



Universidade de Évora

Escola das Ciências e Tecnologia

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**Comparing the feeding ecology of
Propithecus edwardsi in disturbed and
undisturbed forest in Ranomafana National
Park, Madagascar.**

Mariana Duarte Pissarra de Matos

Orientadores: Prof^a. Doutora Patricia Chapple Wright
Prof^a. Doutora Teresa Fernandes

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Comparação da ecologia alimentar de *Propithecus edwardsi* em floresta perturbada e não perturbada no Parque Nacional de Ranomafana, Madagáscar.

Autoria: Mariana Duarte Pissarra de Matos

Orientação: Professora Doutora Patricia Chapple Wright

Coorientação: Professora Doutora Teresa Fernandes

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“Comparação da ecologia alimentar de *Propithecus edwardsi* em floresta perturbada e não perturbada no Parque Nacional de Ranomafana, Madagáscar”

Resumo

Os primatas de Madagáscar, mais conhecidos por lémures, têm vindo a ser muito afetados por práticas humanas insustentáveis que levam ao seu declínio, tornando a sua conservação uma prioridade. Neste estudo pretendemos compreender de que forma a perturbação de habitat influencia a ecologia alimentar de *Propithecus edwardsi*. Os dados utilizados foram recolhidos durante a estação fria/ seca no Parque Nacional de Ranomafana, Madagáscar, através de observações diárias em floresta perturbada e não perturbada. Após o tratamento estatístico, verificou-se que não existem diferenças comportamentais entre sexos em cada local, mas quando comparados indivíduos do mesmo sexo entre locais, as diferenças mostraram-se significativas. Ao nível do comportamento alimentar, indivíduos que habitam na floresta perturbada passam mais tempo a alimentar-se, independentemente do sexo, com diferenças significativas na dieta, em relação aos que habitam na floresta não perturbada. Os resultados foram maioritariamente explicados pelas diferenças existentes na disponibilidade de alimentos causada pela perturbação de habitat, que levam a diferentes dietas e estratégias de sobrevivência.

Abstract

Primates of Madagascar, more known as lemurs, have been greatly affected by several unsustainable human practices that lead to their decline, making their conservation a priority. In this study, we intend to understand in which way habitat disturbance affects the feeding ecology of *Propithecus edwardsi*. The data was collected during the cool/ dry season, at Ranomafana National Park, Madagascar, through daily observations in disturbed and undisturbed forest. After statistical analyses, we observed no significant behavioral differences between sexes at each site, but when comparing individuals of the same sex between sites, the differences appear. At feeding behavior level, individuals living in the disturbed forest spend more time feeding, regardless of sex, with also significant differences in diet compared to those living in the undisturbed forest. Our results, were mostly explain by differences in food availability caused by habitat disturbance, leading to different diets and life strategies.

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1. Introduction

1.1. Primates

1.1.1. Importance, description and classification

Primates have an important role in biological and cultural richness, beyond their close evolutionary history with humans. In many cultures, they are known as central figures in local and regional traditions. Thus, the maintenance of these populations is considered an important issue in conservation to preserve the complex social and cultural relationships between humans and other primates (Chapman and Peres 2001). Besides this role, primates are also an important part of their ecosystems, as prey, predator and mutualist species in food webs. They are considered closely linked with the diversification of angiosperms (especially frugivores), due to their ability to feed on seeds without destroying them and to disperse them over long distances because of their relatively large body size and arboreal mode of locomotion. These traits may augment the regeneration of forests; hence, there is evidence that the loss of primate seed dispersal have negative impacts also in human populations in shared ecosystems (Estrada *et al.*, 2017).

Among mammals, primates are among the oldest and anatomically least specialized group that lives on the planet. Within this group, it is possible to find a high range of diversity, including species with different ecologies and behaviors. In general, primates are known for their shortened nose (related to a decrease in sense of smell) and their binocular vision (high dependence on vision); an unspecialized skeleton with an opposable thumb on the extremities of its limbs and nails rather than claws on fingers and toes; a large brain relative to body size; long periods of development and a placenta that invades the uterus wall. However, not every primate species is representative of these characteristics, but they define a set of closely related species that share a long evolutionary history and reflect the most common trends in the Primate order. Primarily and based on anatomical traits, the primate group is divided into two different sub-groups: Strepsirhini (including more evolutionary primitive families [Prosimians] without tarsiers) and Haplorhini (including more evolutionary advanced families [Anthropoids] plus tarsiers). Prosimians have some distinct characteristics that made them a unique group: they are very dependent on olfaction with having a bare muzzle,

and reproductive biology that includes a bicornuate uterus and a well-defined estrous period (anthropoid females show a true menstrual cycle). This group includes the lemurs of Madagascar, the galagos of Africa mainland, the loris-potto group of Africa mainland and Asia and finally the tarsiers of Southeast Asia. There has been some discordance if the tarsiers should be in the prosimians or in the anthropoid group. If we consider only their morphologic and behavior characteristics, Tarsiers belong to the Prosimian sub-order. But if we take into account the more recent molecular information, we need to consider the classification into Strepsirhini and Haplorhini, including this species in the first one (Groves and Harding 2011). On the other hand, the anthropoid group is divided into the New World monkeys (Platyrrhini; found only in the South and Central America) and the Old-World monkeys (Catarrhini; distributed by Africa mainland and Southeast Asia). This last group can still be divided into Hominoidea (where the apes and humans are included) and Cercopithecoidea (which include the remaining monkeys; Cowlshaw & Dunbar, 2000).

The most recent taxonomic compilation lists 701 primate taxa belonging to 504 species from 79 genera and 16 families; with the Neotropics having 171 species, Africa mainland with 111 species, Madagascar with 103 species and Asia with 119 species (Estrada *et al.*, 2017). The number of taxa is very variable, going from 200 to 500 species (depending on the taxonomic criteria), with new ones continuing to be described (Rowe & Myers, 2016).

1.1.2. Behavior ecology

The life history of most primates includes long life spans and low reproductive rates, being extremely influenced by body size. Within this group, there is an amazing variation of body size, ranging from 30 g of pygmy mouse lemur (*Microcebus myoxinus*) females to 90 kg of Gorilla females. The energy required by an individual for its daily bases routines has implications on its diet and, consequently, in its body size. Thus, linked to their specialized diets and body size, these primate attributes can be associated as: smaller species are usually insectivorous; larger one are usually folivorous; and frugivorous, which can still be divided into two distinct groups according to their protein source (the smaller-bodied species from insects and the larger-bodied ones from leaves). Usually, only species which can survive with small absolute

quantities of food can afford to be exclusive insectivorous, while species with more dietary needs are commonly less selective, using their resources more intensively and they use to be associated with large-bodied species (Cowlshaw & Dunbar 2000). There is also a relation between body size and range size. This relation seems to be mediated by energetic constraints and by individual's dispersal ability. Smaller species tend to be more specialized and tend to occupy relatively small ranges. On contrary, widespread species may be either small or large and tend to be more generalist. Furthermore, among wider-ranging species, species which are more abundant tend to be smaller than the less abundant (Chapman *et al.*, 2006). Body size can also be implicated in the ability of species to survive in variable natural environments. In fact, larger animals tend to have more energy reserves, therefore are able to survive periods of food scarcity in a better way than smaller ones which have smaller energy reserves. To finish, body size is also related with other life history variables associated with many extinction promoting traits. With the increase of body size, birth and death rates decline, while life expectancy and generation time increase (Chapman *et al.*, 2006; Cowlshaw & Dunbar, 2000).

The ecological behavior of primates is dominated by their anti-predator techniques and foraging strategies. In this regard, this group of mammals has developed different combinations of habits, such as arboreal vs terrestrial and nocturnal vs diurnal, and diet. In general, nocturnal animals are always arboreal and feed mostly on insects, while diurnal animals can be terrestrial or arboreal but none of them are insectivorous. These guilds probably reflect a combination of selection pressures including predation risk and the cost of searching for food. There are also some species that are cathemeral (mainly lemurs; Cowlshaw & Dunbar, 2000; Fleagle, 2013).

