strong performances on the prediction of crowned lemur distribution across the protected area (Appendix 6). The low-resolution model produced a mean AUC value of 0.934 (SD = 0.025), while the high-resolution model produced a mean value of 0.950 (SD = 0.033). The AUC values suggest that the two models display strong to outstanding discrimination accuracy. This was supported by a visual inspection of the ENM continuous logistic outputs, to ensure that habitat sections displaying a high probability of occurrence aligned with the known hotspots of occurrence reported by members of the MBG – Oronjia team.

4.3.1 **Probability Distribution of Crowned Lemur Occurrence:**
FIGURE 4.12 – Point-wise mean probability distribution of crowned lemur occurrence across the protected area of Oronjia Park for the (A) low- and (B) high-resolution ENMs.

Continuous logistic outputs of the low- and high-resolution MaxEnt models are presented in Figures 4.12 – A & B. These outputs highlight the point-wise mean probability distribution of crowned lemur occurrence across the protected area, based on how the distribution of background landscape conditions compares to the habitat characteristics at points of occurrence. According to the low-res model, there appear to be two definable habitat sections with a high probability of lemur occurrence. The first section extends from the southern end of Cote 44 to the southernmost edge of the protected area in the vicinity of Mamelon Vert and Baie de Sakalava. The second section extends from the northern portion of Cote 44 to northernmost edge of the site, near the Grotte and Baie des Dunes.

Similar to the low-res model, the high-res ENM highlights the importance of the southern- and northern-most habitat extents of the protected area for the probability of lemur occurrence. More importantly, however, the high-res ENM demonstrates the influence that certain structural components of the Oronjia landscape have on the suitability of specific
locations and the variation of the probability of lemur occurrence throughout the site. For example, by comparing the distribution of background covariates to the continuous logistic output along the southern distribution extent, it becomes apparent that the proximity to water bodies, secondary roads, and trails, in addition to the variation in elevation and the quality of the vegetation coverage, affect the continuity of the MaxEnt logistic prediction (Appendix 6 – Figures A6-1, A6-5, A6-9, A6-12, & A6-13).
Figure 4.13 – Predicated extent of habitat sections suitable for crowned lemur occurrence. Classification of suitable extent done using the 10-percentile logistic threshold (10PLT) for the (A) low- and (B) high-resolution ENMs.

In contrast to the northern- and southern-most habitat extents, the central block of the protected area exhibits a low probability of lemur occurrence. Indeed, the habitat suitability predictions using the 10PLT show that no location within this area exhibits the necessary background conditions to support the niche expressions of crowned lemurs (Figure 4.13 – A & B). Initial consideration of these results could be considered problematic in terms of the potential viability of the crowned lemur population at Oronjia on a day-to-day basis, much less on a long-term basis, as less than 50% of the total protected area is capable of presenting the necessary resources and conditions that influence the presence of the population and support their behavioural and physiological necessities. Nevertheless, given the small size of the site, as well as the relative, though disturbed, continuity of the canopy structure (Appendix 6 – Figure A6-13), it is important to consider the importance that habitat sections with a low probability of occurrence can have for the ecology of the species during specific
circumstance. As Figures 4.12 – A & B show, most locations along the central section of the protected area exhibit a lower probability of crowned lemur occurrence that results from the arrangement of background conditions in this section of the site. Depending on the individual set of conditions available in these locations, they could be beneficial to individuals of the species on an opportunistic basis. Based on the logistic output of the MaxEnt ENMs, then, it is possible to conclude that if the unique arrangement of characteristics that presently structure the southern- and northern-most habitat sections of the protected area were to erode, the population would likely disappear soon after, moving to other fragments across the Ramena complex.

4.3.2 Influence of Background Covariates on Probability Distribution Output:

Partial response curves were used to examine the influence that the interactions of the various conditions and resources included in this study have on the probability distribution of crowned lemur occurrence across the protected area – Note: only results from the low-res NME are presented in this and the following two sections, since there was no key difference between the outputs of the two models. Based on the slope of the partial response curves, variation in the distribution of vegetation quality (NDVI), vegetation moisture content (NDWI), proximity to the edge of water bodies, human settlements, and walking trails, as well as the percentage of canopy cover, appear to have a strong to moderate influence on the predicted probability distribution for the species (Figure 4.14).

Interestingly, similar to the logistic GLMs, the low-res model seems to suggest that the local population of crowned lemurs favour the habitat sections in close proximity to water bodies and the edges of human settlements. The importance that proximity to water bodies has on crowned lemur occurrence is supported by the NDWI and NDVI plots, which suggests that the species is more commonly found along habitat sections with a high moisture content and vegetation quality. The significance of this parallel relationship relies on the fact that the distribution of these two conditions (NDVI and NDWI) rely on the general availability of water to develop. Finally, the positive influence of canopy cover shows that the probability of lemur occurrence is higher along habitat sections with closed canopy structure (similar to the luminance density GLM; Figure 4.5).

In a general sense, then, the low-res ENM demonstrates that habitat sections preferred by the local crowned lemur population exhibit high vegetation richness and quality, which is
expected based on the forest-dwelling nature of the species. Curiously, however, the model also shows that these sections are in close proximity to the influence of anthropogenic activity. Upon initial consideration, this pattern would suggest that crowned lemurs at Oronjia are likely to exhibit a positive response to the presence of humans and anthropogenic features upon their landscape. Nevertheless, this pattern contradicts the negative response that was observed every time the research team encountered a group during the field season – which involved the dramatic flaring of calls and immediate disbanding to escape our presence. As such, further consideration is needed into exactly what this pattern tells us about the niche expression of this crowned lemur population.
Figure 4.14 – Partial response curves showing the influence that each background covariate has on the overall logistic prediction of crowned lemur distribution by the MaxEnt model. Landscape covariates include: (A) Elevation, (B) classification of habitat structure, (C) intensity of anthropogenic disturbance, (D) luminance density, (E) NDVI, (F) NDWI, (G) NDSI, (H) NDBuI, (I) distance from edge of water bodies, (J) distance from edge of human settlements, (K) distance from secondary roads, (L) distance from walking trails, and (M) percentage of canopy cover.