According to their diet, primate species can display several differences in their digestive tract and in intake nutrients. Folivores are the largest primates despite their low-quality diet even if it's wide spread. Leaves have their nutrients locked up inside wall cells and their predators need to have specializations to be able to use their nutrients. Some species have long gut passage times to allow the absorption of nutrients or rely on microbial fermentation to digest the plant cell walls and make nutrients accessible. Besides, folivores are also associated with dental specializations, such as hypsodont molars, which allow shredding or grinding leaves to promote microbial action. Further, frugivores have their nutrients much more accessible but fruits are also

more patchily distributed than leaves and highly seasonal in their availability, presenting their own intrinsic disadvantages. Species which exhibit this diet don't have the specializations that folivores have so they are unable to digest nutrients with the same ability as folivores, even with leaves being a regular part of some frugivores species. Fruit predators need to have other specializations in order to contrast defenses that some plants have evolved to keep their seeds safe, protecting them from premature dispersal or predation. There are also primate species that are gummivorous since they feed on plant gums, others that may also feed on exudates, flowers and nectar, bark by some species in lean seasons, and even small amounts of animal matter. Primates are almost only vegetarians but, because they are not able to synthesize or obtain from nonanimal sources vitamin B₁₂, they need to become occasional carnivores. In most cases, carnivory consists in preying invertebrates, small birds and their eggs or nestlings or other small vertebrates. In contrast, chimpanzees may also be predators of ungulates and some medium-sized primates, and tarsiers are considered the only exclusive faunivorous primate. Within these dietary categories, it's possible to find variations between habitats and within the same species. Even between genders it is possible to find digest differences (Cowlshaw & Dunbar 2000; Mitani *et al.*, 2012).

Males and females present different behavioral strategies according to their ecologic needs. Each individual, by himself, has the purpose to maximize their personal genetic contributions to the next generation. Females have the major investment in each reproductive event since they are responsible for the gestation and lactation period of the newborns. These actions plus the costs of egg production are not comparable with the costs of sperm production in males, resulting in well-marked differences. The reproductive success of a female is defined by the number of healthy offspring produced, which represents the availability of some key ecological resources, such as food, and safety from predators. Further, male's reproductive success is defined by the number of females fertilized, represented by the number of fertile females accessed. The access of these key resources for both females and males, are somehow dependent on the number of conspecific competitors that also want to reach them. Competition for limiting resources in a given environment, has a strong influence on the social relationships among primates, resulting in a dominance rank set by these limitations (Cowlshaw & Dunbar, 2000). Dominance in primate populations is often attributed to males but not always. Among them, lemur species populations are usually dominated by

females and their dominance can range from unambiguous dominance to feeding priority for females. *Propithecus edwardsi*, a folivore species, was described as an example of female dominance in their populations by Wright (1995) and later by Pochron *et al.* (2003). The results of this last study showed that females were dominant towards the males in all contexts, including feeding. As in other species, females are more energy demanding than males, and the costs of motherhood may limit females from storage sufficient fat. In female sifakas, body weight can affect the probability of a successful conception, which can be highly influenced by males. Males submit themselves to female aggressions in a feeding context to be able to increase the number of fertile females available in the next breeding season, and increase their chances of procreation. Unlike females, they do not suffer any disadvantage in a sperm-competition setting related to their body mass, being able to afford a loss of weight without any negative effects in the production of offspring (Pochron *et al.*, 2003).

1.1.3. Social interactions

The subsistence of individuals in social groups describes certain behaviors influenced by the interactions between them. Primates constitute an example of this evidence due to maintenance of affiliative bonds through social interactions (Lehmann *et al.*, 2007). Social behavior can be characterized by agonistic behaviors, involved in the development of dominance relationships, and non-agonistic social interactions (affiliative behaviors; Bekoff, 1972). Interactions of social interest are often constrained by time issues: time invested in these social affairs tends to increase with the increase of group size, while the number of relationships that an individual can keep track of decreases with this incensement. This can result in less cohesive and less stable grouping patterns, possibly leading to group fission. These interactions are both dependent of the size of the neocortex which leads to cognitive constraints, and predation pressure, which affect individual's social time. Affiliative activities include grooming, play, courtship and mating, but only grooming is related to social bonding among adults and is the only one that may seem to occupy a significance proportion of time in some species (Lehmann *et al.*, 2007).

While among New World primates grooming has an hygienic function, in the other non-human primates it is very flexible and varies among species and across

populations. It is mainly considered a primary process whereby relationships are serviced and maintained. Evidences showed that many species spend far more time in this activity than would be necessary only for hygienic purposes, having therefore a greater significance than the mere removal of ectoparasites (Dunbar, 1991; Lehmann *et al.*, 2007; Wright *et al.*, 2009). Another study evidenced that allo-grooming is concentrated in body areas which received less auto-grooming invoking its importance as a protection against ectoparasites (Hutchins & Barash, 1976).

Play is also a social behavior, defined by Bekoff (1972) as a major category of adaptive behavior that must be understood in order to be able to understand primate behavior. The ontogeny of this behavior is responsible for the development of social interactions, performing a crucial element in the development of affectional behavior towards age-mates. This behavior is only possible when individuals have the capability of doing metacommunication, through vocalizations, facial expressions and bodily gestures, indicating that they “are only playing” (Bekoff, 1972). This behavior usually came from the fulfilment achieved after the accomplishment of other activities, like alimentation or reproductive behavior. Play is related with the learning abilities of the individuals and can be very variable in type and complexity among species and populations. It’s usually associated with younger individuals which leads to the discover of how the environment can be changed and manipulated and to build social relationships. Thus, the variable influencing play behavior are gender, age, group structure and population dynamic, and they influence social development, establishment of dominance hierarchy, social integration and social communication (Poirier & Smith 1974).

1.1.4. Conservation status and major threats

The unsustainable human activities are having several negative impacts on primate populations. These activities are responsible for the declining of populations with a recent study pointing to ~60% of primate species being threatened with extinction (Estrada *et al.*, 2017). Ninety percent of these species occur in tropical or subtropical forests which experience losses of 12.5 million hectares per years (Chapman *et al.*, 2006; Chapman & Peres, 2001). Loss of habitat constitutes the main threat to the

survival of these species with several causes and consequences that, because of its importance and extension, are described in the next chapter (“Habitat disturbance”).

Besides habitat loss, primates suffer a great number of other threats that causes the loss of individuals which may lead to local and global extinctions. Hunting may also have a profound impact on forest populations, even if it is for subsistence or commercial purposes (Chapman *et al.*, 2006; Chapman & Peres, 2001; Estrada *et al.*, 2017). Bushmeat hunting provides a major food source for many local communities and primates are usually a target. Their relatively large body size, the fact of being, most of them, diurnal and terrestrial, and living in social groups, make them a prey of high interest for humans (Chapman *et al.*, 2006). Some studies point to the discrepancy found between un hunted and lightly hunted sites and moderately to heavily hunted sites, being primate population densities much higher in those sites where hunting almost not occur (Chapman & Peres, 2001). This activity is hard to track, but some reports described in a recent study (Estrada *et al.*, 2017) indicate that in some African regions about 150.000 carcasses are traded annually. The commercialization of primate’s bushmeat hunting have increased relative to subsistence hunting and, with only a small number of primates living inside protected areas, the populations outside suffer a rapid decline. Besides, the increase in rarity of some species make them more profitable, make poachers to risk themselves to go hunt in protected areas in order to increase their profit (Estrada *et al.*, 2017).

Legal and illegal trade of nonhuman primates is also becoming a driving force for population declines in many species. There are several purposes for this trade including consumption and biomedical research; to become part of zoos and wildlife collections; to become pets; for the sale of body parts to be used in traditional medicine; as talismans and trophies; and in some regions for magical purposes (Estrada *et al.*, 2017). Since the ratification of the Convention of Trade in Endangered Species of Wild Flora and Fauna in 1973, the international live-capture and trade of these species have been reduced, but it still happens in high rates (Chapman & Peres, 2001; Estrada *et al.*, 2017). These activities related with wildlife trade are being facilitated by the expansion of road networks in frontier forest being easier to translocate them to cities and through borders. Also, wildlife laundering (protected species are included in legal shipments with similar species) is happening when these animals are passed off as captive bred (Estrada *et al.*, 2017). Primates being captive as pets can also be a concern, especially at

a national scale. In many cultures, juvenile primates are kept as pets and lactating females are targets of selective harvesting to obtain the infants for this purpose. Thus, there's an increase in mortality pressure especially among infants and juveniles, which are very sensitive to captures: even if these individuals are able to survive the fall and transportation traumas they may not be able to survive in captivity because of its poor conditions and diet and because of the sudden loss of their mother (Chapman & Peres, 2001).

Climate change represents a current threat which effects have been more and more studied and may affect all biodiversity in general including primates. There is still no empirical evidence of its impacts but, according to Estrada *et al.* (2017), a recent global assessment suggests that a large number of primate will be exposed to changing climatic conditions, increasing their vulnerability. Some species are more affected by these impacts than others and thus, these are responsible by the shifting of ecological conditions in several ways. With this shifting, the optimal habitat conditions for a species may change its localization forcing the animals to move. This movement can force them out of protected areas, leaving them more vulnerable to other anthropogenic threats. Primate taxa with limited geographic distributions and species characterized by slow life history traits (reproduction) are more vulnerable to these changes. Interactions between species can also be affected, fetching changes in food supply and in the introduction of new predators, competitors and pathogens. Still, alterations in climate conditions can also have impacts on already existent climate conditions, inducing more droughts, floods, fires, hurricanes and El Niño Southern Oscillations (ENSO) events. Food supply availability will be negatively affected, with impacts on health, fertility and mortality on primate populations. All these changes need to take into account the interactions between climate changes and the other extinction drivers (Estrada *et al.*, 2017).

Not all species are affected in the same way by the same threat, becoming generalizations hard to do. However, a recent review on primate studies showed that the extinction risk does not occur randomly across taxa, at least across mammalian taxa. There are evidences of some relation between closely related taxa and their threat status, i.e., species that are found to be more closely related represent species that are more likely to face the same threat status. The sharing of the same biological intrinsic aspects of related taxa may explain the sharing of the same threats (Estrada *et al.*, 2017). Other

studies found evidences of a relation between body size and range size, being larger bodied species with small range more vulnerable to threats, especially when associated to low population densities (Chapman *et al.*, 2006).

1.2. Habitat disturbance

At a global scale, natural environments have been experiencing great changes in their composition and structure. Most of these changes relate to habitat loss and can be a result of natural events (e.g. cyclones, fires, hurricanes, droughts) and/ or anthropogenic practices (e.g. deforestation; Chapman *et al.*, 2006; Chapman & Peres, 2001; Isabirye-Basuta & Lwanga, 2008). Tropical forests have been devastated by these situations but mainly due to unsustainable human activities. Agriculture practices and large-scale production of non-native crops (for example soybeans and oil palm), livestock (cattle) and tropical hardwoods to respond the great demand by global markets are considerable impacting natural habitats, and thus, are considered main threats for wildlife populations, such as primates (Chapman *et al.*, 2006; Estrada *et al.*, 2017). Other activities, like collection of natural resources by locals, or the promotion of large economic development programs, such as resettlements or construction of infrastructures, can result in deforestation as well (Chapman *et al.*, 2006; Chapman & Peres, 2001). The loss of habitat caused by these activities is responsible for changes in the remaining habitats, causing their degradation and/or fragmentation. Different types of habitat disturbance, lead to different responses by the affected populations, having repercussions in the ecology and behavior of most primates, being mainly affected by limitation in food resources (Chapman *et al.*, 2006; Schwitzer *et al.*, 2011)..

Logging is considered one of the main causes for forest habitats degradation but with no relation to deforestation when in small scale, in fact, selective logging does not decrease forest cover to less than 10% of its original level (Chapman & Peres, 2001). Yet, when logging occurs at industrial scale because of the ever-growing demand for tropical timber, the activity can lead to high rates of deforestation, plus, the additional creation of new roads within forested areas for their transportations which causes habitat fragmentation. This activity is responsible for the reduction of canopy cover, the

destruction of forest undergrowth, and the decline of large tree species (Estrada *et al.*, 2017). The disruption of the forest canopy and the cut of food trees are critical factors to the subsistence of primate populations, representing important sources not only of food, but also shelter (Chapman *et al.*, 2006; Schwitzer *et al.*, 2011). The responses of animals to this disturbance are many, depending on the perturbation levels and the ecology of the affected species, i.e., dietary choices and plant specific composition and abundance in the disturbed area (Isabirye-Basuta & Lwanga, 2008). Species with low ecological flexibility are considered the more vulnerable to these changes due to their high degree of specialization (Chapman *et al.*, 2006). At a community level, some primates may increase, decrease or maintain their population size as a result of this disturbance. Chapman *et al.* (2000), compared the responses of five primate species to both low- and high-intensity selective logging, after decades, on the Kibale National Park, Uganda. Years after logging, there are species population that are still declining, some that recovered and another which population abundance increase in the disturbed area. Selective logging may be responsible for the increase of young leaves production due to an increase of sun light absorption. Body size was found to be also affected by logging; males of one of the study species presented better body conditions in the unlogged habitat. All these differences were only significant when comparing heavily logged areas with lightly or unlogged areas. The decrease of the relative abundance of all studied species, except one, in the heavily logged areas seems to be related to the decline in visibility in this area as undergrowth vegetation became denser (Chapman *et al.*, 2000).

Logging may be responsible for the reduction of food availability that leads to increased infant and juvenile mortality in primates, as well as, it may decrease animal health conditions and increase their vulnerability to disease or parasites (Wright *et al.*, 2009). With the canopy opening by this activity, there may be a reduction in potential canopy pathways, and increase in energy demands, risk of falling and even predation risk (Chapman *et al.*, 2000). Brown & Gurevitch (2004), studied the effects of logging in Madagascar's forests, making reference to the easy colonization of these areas by invasive, nonnative plant species that may become dominant towards the native trees that were removed. In the presence of this activity, native plants diversity tend to decrease, with the presence and abundance of native species being different in logged and unlogged areas, changing forest composition and structure (Brown & Gurevitch,

2004). In general, low-intensity logging is possible to be compatible with primate conservation. For example, in Madagascar, intermediate disturbance might favor some lemur species (by increasing food availability), but with higher disturbances, these species may eventually decline and/ or disappear. Species may present higher, lower or equal densities, when comparing disturbed and undisturbed habitats (Irwin *et al.*, 2010). The increase of some species in disturbed habitats may be explained by the increase exposure of the remaining trees to sunlight, leading to an increase of fruit abundance and in leaves quality eaten by frugivorous and folivores lemurs, respectively. But, when logging becomes more heavy, it may be incompatible with conservation of primate species (Chapman *et al.*, 2000). In general, disturbed habitats are only suitable for some species, and even some populations increase in these areas, species richness usually declines under these circumstances (Irwin *et al.*, 2010).

Natural events (e.g. cyclones (Brown & Gurevitch, 2004), hurricanes, droughts (Schwitzer *et al.*, 2011)) may have the same repercussions as logging in the degradation of habitat. Fires are considered a natural event but in tropical forests, where natural fires are extremely rare, they are usually induced and aggravated by humans. The impacts of fire in natural ecosystems are much larger than the ones provoked by logging. Animals may be directly killed by heat stress and smoke asphyxiation, or may reduce their abundance due to the loss of food resources and habitat (Chapman & Peres, 2001).

It becomes then clear that threats are inevitably correlated, with habitat loss and degradation being responsible for the increased pressure of other threats, such as hunting (Chapman *et al.*, 2006). Climate changes can also be a trigger to increase the negative responses of primates to their common threats (Chapman *et al.*, 2006; Estrada *et al.*, 2017; Karpanty & Wright 2007). Species who have their geographical range size more limited, are more vulnerable to extinction risk. With habitat disturbance, these species may not be able to move to other habitats more suitable to their survival. Endemic and rare species are the most affected by this alterations, being a priority for conservation (Chapman *et al.*, 2006).

1.3. Madagascar

Madagascar is considered the fourth largest ocean island with an area of almost 600 000 km² (Irwin *et al.*, 2010). It's located in the Indian ocean, separated from the southeastern African coast by the Mozambique Channel (Gould & Sauter, 2006).

The island of Madagascar has a long insular history which includes its segregation from the southern supercontinent of Gondwana and displacements until it reaches its actual position. About 160 million years ago, during the Jurassic period, Gondwana started to fragment leaving what we know nowadays as this island attached to Antarctica in the south and to India in the east, while the African mainland was beginning to get behind. This movement had ceased about 125 million years ago, leaving Madagascar in its actual position, and in the late Cretaceous, about 90 million years ago, the island was completely isolated. Since this moment, Madagascar started a new geological chapter as an independent micro-continent with an unique paleontological record, history of local climate change, volcanism and high-plateau formation (Gould & Sauter, 2006; Mittermeier *et al.*, 2010). It has a complex topography with a central high plateau (with almost 3000m high) that drops gradually to coastal lowlands in the west, south and north while in the east, it is separated by a steep escarpment. All these geological characteristics, combined with wind and ocean currents are responsible for the great variability of climates that we can find here. The climate changes from the eastern regions which experience high rainfall, without a true dry season and annual mean temperatures of 20-25°C, to the western regions with moderate rainfall and up to 8 dry months and annual mean temperatures of 24-28°. The south and southwest are semi-arid to arid, with a long dry season and low rainfall, and highly-variable temperatures averaging 23-24°C. Also, the central plateau has its own micro climate with lows temperatures averaging 14-22°C (with frost and possible snowfalls), variable rainfall and a moderate dry season. These variations at climate and geographic levels are responsible for the existence of different kinds of ecosystems with differences in the vegetation. In the east, we have closed-canopy evergreen rainforest, in the west dry deciduous forest, and spiny thicket with gallery forests in the south. We also have the eastern littoral forest on sand and woody formations that used to cover much of the center of the island (Ganzhorn *et al.*, 2001; Irwin *et al.*, 2010).