4.3.3 Influence of Background Covariates on Occurrence Patterns:

Similar to the partial response curves, I present single variable response curves to demonstrate the overall significance of each variable to the prediction of crowned lemur occurrence. Based on the slope of the response curves, then, luminance density (lux), vegetation quality (NDVI), proximity to walking trails, and percentage of canopy cover appear to have a strong positive influence on the differential occurrence of the species across the protected area. Similarly, elevation (m), vegetation moisture content (NDWI), degree of habitat clearing (NDSI), presence of human-made features, as well as the proximity to human settlements and water bodies, exhibit a negative influence on the occurrence patterns (Figure 4.15). The results presented here appear to reflect the same patterns as those from the simple logistics GLMs and the partial response curves.
FIGURE 4.15 – Single-variable response curves showing the dependency that prediction of crowned lemur distribution has on each of the covariates selected for inclusion into the MaxEnt model. Landscape covariates include: (A) Elevation, (B) classification of habitat structure, (C) intensity of anthropogenic disturbance, (D) luminance density, (E) NDVI, (F) NDWI, (G) NDSI, (H) NDBuI, (I) distance from edge of water bodies, (J) distance from edge of human settlements, (K) distance from secondary roads, (L) distance from walking trails, and (M) percentage of canopy cover.
4.3.4 Jacknife Report:

The jacknife report for the low-res ENM shows that the proximity to water bodies and human settlements are the top two predictors of crowned lemur occurrence across the protected area. Comparing the distribution of observation records (Figure 4.1) to the logistic outputs of the MaxEnt models (Figures 4.12 – A & B) and the distribution of these two background covariates across the protected area (Appendix 6 – Figures A6-9 & A6-10) support this report, as all records are located within one km of these features. Other important predictors include NDVI, NDWI, and NDBuI. Percentage of canopy cover, elevation, luminance density at forest floor, and distance to trail showed some low level of importance in comparison to the overall training gain. Interestingly, the classification of habitat structure, distance to secondary roads, and intensity of anthropogenic disturbance failed to provide any considerable amount information to the overall model.

4.4 Socio-Demographic Characteristics of Questionnaire Participants:

A total of 16 questionnaires were completed by Malagasy stakeholders who identified as permanent residents of the villages and smaller communities that surround Oronjia Park. Most participants, which included both male and females, were residents of either Ramena or
Ankorikahely (37.5% each), with a smaller portion (12.5% each) living in either Ambararata or Baie de Sakalava (Figure 4.17 – D). The total age range was 24 to 65 years old, and the proportion of younger (> 40) to older (< 40) individuals was more or less equal (Figure 4.17 – A). Close to 12.5% of participants reported that they had been born in the commune; the remaining 87.5% indicated that they were born somewhere else and had migrated to Oronjia at some point between the last 6 to 53 years (Figure 4.17 – E). Furthermore, the pool of participants reported a wide set of ethnic identities, with the most common ethnic identity being Antandroy (43.75%), followed by Antankarana (18.75%). In addition, participants also identified as Antanosy, Sakalava, Tsimihety, Vezo, as well as other smaller groups like Antemoro/Ajojo and Tsihombe Ambohove (Figure 4.17 – C). While the total number of individuals who participated in the survey represent a small fraction of the total population at Oronjia (0.38% based on 2011 census; Table 2.1), by taking into consideration the socio-demographic characteristics of those who took part, it is possible to consider the range of variation of cultural and livelihood contexts in the peninsula.
4.4.1 Livelihood Dynamics:

The profile of participation in the set of livelihood activities available in the vicinity of Oronjia park shows marked differences between 2007 and 2016. In a general sense, the importance of activities that rely on the direct exploitation of natural resources, like farming and charcoal production, seem to have faltered in the peninsula. While over half of participants reported that in 2007 they considered farming to be of some importance to the subsistence and/or economics of their families, participation in this activity for 2016 was greatly reduced, as less than 20% of participants confirmed that they engaged in the activity. The temporal variation in the importance of charcoal production was even more dramatic. Close to 50% of participants confirmed that it was their most important source of income in 2007; however, during the last 9-years, participation was remarkably reduced, to the point where less than 20% of participants confirmed that they continued practicing the activity today. More importantly, all participants who still practice charcoal production considered it to be a minor source of income, practiced seasonally in conjunction with farming. In addition to farming and charcoal production, participation in the local fishing industry experienced considerable decline during the 9-year interval. In contrast, the importance of livestock rearing rose substantially in comparison to 2007. Indeed, close to 90% of participants considered livestock to be of major or minor importance to their family’s subsistence. Finally, it is important to highlight that while participation in minor resource gathering remained more-or-less stable, some participants have started to consider the activity as an important livelihood source for their families.
Trees for the Primates – Chapter 4

A

Frequency (%)

Livelihood Activity

Importance Score
1 - No Importance
2 - Minor Importance
3 - Major Importance

B

Frequency (%)

Livelihood Activity

Importance Score
1 - No Importance
2 - Minor Importance
3 - Major Importance
Further to the activities listed above, some participants (~ 45%) cited the tourism industry as a source of income that is of either major and minor importance in their families’ economics. Interestingly, while the amount of participation in tourism has slightly increased during the 9-year interval, most participants reported that tourist activities remain of no direct importance to their livelihoods. The livelihood activity that saw the largest rise since the start of MBG operations relates to conservation. Indeed, most participants reported that since 2007, conservation work has become a direct or indirect livelihood source. It is very possible that individuals who agreed to complete the questionnaire were more often than not involved in some capacity with MBG or KODINA, and as such the sample may over-represent the direct impact that conservation activities have had on the livelihoods of local stakeholders. Furthermore, the overrepresentation of individuals association with MBG or KODINA may also lead to explain the drastic drop in charcoal production observed with the interviews.

Nevertheless, the fact remains that to some extent, the model of conservation employed at Oronjia has at least produced some direct benefit to residents of the various communities surrounding the park. Finally, in addition to the set of livelihood activities included in the questionnaire, some participants mentioned other types of jobs that were of major importance to their livelihoods. The most common of these responses included ownership of restaurants or stores, however some individuals also listed government work, construction, or security officer. More importantly, more respondents included alternative livelihood sources during 2016, in comparison to 2007. As a final note, it is necessary to point out that while the questionnaires employed here shows temporal shifts in the livelihood profiles of individuals living in Ramena, there is no clear association that elaborates on a direct causal link, connecting these livelihood shifts to growth of the tourism industry in Ramena and the continued settling of conservation activities in the region. Instead, these results simply help to showcase the type of socio-economic relationships that segments of the Ramena community hold with their local landscape, which permit to better understand the social realities in which MBG and KODINA have to work in to properly develop sustainable conservation avenues.
Chapter 5

5 DISCUSSION AND CONCLUSION:

The purpose of this chapter is as follows: Section 5.1 provides an overview of the general patterns of crowned lemur occurrence across the protected area in context of the ecological and anthropogenic dynamics that contextualize the site. Section 5.2 examines the viability and stability of present hotspots and effective characteristics of crowned lemur occurrence based on current land use patterns and value-judgement of conservation initiatives by local stakeholders. Finally, Section 5.3 highlights general recommendations for future research and the continued conservation of the Oronjia Park landscape.