The geological history and geographic placement of the island are responsible for the unique fauna and flora that we can find in Madagascar. Due to its exceptional

species richness and high number of endemic species, and with a high rate of habitat loss, Madagascar is considered one of the most endangered hotspots and one of the world's 18 "megadiversity" countries (Myers *et al.*, 2000). This biodiversity hotspot stands out, not only because of its high rate of endemic species, but also because of its endemism at higher taxonomic levels (generic and family levels) among fauna and flora (Ganzhorn *et al.*, 2001; Mittermeier *et al.*, 2010). Also, relatively to non-human primate diversity, Madagascar has five primate families and 15 genera found nowhere else. Other groups of vertebrates are well represented here, with a high number of endemism also for amphibians, reptiles and birds. Separated from others mass lands for at least 90 million years ago, all the flora and fauna of Madagascar has evolved in isolation, resulting in this very high levels of endemism (Mittermeier *et al.*, 2010).

Since the arrival of humans, about 2000 years ago, Madagascar has experienced a great number of modifications in its ecosystems. This incursion was responsible for the extinction of the native large mammals and for the loss of a major part of the original cover forest of the island (Irwin *et al.*, 2010). In the case of the non-human primates (lemurs), this arrival was responsible for the extinction of eight genera and at least 17 species, corresponding to 15% of all known lemur' species (living and extinct species; Mittermeier *et al.*, 2010). Regarding habitat loss, in spite of not known for sure how much of Madagascar was originally forested, it's estimated that only 10% of the original forest remains (Ganzhorn *et al.*, 2001; Ratsimbazafy *et al.*, 2013). Among the years, Madagascar has been struggling with severe problems of deforestation in favor of agriculture and pasture, mining, extraction of precious hardwoods and other products, and a diversity of other activities. There are many reasons for this massive destruction. The population growth rate is one of them, with Malagasy population experiencing growing at 3% per year. In a country where only 5% of the land is arable and where 80% of the population depends on small-scale agricultural practices, there is an inevitable increase in land-use pressure (Clark, 2012; Ganzhorn, 1987; Ratsimbazafy *et al.*, 2013). Rice-growing is an example of agricultural land use that occurs here and are not well adjusted to these unique ecosystems. These practices come from the clearance of a plot of forest of its natural vegetation which is then burn. In fact, this leads to very problematic cases of erosion with a lot of negative effects on the ecosystems. The original flora of the island was also targeted by artisanal loggers through the removal of high-value trees. All these practices opened the way to the spread of non-native species,

an issue that has become increasingly important in conservation. Malagasy trees have a slow regeneration process, and once primary forest is cleared, invasive species, like strawberry guava (*Psidium cattleianum*), tend to be more able to take over these areas than native species (Wright, 1992). Other practices, like use of fuelwood, cattle-raising and mining, also have negative impacts on the ecosystems. The use of fuelwood is responsible for the cut down of large areas of natural forest contributing for increased hunting, introduction of invasive species and localized drying of forests leading to increase fire risk. In order to guarantee the survival of the cattle, clearance of forests takes place followed by a periodic burning that provides new grass to feed the animals. Thus, these are extended to the whole island, and in a country where there are as many cattle as people, they have a great negative impact in the most delicate areas. These activities gradually eroded the edges of forest fragments, preventing its regeneration and allowing the invasion by non-native species into primary forest. Mining has also been responsible for the degradation of many areas because of deep holes digging to found all kind of minerals (Mittermeier *et al.*, 2010). In addition, other important issue, coming from the high rate of population growth and the continued forest fragmentation is the possibility of cross-species disease transmission. Although there are still no documented cases of this situation, conservationists need to be aware of this possibility (Ratsimbazafy *et al.*, 2013).

Besides anthropogenic activities, there are also some natural events that occur in this island that are responsible for the decline of some lemur populations. Global climate cycles, such as ENSO events, have some major effects on the viability of wildlife populations. In Madagascar, these events have been documented to cause drought and changes in vegetation indices that negatively affect the ecological standards of Malagasy ecosystems. Also, the increasing of global warming may produce an increase of ENSO frequencies and intensities, becoming a growing concern for conservation (Dunham *et al.*, 2008). Other climatic events, like cyclones, can also be a disturbance fact in ecosystems and there are records of lemur populations declining after this events (Dunham *et al.*, 2011; Ratsimbazafy *et al.*, 2013).

With all its unique characteristics and threats, Madagascar is in the top global conservation priority list. Nowadays, Madagascar has an extensive network of national parks and reserves that had its beginning in 1927. It has an area corresponding to 2.3 million ha, organized in 47 protected areas (corresponding to IUCN Protected Areas

categories I, II and IV) managed by Madagascar National Parks (formerly ANGAP). There are also 27 new protected areas (2.6 million ha, corresponding to IUCN categories III, V and VI), managed directly by the Ministry of Environment and Forests with community groups and NGOs. Besides, there are more 40 areas (1.1 million ha) that have been identified as priorities. In fact, there are a large number of international and national non-government organizations working and developing partnerships in order to preserve what's left from this hotspot and at the same time make local people benefit from conservation (Mittermeier *et al.*, 2010; Wright & Andriamihaja, 2002, 2003). The World Database on Protected Areas (WDPA), in 2017, records 147 protected areas in Madagascar, including terrestrial (31.214 km²) and marine (4.308 km²) components (World Database on Protected Areas, 2017).

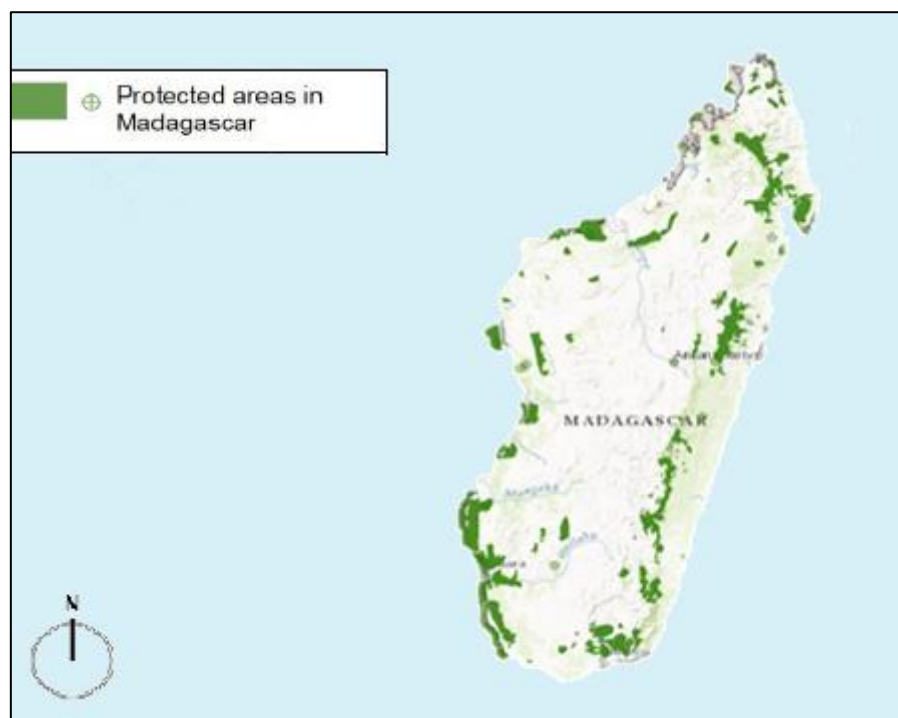


Figure 1 Map of protected areas in Madagascar (adapted from World Database on Protected Areas (2017)).

Ranomafana National Park

Ranomafana National Park (RNP) started its creation in 1986 and was designated a national park in 1991 (Wright & Andriamihaja, 2002, 2003). The discovery of the golden bamboo lemur (*Hapalemur aureus*), new species for science, and the rediscovery of the greater bamboo lemur (*Prolemur simus*) led to the institutionalization of this new protected area. The park project was influenced by the primatologist Patricia Wright who made the discoveries above mentioned, motivated by timber exploitation during the mid-1980s in this area. Actually, it's possible to find 13 lemur species in this park (six nocturnal and seven diurnal) and also an amazing biodiversity in other taxonomic groups (Wright *et al.*, 2012). From this 13, eight taxa had been focus of long term research. These researches have their major attention turned to behavioral ecology and population demographics of the diurnal lemurs including life history, reproductive biology, stress and reproductive hormones, parasites, feeding and nutritional ecology, morphometrics, predation, communication and cognition, seed dispersal, climate change, and conservation (Wright *et al.*, 2012). They are based in some three major components described by Wright *et al.* (2012) as: 1) the permanent identification of individuals for behavioral observation and censusing, 2) the collection of routine phenological data to understand when and what foods are available in the forest, and 3) the documentation of daily fluctuations in temperature (minimum and maximum) and rainfall (Wright *et al.*, 2012).

Throughout the years, there have been captures and marking of adult individuals of *Propithecus edwardsi*, *Hapalemur aureus*, *Prolemur simus*, *Eulemur rubriventer*, *Eulemur rufifrons* and *Varecia variegata* in the main study sites to become possible their identification in a long distance and usually there are also placed radio collars for an easiest location. While the animals are tranquilized, there are additional information collected: weight, reproductive state, general physical condition, body measurements, hair samples, external parasite samples, fecal samples, blood samples, and dental casts. With the combination of body weights, canine eruption patterns, general tooth wear, nipple length for females, and presence or absence of testes in males is also possible to know the age categories (infant, juvenile, young adult, prime adult, and old adult) of each individual. Also the main trees used by lemurs has been checked monthly for fruiting, flowering and new leaves, and matched with climate data to understand fluctuations in food resources (Wright *et al.*, 2012).

Nowadays, the park has more than four study sites where it's possible to do research on lemurs and other taxonomic groups. Some of them are in undisturbed or minimally disturbed rainforest and with bush camp facilities (e.g. Vatoharanana, Valohoaka and Mangevo), while others are more close to the road (Route 25) and had experienced intensive logging before the creation of the park (e.g. Talatakely and Vohiparara). At this moment, the major disturbance factors in RNP are the ecotourism with an estimate 25.000 tourist per year visiting one of these sites (Talatakely) and the introduction of the Chinese guava (*Psidium cattleynum*), an invasive species, in the early 1950s that covers several hectares of forest (Wright *et al.*, 2012).

Centre ValBio Research Station, inaugurated in 2003, is located closely to the park entrance, north of the Namarona River and on Route 25, and is the heel of scientific research in RNP. This research station provides logistical support, modern facilities and access to technology to the ones who are working within the park. In fact, there is local staff of trained lemur technicians and Malagasy biodiversity experts working here. Some of these technicians are responsible for the long-term studies conducted at the center. It's also involved in health, hygiene and education projects extend to villages all around the southeastern Madagascar. There are also some ongoing reforestation programs to improve a more sustainable use of resources. Thus, Centre ValBio has an important and active role in the conservation of the rainforest and in the welfare of the human populations that dwell in the surroundings of the park (Mittermeier *et al.*, 2010; Wright *et al.*, 2012).

1.4. Primates of Madagascar

The non-human primates of Madagascar, lemurs, are with no doubt the most diverse and acclaimed group of mammals within the island. Belonging to the Strepsirrhine group, these are classified into seven families, including the extinct “subfossil” forms: Cheirogaleidae, the dwarf lemurs, with five living genera; Lemuridae, considered the “true” lemurs and their close relatives, with four living genera and one extinct; Lepilemuridae, the sportive lemurs, with one living genera and one extinct; Indriidae, with three living genera; Archaeolemuridae, with two extinct

genera; Palaeopropithecidae, with all four genera extinct; and Daubentoniidae, the aye-ayes, with a single living genus and species (Gould & Sauther, 2006; Mittermeier *et al.*, 2010). More recent studies recognize 99 lemur species with a major increase in the beginning of the 20s (Ratsimbazafy *et al.*, 2013). Madagascar has a unique diversity of ecological settings that offer primates and other mammals conditions that can't be find nowhere else. All species of lemurs are endemics to the island, accepting the idea that the evolution of this group has an independent course for an unknown period. Because Madagascar has been essentially where it is now in relation to Africa for about 90 million years, the presence of lemurs in this oceanic island can not be explained by the African "founder effect" (nevertheless this theory may explain the presence of some of the more ancestral biota in the island). In fact, the first fossils records of Malagasy primates appear in the beginning of the Eocene. This group is assumed to be a morphometric group, i.e., all lemurs are descendants of a single successful colonization event. The most accepted hypotheses for this colonization event is that the ancestor of today's lemurs reached Madagascar by sea crossing from Africa. As explained by Mittermeier *et al.* (2010), "large, matted clumps of floating vegetation are routinely washed down major rivers and out to sea, sometimes carrying unwilling mammals or other passengers". This theory is supported by the climatic conditions and sea currents that are thought to exist at the time of this event, which has been changing over time (Gould & Sauther, 2006; Mittermeier *et al.*, 2010).

In the wild, lemurs face several anthropogenic threats that are responsible for the decline of species. The degradation and destruction of habitat is the most concerning cause of loss of species in Madagascar, but these primates also have other issues with major effects on their wild populations. Hunting lemurs is illegal in the country but in regions far from authorities and outside protected areas it still happens. Besides the use of bushmeat hunting as a food resource, there is also a traditional use for some species. For example, in some regions, hunters may use hair from their hunting object to make tea, used in the treatment of some illnesses. The larger species are the ones who suffer the most with hunters but many of them may prefer the smaller ones because of their taste. There are some traditions that benefit some species, such as the taboo against hunting *Indri* and *Propithecus*, but there are also some that requires their effective killing to protect from bad luck. The most known case is the aye-ayes (*Daubentonia madagascariensis*), who are usually considered a bad omen in northern Madagascar

traditions. Therefore, the subsistence hunting of Malagasy primates is widespread and an important matter in the conservation of this group and without alternative sources of protein, these practices are unlikely to decline (Golden *et al.*, 2011). Lemurs may also be target of live captures for local use as pets or for export but this does not represent a major problem for the conservation of this group. Within the island, it is possible to find some species (e.g. *Lemur catta*, *Varecia* and *Eulemur*) kept as pets from local people but at a much lower level than in most regions where other primates occur. However, the information on this subject is little so further investigation is needed to take more conclusive ideas. Also, because these species are all protected by Malagasy laws and are all listed in the appendices of CITES, the export of lemurs to other countries does not appear to be a serious issue. The only exports of lemurs that are documented in the last two decades only reveal scientific purposes, like for conservation-oriented breeding programs, and only a small number of individuals was taken from the wild without constituting a threat (Mittermeier *et al.*, 2010).

1.5. Significance of study

Several studies on habitat condition have been conducted using lemurs as study subject because they represent one of the largest forest dependent vertebrate species of Madagascar and can therefore be considered “umbrella species” (Ganzhorn *et al.*, 2000). In this study, *Propithecus edwardsi*, is excellent for this type of comparison; because of its large body size, it would be expected that this species would alter its feeding behavior and/or ranging behavior in the presence of habitat disturbance, even in moderate levels. Thus, they may be at high risk of localized extinctions succeeding habitat modification. It’s also expected that sifakas may have a behavior plastic enough to change in response to habitat disturbance because of their long-life spans and high variability of social structure (Pochron & Wright, 2003). To finish, although their dental and gut morphology suggest evolutionary adaptations to folivory, there have been controversy between observational data regarding exactly how obligatory folivory it is. Most studies point that their diet consists of almost equal proportions of leaves, fruits and seeds with some amendments with regard to the level of habitat disturbance where each population are (Arrigo-Nelson, 2006; Hemingway, 1996, 1998).

Through the comparison of the feeding behavior of this specie in disturbed and undisturbed forest we may be able to predict population changes in relation to habitat modifications and its vulnerability to habitat disturbance (Chapman *et al.*, 2006; Wright *et al.*, 2009). This can be relevant in view of ongoing habitat degradation and can be applied in conservation and reforestation efforts (Schwitzer *et al.*, 2011). These kind of comparisons can allow the researchers to test their results obtained from one of the study sites and also the creation of a baseline data set for similar phenomenon (Chapman & Peres, 2001).

1.6. Main goals

The overarching goal of this research is to better understand feeding differences between males and females in disturbed and undisturbed forest. Thus, the main goals of this study are: 1) compare the time each gender within the studied populations spent feeding in the disturbed and undisturbed habitats, 2) compare the time each gender within the studied populations spent in social activities in the disturbed and undisturbed habitats, and 3) compare the time each gender within the studied populations spent feeding on leaves *versus* fruits/seeds in the two distinct habitats.

2. Materials and methods

2.1. Study site

Ranomafana National Park (RNP) is located in a southeast mountain rainforest of Madagascar, 21°16'S latitude and 47°20'E longitude, in the province of Fionarantsoa, with altitudes ranging from 600 to 1.487 m. The park contains moist evergreen forest and the canopy height ranges from 18 to 25 m and the most common plant family found here is Monimiaceae. The yearly average rainfall is over 3.000 mm, but there is a considerable interannual variation. The climate conditions vary seasonally with rainfall and temperatures reaching its highest levels from December through March (King *et al.*, 2012; Wright, 1995; Wright *et al.*, 2012).