5.1 Summary of Crowned Lemur Occurrence Patterns:

The results of my probability distribution ENMs show that the suitability profile of the protected forest in Oronjia Conservation Park exhibits a substantial degree of spatial variation that limits the realized niche expression of the local crowned lemur population to a subset of the total area. Moreover, the findings of these models, coupled with the simple logistic regression GLMs of the individual background landscape covariates, show that the limited suitability of the site is best explained by the combined effect of its ecological and anthropogenic contexts. Specifically, the differential habitat use patterns observed at Oronjia are primarily influenced by the variation in the quality and continuity of the forest, in addition to the availability of water resources within the protected area. Crowned lemur habitat use patterns are also influenced by the proximity of human settlements and other anthropogenic features that are immediately located in the vicinity of the protected area. Overall, the realised niche patterns shown here reveal that the distribution of crowned lemur is strongly influenced by the heterogeneous structure of within-habitat degradation observed across the protected area, which has reduced the total extent of the forest habitat capable of presenting the full set of necessary resources required to support the behavioural processes needed by the population.

Several mechanisms may be responsible for the influence that habitat degradation and anthropogenic factors have on the niche expression of crowned lemur. At the most basic level, anthropogenically-modified habitats, as a result of the intensity of human activities and
land-use patterns, have been shown to have limited availability of effective habitat characteristics that may facilitate lemur occurrence (Harris, 1984; Chapman, 1986; Lammertink et al., 2003; Lehman, 2006; Lehman et al., 2006a; Liao et al., 2013; Kamilar and Tecot, 2016). As previously mentioned, crowned lemurs are an “obligate” forest dweller, usually found in the forest understory, below the upper canopy level and above the shrub level (Freed, 1996; Solomon, 2009). Furthermore, like other members of its genus, crowned lemurs exhibit a necessity to maximize their food and water consumption to stay nutritionally balanced and properly hydrated (Colquhoun, 1993; Freed, 1996; Sato et al., 2016). In dry and highly disturbed habitats with high maximum temperatures and poor availability of water resources, such as Oronjia, this species is known to employ a flexible feeding strategy in which they consume high amounts of available foods that are low in fibre and high in moisture; in certain occasions this may include young leaves and flowers, as well as certain juicy fruits. They have been observed to accomplish this by expanding the total area of their home ranges, in which they increase their energy expenditure to exploit scattered resources across heterogeneously disturbed sites (Wilson et al., 1989; Freed, 1996; Sato et al., 2016). For example, Wilson (1989) previously showed that at Ankarana National Park, crowned lemurs will traverse the patchy habitat in search for specific subsets that best provide the necessary resources that they may need (i.e., abundant water, good quality food, or safe resting places). Similar to this, Lehman (2006) has suggested that density patterns of red lemurs (Eulemur rufus) in hedge habitats, in comparison to forest interiors, are negatively affected by the low availability of fruits and other preferred resources.

Based on these previous studies, then, it can be summarized that the differential habitat use patterns observed at Oronjia are a form of adaptive response by crowned lemur to the limited occurrence of effective foraging resources, water availability, and canopy coverage observed across the protected area (Appendix 6 – Figures A6-5, A6-6, A6-9, A6-13). Indeed, as Figures 4.13 – A & B, 4.14 – A to M, and 4.15 – A to M show, the heterogenous arrangement of background landscape conditions across the protected area is such that, suitable locations for crowned lemur occurrence appear to be only found across the northern- and southern-most sections of the protected area. These two ‘hotspots’ exhibit high vegetation quality and moisture, close proximity to water bodies, closed canopy structure, and are distant from walking trails. In contrast, beyond certain opportunistic chances to encounter effective characteristics of occurrence, the central section of the protected area
appears to show little potential for the continuous occupation of the population. Based on these patterns, it is apparent that the long-term likelihood of the sustained occurrence of crowned lemurs at Oronjia Park deeply depends on the stability of current landscape conditions and resources that make-up the structure of the northern and southern suitability ‘hotspots’.

It is important to note, however, that my vegetation data are an indirect approximation of actual on-site structural characteristics, and as such may only offer an overly optimistic indication of the abundance of foraging resources within the protected area. Although I took some steps to assess the reliability of the indicator by comparing areas highlighted with a high probability of lemur occurrence to my own-field observations of the range of behaviours displayed at points where the presence of the population was visually confirmed, this approach was not without problems. After all, the protocol employed here is only capable of highlighting areas of high vegetation quality, which may contain a combination of plants that are utilized by the species in addition to plants ignored by them because they do not provide necessary resources. As such, potential relationships between crowned lemur occurrence and vegetation characteristic highlighted here should be considered with caution (Lehman, 2006).

In addition to the availability of relatively higher-quality ecological resources and structural characteristics of the two occurrence hotspots, these habitat sections appear to also exhibit patterns of anthropogenic disturbance that differentiate them from the central section of the site – defined by a close distance to the location of human features altering the landscape, such as settlements and roads. Interestingly, however, these findings appear to suggest that crowned lemurs exhibit a positive adaptive distribution in response to the relative intensity of anthropogenic influence (Figure 4.4) as well as to the proximity of human features and settlements (Figure 4.9 to 4.11, 4.14, and 4,15). In other words, the results of my occupation and distribution models suggest that the occurrence of the species within the protected area is not afforded by the direct presence of people, only by the aftermath of their actions whenever it directly affects the availability of effective resources. These patterns, however, should be viewed with caution, because their implications do not properly reflect the alarm-calling and fleeing responses that crowned lemur groups would display when coming into contact with the observation team or other people local to the area. Furthermore, these findings contradict previous studies, which have shown that crowned lemurs, and other closely related members of the genus, react negatively to the encroachment
of anthropogenic features upon their home ranges (Freed, 1996; Solomon, 2009; Rakotondraparany & Andriambeloson, 2015; Kamilas & Tecot, 2016).

**FIGURE 5.1** – Southern edge of the protected area at Oronjia Conservation Park; the sharp transition from the dense forest located along the southern slope of Mamelon Vert and the farmlands located immediately next to the park, is clearly visible.

A more likely scenario is that crowned lemurs occur within these subsets of the site in spite of the patterns of anthropogenic pressure present along these locations, not because they exhibit a preference for these characteristics. Indeed, a possible scenario is that crowned lemurs show preference for these sections of the site because they contain the best foraging resources that are available throughout the site. In order to maintain access to these resources, the crowned lemur population might employ cryptic distribution strategies that can facilitate their presence in these human-dominated sectors without habituating to humans. The exact characteristic of these cryptic mechanisms, however, remain undefined and need further research. These findings reinforce earlier conclusions that the prospects for the long-term
occupation of the species depends on the stability of the current resource-driven effective conditions differentiating the suitability of the northern- and southern-most hotspots from the rest of the site. They show that the population’s adaptive distribution patterns are likely occupying the maximum habitat range that supports their niche requirements while also avoiding areas where levels of disturbance are too extensive for the population to handle (Chapman, 1986; Lammertink et al., 2003; Hardin & Remis, 2006; Remis & Jost Robinson, 2012). This is concerning since the suitable hotspots are already at the very edge of the available forest habitat for this site (Figure 5.1).

Indeed, Figures 4.14 and 4.15 show that areas with a high probability of lemur occurrence are in close proximity to human settlements. This is best exemplified by the southern edge of the protected area, along the boundary between Mamellon Vert and communities and farmland found in the immediate vicinity of the protected area (Figure 5.1). This area is in close proximity to the largest seasonal body of water available at Oronjia (Appendix 6 – Figures A6-9), it boasts the highest measure of vegetation moisture as a result of its low elevation (Appendix 6 – Figures A6-1 & A6-6), and exhibits a relatively high degree of vegetation diversity and canopy cover along the forest found within the protected area (Appendix 6 – Figures A6-6 & A6-13). Because of these characteristics, this section of the protected area and the human-dominated landscape immediately adjacent to it makes the best suitable location for both the occurrence of the local crowned lemur population and the undertaking of livelihood activities commonly practiced by local residents (i.e., farming). In addition, due to the close proximity of this habitat section to the peninsula’s eastern shoreline and the relative aesthetic quality of the forest, this section sees a large proportion of tourist activities carried out in the peninsula. Most of the tourist lodges are found in close proximity to this section of forest, and the secondary road that cuts across this area is also travelled quite frequently by cars transporting people from the main road and all-terrain vehicles that are commonly driven at high speeds.

In summary, then, my findings show that the protected area of Oronjia Park is suitable to host the local crowned lemur population as a result of two definable sections of the forest that bear the necessary suite of effective characteristics capable of supporting the day-to-day niche requirements of the species. However, due to the close proximity of human settlements and features related to their main livelihood patterns of local stakeholders, there is ample cause to be concerned about the viability of this habitat pattern. As such, I will now review
the potential for current livelihood patterns practiced in the vicinity of the protected area, as well as local-stakeholder’s value-judgements of conservation initiatives to hinder or support the stability of habitat hotspots suitable for crowned lemur occurrence.

5.2 Potential for Effective Conservation at Oronjia:

As explained in Section 2.2, the conservation model at Oronjia Park is based on the ideals of community-based action. This means that operation of the site emphasises the importance of working with the local community to generate sustainable livelihood systems that reinforce the conservation initiatives employed in the management of the park, used to protect and restore the local environment (Pollini et al., 2014). Following this system of operation, the work of MBG – Oronjia and KODINA has already produced measurable improvements for the quality of the local environment. For example, since the start of operations in 2007, charcoal production within the boundaries and in the immediate vicinity of the protected area has come to a stop (Figure 4.18). Indeed, no new charcoal pits were observed within the forest during this study. Moreover, the few cases of charcoal production were contained within farmlands, as well as private property in the villages of Ramena and Ankorikahely, using sustainably sourced or self-grown wood (For more information on this process, see: Gardner, 2014; Minten et al., 2013). With regards to older, now out of use, charcoal pits, members of MBG and KODINA reported that these areas were being left alone to permit their restoration. This was supported by the thick layers of grasses witnessed by the observation team along all of the older pits located within the protected area.

The halt of unregulated charcoal production that relies on raw materials from Oronjia forest is a clear example of success for the conservation model employed at the site. All interview participants who reported the cessation of their charcoal activities since the start of park operations commented that their decision was a result of: (1) the incorporation of new sets of Dinas that, through their enforcement by other members of the community serving a term with KODINA, reduced the chances of the activity because transgressors could be fined; and, (2) the availability of alternative livelihood opportunities in the traditional fishing and/or tourism industries – in addition to conservation work for handful of residents – facilitated by the intervention of MBG – Oronjia, who worked with local residents to ensure they had the necessary resources and organisation to participate with these activities (conversations with Oronjia residents, recorded in author’s fieldnotes; Missouri Botanical
Gardens, 2015). The combination of these two causes demonstrates the parallel approaches that MBG and KODINA use to deliver on their management goals for the park. This involves a combination of the establishment of specific management rules requiring the types of activities allowed within explicit areas of the park and its surrounding, which are to be followed and enforced by all residents, along with socioeconomic programs capable of ensuring that individuals who are at risk of being most affected by these rules have the means to actually change their behaviour. Essentially, then, the system of conservation employed by MBG at Oronjia tries to strike a balance between environmental protection and financial sustainability, by ensuring that their management actions generate change not by force, but through the availability of alternative options that are equally appealing – or as equally appealing as possible –as the livelihood pattern they seek to replace (Hardin, 1968; Hardin & Remis, 2006; McConnell, 2009; Colquhoun, 2015; Oldekop et al., 2016).

This approach to conservation has seen comparably successful results in other circumstances. Recent research by Oldekop et al. (2016), who conducted a global meta-analysis comparing the management systems employed by 165 different protected areas, shows that protected areas that attempt to integrate positive socioeconomic outcomes by empowering stakeholders, reducing systematic inequality, and maintaining cultural and livelihood benefits, are more likely to report successful conservation outcomes. In contrast, strict management systems that ignore socioeconomic necessities, while maintaining the effective structure of their environment, ultimately became vulnerable to rule breaking in situations of high economic scarcity or social necessities.

Even though the case of charcoal production illustrates the clear benefits of the conservation system employed in Oronjia Conservation Park, it is necessary to note that further work is still necessary in order to ensure the long-term protection of current habitat characteristics maintaining crowned lemur occurrence within the protected area. This note of caution is owed to the problematic expression of other intrusive types of livelihood activities that continue to be carried within and around the protected area. Here I refer to the persistence of unregulated collection of natural resources – i.e., yams and selective wood extraction – that a small segment of the population continues to practice (Figure 4.18). My note of caution, however, is not regarding the potential disturbance that these activities can continue to impose upon the habitat quality of the forest. This issue is problematic since it inflicts a great deal of pressure on endemic plant species whose persistence in the site is at
high risk (Figure 2.8; Wilkin et al., 2009). The direct effect of these activities on the persistence of the crowned lemur are nevertheless minimal, and as such, not of primary significance to this study. My concern, instead, relates to the socioeconomic issues these activities represent. Participants who admitted that they collected natural resources from the protected area on a regular basis explained that they did so as a result of not possessing the financial capacity to obtain food for their family or raw materials from their homes in any other way. As one villager put it:

I am proud and happy of the beauty of my forest, it shows that what MBG is doing here is good. Thanks to them, I have access to plenty that I would not have otherwise. However, at the same time, because of them, I sometimes feel like the forest is no longer mine. For example, when I need wood to fix the broken wall of my house, I am supposed to petition it through an official process that takes long to fulfill. Weeks can go before I receive a response, and then weeks can go before [KODINA] is able to locate a tree that can be logged. In the mean time, my wall is broken, and I am not supposed to do anything about it even though there is a good tree a short walk away.