This study was carried out in two different study sites within RNP (Fig. 2), one consisting in disturbed forest (Vohiparara) and the other in undisturbed forest (Mangevo), which were selected for their past 'use' histories. Mangevo (S21° 22' 22.8" E047 26' 59.1"), corresponds to the study site in the pristine forest. It's located about 20 km from Centre ValBio Research Station and the park entrance, with an altitude range from 565 to 1065 m. This area has the characteristics of a primary forest without any perturbation, and it's in one of the most remote parts of the park. It's possible to find the lemur species *Varecia variegata* in this habitat, a forest ecological specialist that only subsists in pristine habitats (Baden, 2016; Wright, 1999). Vohiparara is the second study site, close to Route 25 with altitudes that ranges from 1075 to 1275 m. The localization of each study site within the park is represented in Figure 2. The forest in this area has a structure characteristic of disturbed areas, because of the intense selected logging that occurred here in the latest 20s (Wright *et al.*, 2012). Thus, it's characterized by decreased tree height, basal area and crown volume, and an increase in the forest's species diversity, compared to the undisturbed site. The previous removal of some trees through selective logging, also changed the dominance and abundance of the selected tree taxa, favoring fast growing species (native and non-native species; Arrigo-Nelson, 2006). Therefore, this area consists of low, discontinuous canopy with an high understory density (Herrera *et al.*, 2011).

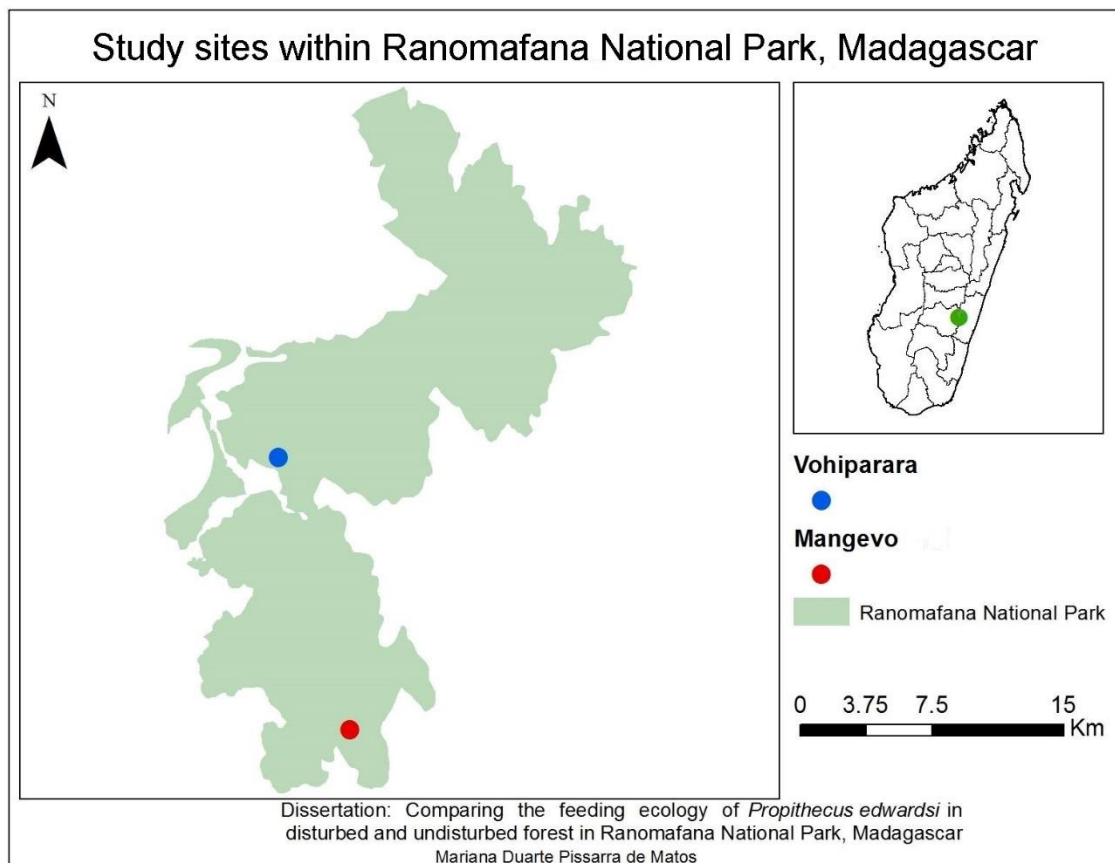


Figure 2 Map of Ranomafana National Park with the localization of the study sites (Mangevo: undisturbed habitat; Vohiparara: disturbed habitat).

2.2. Study groups

The study species represented in this study is *Propithecus edwardsi* (Fig. 3), the largest non-human primate found in RNP (average weight of 5.0-6.5 kg). It's a diurnal species without sexual dimorphism and, previously described as an anatomical folivore. Their diet is a combination of leaves, fruits and seeds that vary seasonally, strengthened with the occasional consumption of soil and the seasonal consumption of insect larvae. In fact, sifakas have spiral shaped colon which permits hindgut fermentation and make them more like seed predators. During the long-term study that last for 20 years the drinking of water was never noticed (Arrigo-Nelson, 2006; Hemingway, 1998). Their total social group size ranges from 2 to 9 individuals and the groups territory ranges from 30 to 55 ha (Arrigo-Nelson, 2006; Pochron & Wright, 2003; Wright, 1995), and they can only be found in the rain forest of southeastern Madagascar (Irwin *et al.*, 2005;

Mittermeier *et al.*, 2010). Belonging to the Indriidae family, this sifakas are classified by the 2008 IUCN Red List as Endangered (EN), due to the massive loss of habitat and hunting to which they are subject (Dunham *et al.*, 2008; Mittermeier *et al.*, 2010). There are also natural



causes that contribute for the current decline of this specie. Death by predation is one with their major predator being the fossa, *Cryptoprocta ferox*, without evidences of any aerial predators (Irwin *et al.*, 2009; Karpanty & Wright 2007). Also, ENSO events can cause periods of reduced fecundity (about 65%) which may be related to reduction in precipitation (Dunham *et al.*, 2008).

2.2.1. Group composition

In total, there were followed 16 individuals organized in five social groups: two in the undisturbed area (total of 6 individuals) and three in the disturbed area (total of 10 individuals). In the undisturbed area, two of the females were in lactation and in the disturbed there were also two females lactating but one of them lost her infant when a new male arrived in the group. All information about groups composition and individual's characteristics is given in Annex 1.

2.2.2. Capture methods

In continuation of long-term study of *Propithecus edwardsi* carried out in Centre Valbio and to help in this study, animals from both study sites were captured using a well-established and successful protocol (King *et al.*, 2010). There were five individuals in total that were capture and release by a team of trained technicians: four in the undisturbed habitat and two in the disturbed habitat. The animals were darted in the morning using a Tranquilizer gun with darts using a mixture of ketamine hydrochloride and diazepam. Each animal was given a nylon collar that allows the identification of

each individual and differentiate the sex from long distances. The females use a collared collar with a collared tag and the males only use a collared collar to prevent the tags to interfere with the scent marking with the chest gland. Captured animals also received a subcutaneous microchip (AVID, HomeAgain®) if it's the first time they are darted, and usually at least one radio collar is placed in each group (King *et al.*, 2010; Wright *et al.*, 2012), but this year due to found lacking there were no radio collars placed. There was also collected morphometric and health data on each individual captured, as described previously.

Before start data collection, in the study site corresponding to the undisturbed habitat, it was fundamental to habituate some groups there. This procedure consists in frequent contacts with the same individuals or groups to make them aware of human presence and at the same time learn how to ignore it. To do this, it was necessary to find and follow them for as long as possible, every day, until the individuals would stay all together as a group and not running away when they contact with human beings (Williamson & Feistner, 2003). Because the animals weren't radio-tagged, it was unavoidable to locate them by hiking through the forest. This task was easier due to the previous knowledge of the group's territories by the team of technicians. The procedure last for about five days for one of the groups and nearly nine for the other one with an average of seven hours daily. After this it was possible to follow each one of these groups for full days, from dawn to dusk.

2.3. Data collection

The data used in this study was collected every day (from Monday to Friday) from all the study groups from July through September 2016. The author and a team of trained Malagasy research technicians followed a group each week, observing two different individuals from the same group each day, for seven weeks. Scan samples were collected at five-minute intervals from dawn to dusk and only adults and sub adults (from 3 years old) were followed. Due to the small sizes and spread of the study groups, and the research team's ability to recognize all study animals individually it was

possible to use this method of sampling without any inconvenient (adapted from Arrigo-Nelson, 2006).