(Conversation with Oronjia Resident, recorded in author’s fieldnotes).

Indeed, the persistence of such small-scale natural resource-based activities by a small portion of the resident Malagasy population signals that the current conservation model is not taking proper care of all members of the society. As one villager who admitted that their family regularly collected wild yams explained when asked if they feel that they have personally benefitted from the conservation and tourism activities conducted on the peninsula:

No, conservation helps the forest and it helps the animals, but it does not help me. Tourism helps the young and the people of Diego. I am too old, all I have to feed myself and my grandchildren are my crops and what little my children send. When that is not enough, I have to find what I can from the forest or the sea.

(Conversation with Oronjia Resident, recorded in author’s fieldnotes).

This conversation was of particular interest because it shows the inherent limitations of conservation management systems based on tourism as the main employment alternative to achieve mutual biological conservation and socioeconomic development outcomes – such as is the case in Oronjia. As Hardin and Remis explain (2006), even when the necessary steps are taken to ensure that the direct socioeconomic and cultural benefits of tourism and conservation are fairly distributed among members of the local community, there is a certain degree of bias that may impede some individuals from obtaining the opportunity to participate and directly benefit from these activities. Specifically, a person’s level of
education, age, and sometimes sex can mean that they are either passed over for these opportunities or that they are simply not interested in pursuing them (See also Remis & Hardin, 2009; Wilson, 2012). Simply put, for management systems to best integrate positive socioeconomic benefits that can help alleviate the pressure of the exploitation of the local environment, it is best that they do not put all their eggs in one basket. Instead, it may be necessary to diversify the offering of socioeconomic programs that the conservation model can offer (Harper, 2002; Gezon, 2006). MBG – Oronjia have shown their interest in alleviating the effects of this bias as best as possible. Indeed, during my stay on the peninsula I had the opportunity to attend several community meetings that had the goal of helping stakeholders establish committees to regulate and increase the benefit of alternative livelihood activities that can indirectly benefit from the regular traffic of tourists visiting the peninsula. This included: manufacture and sale of traditional crafts and textiles, massage parlors, as well as further support of the traditional fishing industry. If properly implemented, the support of these livelihood forms into the conservation model employed at Oronjia could continue to displace local reliance for natural resources from the forest.

Nevertheless, the inclusions of these livelihood alternatives do not limit the overall reliance that current conservation practices employed at Oronjia and the greater Ramena Complex have on the continued popularity of local tourism. Given how many of the peninsula’s more popular tourist amenities are in close proximity to the northern- and southern-most habitat hotspots of the crowned lemur population (Figure 2.1; Figure 4.13), it is necessary to note the unintended and problematic physiological impacts that close proximity to human populations can have on crowned lemurs. As noted by Rakotondraparany & Andriambeloson (2015), crowned lemur groups occupying the southern portion of the site were commonly observed sleeping in the sub-canopy level of trees adjacent to the tourist lodges near Baie de Sakalava. Furthermore, in certain situations, some of the members of these groups would come in close proximity of tourists offering treats. Past research has shown that in members of the genus Eulemur whose diets include high proportion of human foods can exhibit imbalanced hormonal levels. Similarly, constant and unregulated contact with human populations can increases the chances of pathogen transmission (Kamilar & Tecot, 2016). Based on these risks, then, it is necessary that as tourism activities increase in the peninsula, specific management rules limiting the contact of people with lemurs be developed.
Another point that should be further considered as conservation activities at Oronjia and the greater Ramena Complex continue to develop, is the reliance that their current management model places on the continued viability of tourist activities. As explained in Section 2.1.2, current management operations by MBG – Oronjia and KODINA appear to be focused on establishing a stable tourist industry that can be easily accessed by local residents from most sections of the community. The goal of this is to ensure that participation and collaboration with the local tourism industry is directly or indirectly, a sustainable and enticing socioeconomic alternative for people that give them the capacity to not take part in other livelihood activities available in the region (Pollini et al., 2014; Missouri Botanical Gardens, 2015; Randriamahefa, 2016).

Understandably, pairing conservation management activities alongside the tourism industry is, at the present moment, a viable mechanism to decrease the historic reliance that local livelihoods have on unsustainable industries. Nevertheless, it is also necessary to mention the fact that in Madagascar, the viability of tourism tends to show a capacity for much interannual fluctuation. Indeed, the number of tourists coming to Madagascar each year is known to vary alongside tangentially related events that include, to name a few, political instability, extreme climatic events, and health-related issues. The most well known of these instances is the political unrest that developed as a result of the coup d’état in 2009, which had a negative influence on the number of international tourists coming to the island for the following 2-3 years (Schwitzer et al., 2013; Volampeno et al., 2013; Colquhoun, 2015). Due to the negative impact in tourism, it has been shown that community-based conservation projects that primarily depended on the viability of tourism as the mechanism to shift the livelihood styles of local stakeholders, were forced to reduce the capacity of their operations or close down (Colquhoun, 2015). Furthermore, from the perspective of local stakeholders, experiencing a decreased return from tourism-related employment could force them to find livelihood alternatives that may not necessarily follow a sustainable framework (Gezon & Freed, 1999; Hardin & Remis, 2006; Gardner, 2014). As such, to ensure that the efficacy of conservation at Oronjia is not severely affected were a temporary – or more prolonged – crash in local tourism to occur, it is necessary that MBG – Oronjia and KODINA diversify their intervention with the development of sustainable livelihood opportunities. The support that MBG provides to traditional fishermen in the peninsula is a realised example of possible avenues of diversification. It might also be worthwhile to consider whether opportunities for
the implementation of other sustainable industries like agroforestry and ‘green-charcoal’ production could be successfully implemented in this region (Carret, 2013; Gardner, 2014); nevertheless, more locally-based work is needed in this avenue to properly understand what livelihood opportunities may prove most useful in this community.

In summary, my research has shown that the conservation management model employed at Oronjia is well aware of the complex social-ecological realities that characterise the relationships that exist between the Malagasy people of this region, the local crowned lemur populations, and the landscape inhabited by this inter-species community. This model shows that for conservation and sustainable land stewardship to succeed in deteriorated and human-dominated forest fragments, it is necessary for our work to address the reasons why people undertake activities that have negative effects on the local environment and create opportunities for sustainable livelihoods with an equal capacity as those causing the issues. Nevertheless, the application of this vision still needs further work to ensure it can foster viable sustainable relationships between people and their environment that require no outside intervention. At the moment, it is clear that individuals in certain sections of the Ramena Commune feel as if the work of MBG – Oronjia and KODINA is constraining their livelihoods. Furthermore, basing such a great portion of the capacity of local conservation initiatives on the viability of tourism to shift the livelihoods of people towards a sustainable end-goal is problematic because of how much the efficacy this industry has tended to fluctuate historically.

Finally, my research shows that similar to lemurs, the two areas that comprise the crowned lemur occurrence hotspots are very well favoured as the setting of many of the human activities that occur within, as well as in the immediate vicinity of the park. In order to ensure that stability of these hotspots remains, so as to foster the continued presence of this lemur species, MBG – Oronjia and KODINA will have to develop specific management guidelines that ensure to maintain the quality of local vegetation while still supporting sustainable human activities in these valuable landscape sections. This last point is, in my opinion, the most important conclusion of this study and the reason for which I chose the main title of this thesis – *Trees for the Primates*. As I have shown here, understanding the complex set of relationships that structure the interactions between the two primate groups that are considered in this work, humans and lemurs, is key to understanding both, the mechanism influencing the ecologies of organisms in disturbed habitats and the proper
pathways for conservation (Ingold, 2000b; Colquhoun, 2005; Hardin & Remis, 2006; Fuentes, 2012; Bracebridge et al., 2013). Indeed, as human action has become such a significant influence on the vast majority of all modern environments, it is necessary that future ecological and conservation work continues to consider a more nuanced understanding of the mechanisms by which socioeconomic and cultural factors of people influence nature and other organisms (Fuentes, 2012).

5.3 Recommendation for Future Directions:

Future research should focus their attention on formulating the metapopulation dynamics that connect the crowned lemur population found at Oronjia Conservation Park to the neighbouring populations located in Montagne des Français and other nearby habitat fragments (Freed, 1996; Wiens, 1997; Sabel et al., 2005; Missouri Botanical Garden, 2015). In this thesis, I focused exclusively on within-habitat patterns of crowned lemur occurrence and the potential influence these have on the persistence of the local population. This research showed that the availability of suitable ecological and anthropogenic characteristics, as well as the effectiveness of community-based conservation initiatives following the Category V management model NPAs influence the distribution of the species in this fragment. This scale of analysis treats the crowned lemur population in isolation, ignoring its relationships to closely available populations.

The gap in knowledge highlighted here means that it is necessary that future population studies in this area expand from the limits of the present study to compare how the various populations found scattered across the fragments that make-up the Ramena complex relate to each other. It is likely that possible metapopulation dynamics found here could help to better explain the long-term persistence of the Oronjia population in this fragment – which remains a point of concern given the small size and density of this population, as well as the limited availability of suitable habitat characteristics within its home-range (Arroyo-Rodriguez & Fahrig, 2014; Johnson et al., 2016; Kamilar & Tecot, 2016). It is likely that the results of a meta-population focus for the crowned lemur groups found throughout this region could show the effective characteristics influencing the presence of the species within fragments explain how the species realises their day-to-day niche necessities. The long-term persistence may in fact be due to metapopulation dynamics
that ensure low-quality, sink fragments remain inhabited (Wiens, 1997; With, 2004; Arroyo-Rodriguez & Fahrig, 2014).

It is also recommended that future research should explore the influence that variation in habitat configuration between fragments along the Ramena Complex have on the niche expression patterns of the various crowned lemur subpopulations. As discussed above, the effective habitat characteristics available at Oronjia are likely to sustain the bare minimum niche requirements of crowned lemurs (Hutchinson, 1957). It would thus be interesting to see how the realised niche expression of the crowned lemur meta-population vary as a result of the variation in habitat quality and intensity of anthropogenic disturbance seen throughout the Ramena Complex. Similarly, it would be worthwhile to observe the degree of variation in the population processes and distribution characteristics of the species that occur in settings where availability of effective resources and conditions is more reliable (Wilson et al., 1989; Arroyo-Rodriguez & Fahrig, 2014; Sato et al., 2016). This would permit a more comprehensive appreciation of how the behavioural flexibility that this species, and other members of the genus *Eulemur*, exhibit is influenced by temporal and spatial variation in the availability of resources and intensity of disturbance.

Finally, with regards to the continued conservation of the protected area in Oronjia Park, while immediate operations should focus their attention on ensuring that the effective characteristics making-up the northern- and southern-most suitable habitat are stable, this is at most a short-term measure. Indeed, to ensure that the crowned lemur population is capable of thriving in this habitat, it is necessary that future management initiatives focus their attention on restoring the continuousness of the canopy structure in the central sections of the protected area. Specifically, MBG – Oronjia should seek to replant native hard- and soft-wood species within the old charcoal pits, which currently remain unattended, having been left to regenerate on their own. Without direct restoration intervention, these pits could be dominated by invasive species and will continue to limit the availability of effective vegetation (Liao et al., 2013). While it is likely that the quality of this section of the forest will remain less preferable due to the lower availability of water, it would at least help to lower the intense reliance that crowned lemurs currently hold over the northern- and southern-most suitable hotspots.
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Trees for the Primates – Works Cited


2006-01-01 to 2016-12-26, and subset size: 15 x 15 km.
http://dx.doi.org/10.334/ORNLDAAC/1241.


APPENDICIES

APPENDIX 1: Additional satellite scenes from northern Madagascar

**FIGURE A1-1** – Location of the city of Antsiranana (Diego Suarez) in relation to the Oronjia peninsula. Also visible is the northern section the NPA Montage des Français (green patch in centre-south of the scene). Obtained from Google Earth Pro, 2015.

APPENDIX 2: Datasets utilized in this study.

**TABLE A2-1** – Structural summary of geospatial dataset.

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<td>$ LUX          : int 742 521 97 896 875 831 299 777 870 878 ...</td>
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**TABLE A2-2** – Structural summary of transect dataset.

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### Table A2-3 (Part 2) – Livelihood dataset.

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APPENDIX 3: Ordinary Classification Keys.