During each instantaneous group scan, the activity (e.g. feeding, resting, traveling, self-grooming and social grooming; Annex 4), height and distance from all group members (until 10 m) were recorded for each focal individual within a group. When the focal animal was observed feeding, there was additional information that was recorded on the specific food item consumed, including the plant part and maturity level of the food consumed. Additionally, there was also recorded the duration of each feeding and social activity bout (e.g. social grooming and play). Only behavioral records collected during full day (dawn-dusk) or complete half day (dawn-midday or midday-dusk) group follows with a minimum of 6 continuous observation hours have been included in the following analyses (adapted from Arrigo-Nelson, 2006), resulting in a total of 488,25 hours of group observations and a total of 5859 scan samples.

2.4. Data analyses

The data from scan samples were used to determine the proportion of each of the considered activities (e.g. rest, self-groom, travel, feed, social activities, and sense marking) for each gender within each study site. Hypothesis test for proportions were applied to each behavior in order to verified if there were significant differences between study sites and sexes (Afonso & Nunes, 2010).

The data collected corresponding to durations, were used to determine the daily average time males and females spend in feeding behaviors and social activities in each study site. The behavior “play”, included in “social behaviors”, was only found during one day of observations and in one adult individual, hence, this behavior was not used in the statistical analysis. Before any statistical test, these data were arcsine transformed to reach the assumptions needed to do analyses using parametric tests. Pared-sample T tests were used with the durations of feeding and social activities, separately, in each study site. It was also a goal to find with which type of food they spend more time on. It was necessary to group each food item into: “Leaves” which include both mature and immature leaves; “Fruits and seeds” which include both ripe and unripe fruits and also

seeds; “Flowers” including any flower or bud; and “Soil” including any substrate that is possible to find on the floor. This data was analyzed using the Kruskal-Wallis test used to compare the time, in minutes, each sex in each study site spent feeding on each food type (Afonso & Nunes, 2010).

Some correlation tests were also applied to these data in order to measure the degree of relationship between variables. It was applied the Spearman's rank correlation coefficient to measure the relationship between the time sifakas spent feeding and their sex, study site and food type consumed, and the time sifakas spent in social grooming and their sex and study site. This test uses non-parametric data, being the only one possible to use with this data. To verify the existence of correlation between the time spent feeding and social grooming, it was applied the Pearson's correlation coefficient, which can only be used with parametric data (Afonso & Nunes, 2010).

3. Results

Focal samples

In general, individuals from both study sites presents differences in their daily activities (Fig.3). In Mangevo, individuals spent more time on resting and social activities, with a percentage difference of 9,9% and 1,7% respectively. However, only the differences found in resting activities are significant (*). The individuals in Vohiparara, on the contrary, seem to spend more time on feeding behavior (10,4%). Activities like “Self-grooming”, “Scent marking” or others related with movement (“Travel”) showed very small differences. The “OOS” corresponds to those moments when the author and the technicians were not able to see the focal individual at the time of registration the activity. The number of “OOS” were higher in Vohiparara than in Mangevo, due to technical difficulties during field work.

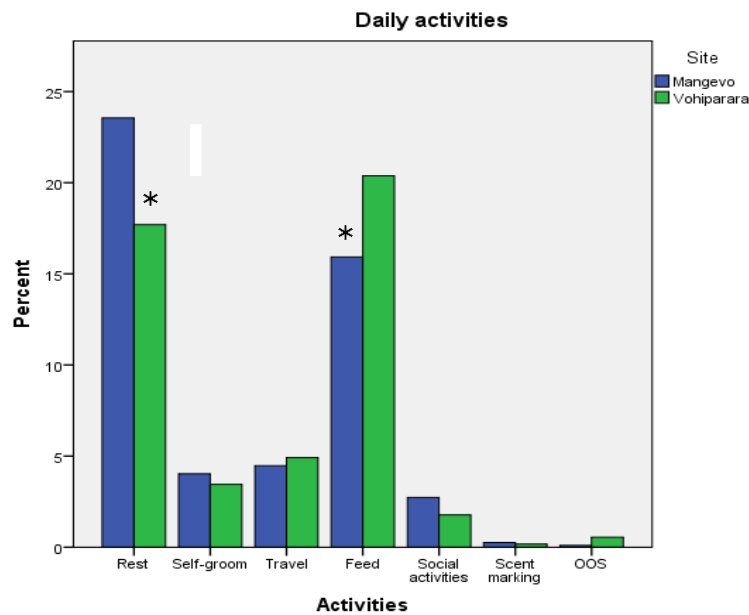


Figure 4 Comparison of daily activities of *Propithecus edwardsi* in disturbed (Vohiparara) and undisturbed (Mangevo) habitats, measured by % of each activity (* significant differences). OOS represent the “out of site” observations, when focal individuals were not possible to visually.

When comparing the proportion of these daily activities between sexes in each study site, according to the proportion tests applied, no significant differences were found (Fig. 4). The percentage of each activity is very similar within each study area for females and males.

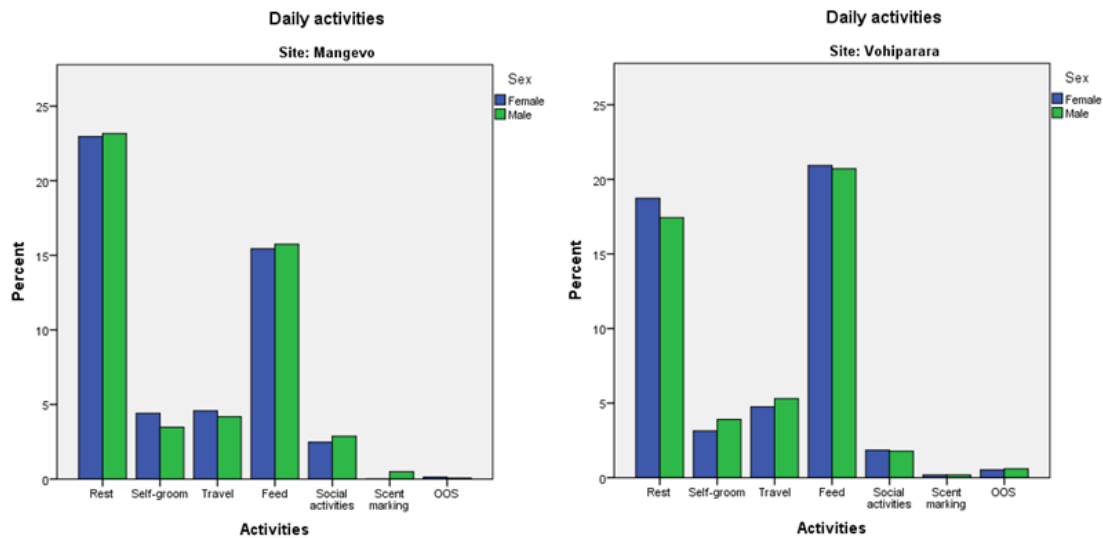


Figure 5 Graph 1: Comparison of daily activities of each sex of *Propithecus edwardsi*, in undisturbed habitat (Mangevo). Graph 2: Comparison of daily activities of each sex of *Propithecus edwardsi*, in disturbed habitat (Vohiparara). Both graphics are measured by % of each activity.

Further, when comparing each sex from both study sites, the differences start to show up. In Graph 1 from Fig. 5 is shown the proportion differences of each daily activity from both study sites only for females. The only activities who showed significant differences among females from both sites were “Rest”, “Self-groom” and “Feed”. In Mangevo, females were seen more times resting and self-grooming than the females in Vohiparara. Here, females were seen more times engaged in feeding activities than any other daily activity.

In Graph 2 from Fig. 5, its represented the frequency of each daily activity for males from each study site. The only activities who showed significant differences between sites were “Rest”, “Feed” and “Social activities”. In Mangevo, males of *P. edwardsi* were seen more frequently in resting and social behaviors than the ones in Vohiparara. The remain activities were more frequent in Vohiparara than in Mangevo. However, the differences found in social activities for males, were not considered once

the results from the total duration of those behaviors do not support this difference, as we will see in Table 3.