**TABLE A3-1 – 5-point habitat-type classification key**

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<tr>
<th>Level</th>
<th>Type</th>
<th>Description</th>
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<tbody>
<tr>
<td>1</td>
<td>Bare rock/soil</td>
<td>Bare, dry soil with no canopy cover.</td>
</tr>
<tr>
<td>2</td>
<td>Wooded grassland/brush thicket</td>
<td>Tall grasses. Shrubs, small vegetation.</td>
</tr>
<tr>
<td>3</td>
<td>Degraded/mixed forest</td>
<td>Mosaic habitat microsections, exhibiting forest, brush thicket, and grassland traits.</td>
</tr>
<tr>
<td>4</td>
<td>Intact forest</td>
<td>Relatively intact forest structure, containing primarily trees and mid to dense vegetation</td>
</tr>
<tr>
<td>5</td>
<td>Anthropogenic landscape</td>
<td>Land utilized for livelihood activities or in close proximity to human settlements and other features.</td>
</tr>
</tbody>
</table>

**TABLE A3-2 – 5-point intensity of anthropogenic disturbance classification key, adapted from Lehman et al. (2006b).**

<table>
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<th>Level</th>
<th>Type</th>
<th>Description</th>
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<tr>
<td>1</td>
<td>None</td>
<td>Sections exhibiting no current evidence of anthropogenic forest use – Agriculture, deforestation, trails, wild-yam collection, cattle grazing, or charcoal production</td>
</tr>
<tr>
<td>2</td>
<td>Light</td>
<td>Sections exhibiting low levels of anthropogenic forest use. Includes past evidence of tree extraction, wild-yam collection, no direct sign of cattle grazing, and no evidence of charcoal production. May contain minor trails.</td>
</tr>
<tr>
<td>3</td>
<td>Moderate</td>
<td>Sections exhibiting recent evidence of logging, wide trails with minor canopy openness, direct evidence of some cattle grazing and wild-yam collection. No evidence of agricultural activity.</td>
</tr>
<tr>
<td>4</td>
<td>Heavy</td>
<td>Sections exhibiting direct and persistent evidence of tree extraction, charcoal production, high number of freshly dug wild yams, and high cattle density. No evidence of agricultural activity.</td>
</tr>
<tr>
<td>5</td>
<td>Dominated</td>
<td>Sections exhibiting evidence of tempo/spatial continuous human action like long term agricultural fields and settlements.</td>
</tr>
</tbody>
</table>
APPENDIX 4: Research questionnaire

Livelihood Dynamics and Social Attitudes towards Conservation Action

Interviewer: 
Interview ID: 
Date: 
Recording Done? [Y/N]

How did you approach this participant?

1 – Basic Information:

A) How old are you?


B) Are you the (or one of the) primary financial provider(s) for your family?

C) What is your ethnicity?

D) Do you live in one of the villages of this commune [yes | no]?

E) If yes, how long have you been living here?

F) If no, where do you live (village, commune)?
2 – Livelihood Activities*:

The group of questions that follows are about the activities that you carry out day to day to get food and money for yourself and your family. I am going to give you a list of activities, and for each one I would like you to tell me how important it is for you (and your family) as a source of income. For each activity, please, give me a score of 1 to 3 depending on how important it is for you.

1 – I never carry out this activity.

2 – I sometimes carry out this activity, but not very often. It brings some revenue to my household but it is small compared to other activities.

3 – I carry this activity quite often. It is an important source of revenue for my household.

<table>
<thead>
<tr>
<th>Activity</th>
<th>Score</th>
</tr>
</thead>
<tbody>
<tr>
<td>A) Farming in fixed plots.</td>
<td></td>
</tr>
<tr>
<td>B) Producing Charcoal.</td>
<td></td>
</tr>
<tr>
<td>C) Keeping livestock.</td>
<td></td>
</tr>
<tr>
<td>D) Fishing.</td>
<td></td>
</tr>
<tr>
<td>E) Tourism/Ecotourism Industry.</td>
<td></td>
</tr>
<tr>
<td>F) Conservation.</td>
<td></td>
</tr>
<tr>
<td>G) Wood cutting.</td>
<td></td>
</tr>
<tr>
<td>H) Sand Mining.</td>
<td></td>
</tr>
<tr>
<td>I) Other [Please specify]:</td>
<td></td>
</tr>
</tbody>
</table>

Now, I would like to ask the same questions again, but about how important each activity was seven years prior. Before MBG started operations in the area. The reason for this is to know if the conservation efforts of MBG have had any impact in your life. I will be using the same scoring system as before, from 1 to 3.

1 – I never carry out this activity.

2 – I sometimes carry out this activity, but not very often. It brings some revenue to my household but it is small compared to other activities.

3 – I carry this activity quite often. It is an important source of revenue for my household.

<table>
<thead>
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<th>Activity</th>
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<td>H) Sand Mining.</td>
<td></td>
</tr>
<tr>
<td>I) Other [Please specify]:</td>
<td></td>
</tr>
</tbody>
</table>

* Adapted from Gardner (2014).
3 – Attitudes Towards Conservation Action:

A) Do you think conservation action in Madagascar is important? [yes | no]

B) Do you think conservation action at Oronjia is important? [yes | no]

C) Do you know of the work that the Missouri Botanical Gardens is doing in the area? [yes | no] Do you find it beneficial or problematic? [If the respondent does now know much about MBG of what they do in the area, then you can provide a brief explanation].

D) What are your thoughts about ecotourism in the area? [Good, bad, no opinion]

E) Do you feel like you have personally benefited from the conservation and ecotourist activities in the area? [yes | no]
4 – Attitudes towards lemurs at Oronjia and the forest:

A) Do you know what lemur species are present at Oronjia? Can you name them? [Aided with field guide]

B) Do you consider lemurs to be important? [yes | no] Why?

C) Do you normally use the forest for reasons not related to your livelihood activities? [Always, sometimes, never]

D) What makes the forest important for you?

E) How significant do you think is it for the next generation to have Oronjia Forest?

F) Do you remember what the forest was like 10 years ago, in 2006? If yes, which forest do you prefer, the one you have today or that one you had then?

Thank you for your time and for participating in this interview, goodbye.
APPENDIX 5: Variation of background landscape covariates occurring between presence and absence transects for the simple logistic GLMs

**FIGURE A5-1** – Elevation (m) boxplot.

**FIGURE A5-2** – Habitat classification boxplot.
**FIGURE A5-3** – Intensity of anthropogenic disturbance boxplot.

**FIGURE A5-4** – Luminance density (LUX) boxplot.
FIGURE A5-5 – NDVI boxplot.

FIGURE A5-6 – NDWI boxplot.
FIGURE A5-7 – NDSI boxplot.

FIGURE A5-8 – NDBuI boxplot.
**FIGURE A5-9** – Distance (m) from the edge of water bodies boxplot.

**FIGURE A5-10** – Distance (m) from the edge of human settlement boxplot.
FIGURE A5-11 – Distance (m) from secondary roads boxplot.

FIGURE A5-12 – Distance (m) from walking trails boxplot.
APPENDIX 6: Spatial variation of landscape covariates selected for inclusion in MaxEnt ENMs.

**FIGURE A6-1** – Digital elevation (m) model.

**FIGURE A6-2** – Habitat configuration model.
**FIGURE A6-3** – Intensity of anthropogenic disturbance.

**FIGURE A6-4** – Spatial heterogeneity of luminance density (LUX).
**FIGURE A6-5 – NDVI.**

**FIGURE A6-6 – NDWI.**
FIGURE A6-7 – NDSI.

FIGURE A6-8 – NDbuI.
FIGURE A6-9 – Distance (m) from edge of water bodies.

FIGURE A6-10 – Distance (m) from the edge of human settlements.
FIGURE A6-11 – Distance (m) from secondary roads.

FIGURE A6-12 – Distance (m) from walking trails.
FIGURE A6-13 – Percentage of canopy cover.
APPENDIX 7: Receiver-operating characteristic (ROC) curves

**FIGURE A1-1** – ROC curve for low-resolution model.

**FIGURE A7-2** – ROC curve for high-resolution model.
APPENDIX 8: Ethics approval form

Western University Non-Medical Research Ethics Board
NMREB Delegated Initial Approval Notice

Principal Investigator: Dr. Ian Colquhoun
Department & Institution: Social Science/Antropology, Western University

NMREB File Number: 108010
Study Title: Trees for the Primates: A Community-Based Assessment of the landscape ecology of Crowned Lemurs (Eulemur coronatus) in Northern Madagascar

NMREB Initial Approval Date: August 17, 2016
NMREB Expiry Date: August 17, 2017

Documents Approved and/or Received for Information:

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<th>Document Name</th>
<th>Comments</th>
<th>Version Date</th>
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<tr>
<td>Other</td>
<td>Informed Consent Script - Received May 25, 2016</td>
<td></td>
</tr>
<tr>
<td>Instruments</td>
<td>Data Collection Form - Received May 25, 2016</td>
<td></td>
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<tr>
<td>Instruments</td>
<td>Questionnaire - Received May 23, 2016</td>
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<td>Western University Protocol</td>
<td>Received August 6, 2016</td>
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<tr>
<td>Letter of Information &amp; Consent</td>
<td>2016/09/25</td>
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<td>Instruments</td>
<td>Interview Guide - 2016/07/29</td>
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<tr>
<td>Other</td>
<td>Confidentiality Agreement - 2016/07/29</td>
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<tr>
<td>Other</td>
<td>Received August 6, 2016 - Tracking Log</td>
<td></td>
</tr>
</tbody>
</table>

The Western University Non-Medical Research Ethics Board (NMREB) has reviewed and approved the above named study, as of the NMREB Initial Approval Date noted above.

NMREB approval for this study remains valid until the NMREB Expiry Date noted above, conditional to timely submission and acceptance of NMREB Continuing Ethics Review.

The Western University NMREB operates in compliance with the Tri-Council Policy Statement Ethical Conduct for Research Involving Humans (TCPS2), the Ontario Personal Health Information Protection Act (PHIPA, 2004), and the applicable laws and regulations of Ontario.

Members of the NMREB who are named as Investigators in research studies do not participate in discussions related to, nor vote on such studies when they are presented to the REB.

The NMREB is registered with the U.S. Department of Health & Human Services under the IRB registration number IRB 00000941.

Ethics Officer: Erika Basile ⎜ Nicole Kaniki ⎜ Grace Kelly ⎜ Katelyn Harris ⎜ Valki Tran ⎜ Karen Gopaul

Western University, Research, Support Services Bldg., Rm. 5150
London, ON, Canada N6G 0B9 t. 519.864.8396 f. 519.865.2456 www.uwo.ca/research/ethics
CURRICULUM VITAE

NAME: Fernando Mercado Malabet

EDUCATION:
2015 – 2017 Master of Arts, Department of Anthropology (Environment & Sustainability), Faculty of Social Science, the University of Western Ontario, London ON Canada. Supervisor: Dr. Ian C. Colquhoun.
2011 – 2015 Bachelor of Science in the Honours Program, Departments of Anthropology and Biology (joint majors), Trent University, Peterborough ON Canada.

ACADEMIC AND RESEARCH AWARDS:
2017 Environment & Sustainability Graduate Student Award (Masters Continuing), Centre for Environment & Sustainability, the University of Western Ontario.
2016 – 2017 Ontario Graduate Research Scholarship, School of Graduate and Postdoctoral Studies, the University of Western Ontario.
2016 – 2017 Western Graduate Student Research Scholarship, Department of Anthropology, the University of Western Ontario.
2016 Environment & Sustainability Graduate Student Award (Masters Entrance), Centre for Environment & Sustainability, the University of Western Ontario.
2015 – 2016 Western Graduate Student Research Scholarship, Department of Anthropology, the University of Western Ontario.
2012 – 2015 Trent National Renewable Scholarship, Faculty of Arts & Science, Trent University.
2011 – 2012 Trent’s Entrance Scholarship, Faculty of Arts & Science, Trent University.
HONORARY DISTINCTIONS:

2015  President’s Honour Roll. Awarded for graduating with outstanding academic achievement from Trent University.

2012 – 2015  Dean’s Honour Roll. Awarded for outstanding academic achievement throughout the academic year in the Faculty of Art’s and Science at Trent University.

NON-PEER-REVIEWED PUBLICATIONS:


OTHER PEER-REVIEWED CONTRIBUTIONS:

2017  Mercado Malabet, F.M. & Colquhoun, I.C. Validating the use of canopy cover as a proxy predictor of human disturbance across forest habitats in northern Madagascar. Poster Presentation. Canadian Association of Physical Anthropology, 44th Annual Meeting. Trent University, Peterborough, ON.


NON-PEER-REVIEWED CONTRIBUTIONS:

2017  **Mercado Malabet, F.M.** Habitat preferences of crowned lemurs (*Eulemur coronatus*) in disturbed forest settings: A case study of flexibility in human and non-human interactions? Paper Presentation. 5th Annual Western Anthropology Graduate Student Conference – Community and Anthropology. Department of Anthropology, the University of Western Ontario, London, ON.

2016  **Mercado Malabet, F.M.** Beyond the shores of an ‘island’: A conceptual model of socio-ecological space for conservation action in Madagascar. Paper Presentation. 4th Annual Western Anthropology Graduate Student Conference -- Conflicting Voices in Cultural Spaces. Department of Anthropology, University of Western Ontario, London, ON.

**INVITED LECTURE:**

2016  ANTHRO 2265F – Primate Behaviour, Department of Anthropology, University of Western Ontario.

Conservation Research of a Small Population: Understanding habitat preferences of crowned lemurs in disturbed forest settings.

**PUBLIC PRESENTATIONS:**


**EMPLOYMENT:**

2015 – 2016  **Graduate Teaching Assistant, University of Western Ontario,**
**Department of Anthropology.**
ANTHRO 2265F - Primate Behaviour
ANTHRO 2264F - Issues in Primate Conservation.
ANTHRO 2100 - Introduction to Archaeology and World Prehistory.