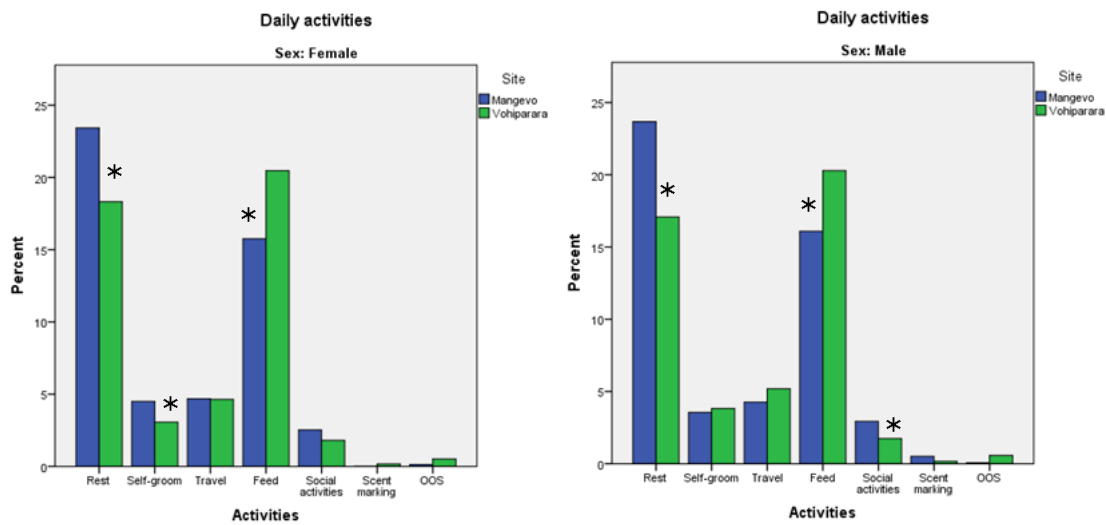


Figure 6 Graph 1: Comparison of daily activities of *Propithecus edwardsi* females, between undisturbed (Mangevo) and disturbed (Vohiparara) habitats. Graph 2: Comparison of daily activities of *Propithecus edwardsi* males, between undisturbed (Mangevo) and disturbed (Vohiparara). Both graphics are measured by % of each activity (* significant differences).

Feeding behavior

In addition to focal sample collection, we recorded the duration of each feeding bout which gave us the time each gender spent in each bout in each study site (Table 1). Applying statistical analyses to these data, there were no significant variation between females and males in each study site ($p > 0,05$), but there were significant differences between study sites for individuals of *P. edwardsi* in general ($p < 0,05$). Though, when these analyses were applied to compare each gender between study sites the results are very different. Females presented a significant difference ($p = 0,00$) in their feeding bout duration when comparing the times in each study site, with Vohiparara having the longest durations. Comparing the same data on males, the differences in their feeding duration in each site are also significant ($p = 0,004$).

Table 1 Differences among study sites for each sex of *Propithecus edwardsi*, in feeding time.

Sex	Site	Feeding Time (%)	Feeding Hours	Total Observation Hours	P
Females	Mangevo	30,9	36,77	118,42	0.000**
	Vohiparara	41,8	46,45	126,67	
Males	Mangevo	31,5	36,26	118,42	0,004**
	Vohiparara	41,5	44,55	126,67	

** P < 0,01

Comparing the time individuals spent feeding on each food type, there were found some significant differences. The Kruskal-Wallis Test rejected our null hypothesis that the distribution of the time is the same across categories of food type, for each gender in both study sites. However, when the time spent feeding in each food type is analyzed for both sexes in each study site, no significant differences were found. Table 2 presents the results the differences between sites for sexes and we can see that leaves were the most used food type among individuals of *P. edwardsi*, both for females and males in the two study sites. The study site where more leaves were eaten was Mangevo, however, only females presented significant differences between sites ($p < 0,05$). Contrary, soil was the food time less seen to be eaten in both study site, and both sexes spent more time feeding soil in Mangevo than in Vohiparara. However, these differences were only significant for females ($p < 0,01$). The time individuals spent feeding on fruits and seeds, and flowers, are placed between leaves and soil, with the values being always higher in the disturbed site. Vohiparara was the site were individuals from both sexes were seen eating more fruits and seeds, but when sites are compared for each one of them, females were the only presenting significant differences ($p < 0,05$). When comparing, the time spent in the food type corresponding to flowers and but, Vohiparara also had the highest duration times but significant differences were only found in male sifakas ($p < 0,01$).

Table 2 Differences among study sites for each sex of *Propithecus edwardsi*, in feeding time devoted to different food types.

Food type	Sex	Site	Feeding Time (%)	Feeding Hours	P
Leaves	Female	Mangevo	75,6	24,27	0,044*
		Vohiparara	64,3	23,52	
	Male	Mangevo	76,7	25,16	0,423
		Vohiparara	60,5	20,46	
Fruits and seeds	Female	Mangevo	20,2	11,77	0,021*
		Vohiparara	21,7	14,50	
	Male	Mangevo	17,1	10,44	0,429
		Vohiparara	22,5	13,60	
Flowers	Female	Mangevo	2,3	35,5 min	0,051
		Vohiparara	12,6	8,02	
	Male	Mangevo	3,7	25,5 min	0,000**
		Vohiparara	15,5	10,33	
Soil	Female	Mangevo	1,8	8,5 min	0,007**
		Vohiparara	1,4	14 min	
	Male	Mangevo	2,6	14 min	0,499
		Vohiparara	1,5	10 min	

* P < 0,05; ** P < 0,01

Social grooming

The duration of social grooming has not presented any significant difference between sexes in each study site ($p > 0,05$). When this data is analyzed comparing each gender between study areas, females are the only ones who showed a significant difference ($p < 0,05$; Table 3). Females in Mangevo spent more time engaged in social grooming than females in Vohiparara.

Table 3 Differences among study sites for each sex of *Propithecus edwardsi*, in social grooming time.

Sex	Site	Grooming Time (%)	Grooming Hours	Total Observation Hours	P
Females	Mangevo	4,9	6,40	118,42	0,024*
	Vohiparara	3,7	3,84	126,67	
Males	Mangevo	5,7	7,63	118,42	0,656
	Vohiparara	3,6	3,36	126,67	

* P < 0,05

Correlations between variables

Statistical tests were applied to this data in order to find any correlations between the study variables. Table 4 shows the results of those tests with the corresponding variables. Feeding time variable showed significant correlation with variables, such as site and food type ($p=0,00$). Variable correspondent to sex, didn't correlate with any other variable, the same as grooming time. For those variables, it was used Spearman's rank correlation coefficient. Also, correlation tests showed that the duration of feeding and social grooming behaviors do not correlate between them. A Pearson's correlation coefficient was used to test these two variables and the results showed a very weak relationship between the two variables ($p>0,05$).

Table 4 Correlation values for the study variables.

Correlated variables		N	Correlation Coefficient	P
Feeding time	Site	1765	0,109	0,000**
	Sex	1765	-0,029	0,217
	Food type	1765	0,160	0,000**
Grooming time	Site	661	0,066	0,088
	Sex	661	0,025	0,529
Feeding time	Grooming time	324	0,028	0,621

Cell values denote Spearman's rank-order correlation coefficient with exception to the last line, which denote Pearson's correlation coefficient.

**P < 0,01

4. Discussion

There were very few differences in the type of behaviors observed in individuals of *Propithecus edwardsi* between the disturbed and undisturbed habitats, however their frequency showed some significant differences. Previous studies on primate behavior have shown a decrease in behavior diversity (Negrín *et al.*, 2016), or alteration in behavioral frequencies (Nijman, 2006), in habitats with higher degree of human disturbance. Others report the effects of selective logging in forest composition and structure, and their implications in food availability (Arrigo-Nelson, 2006; Brown & Gurevitch, 2004; Chapman *et al.*, 2000; Ganzhorn, 1995), making feeding the behavior more predicted to be change due to habitat disturbance. The results of our study showed significant differences between the time adult and sub-adult sifakas spent feeding in disturbed and undisturbed forests. Both sexes were found to spent more time feeding in the disturbed forest than their counterparts in the undisturbed forest. These results show differences in diet, suggesting differences in food quality and/ or availability; if in the disturbed habitat food quality is lower, animals are forced to spend more time feeding to reach the same nutritional levels than their counterparts in the pristine forest. Arrigo-Nelson (2006), pointed out the impacts of small crown volumes and basal areas in the production of new leaves, flowers and fruits by trees in disturbed habitats. Malagasy trees are usually much smaller than those found in other tropical forests, both in terms of crown size and tree stature (Ganzhorn *et al.*, 2009), thus, when affected by selective logging, the impacts may be much more severe. Arrigo-Nelson (2006) showed the same results for the same study species, which spent more time feeding in the disturbed habitat than in the undisturbed habitat, during the cool/dry season. For *P. diadema*, Irwin (2008) also found that sifakas in fragmented forests spent more time feeding than their counterparts in the continuous forest.

Looking at their diet profile, our results are consistent with those detected in other studies (Arrigo-Nelson, 2006; Hemingway, 1998; Wright *et al.*, 2005), with sifakas found feeding on leaves, flowers, fruits, seeds and soil, being leaves the food item more consumed. Several studies showed that selective logging is, due to the increase of the remaining trees to sun exposure, responsible for increasing protein and phenolic levels in leaves (Arrigo-Nelson, 2006; Ganzhorn, 1995; Herrera *et al.*, 2011). Our results showed significant differences for time spent on leaves consumption in females. The higher quality of leaves in the disturbed habitat, enables individuals from

spending less time feeding on this food item to reach their protein requirements. In the undisturbed forest, leaves protein rates are considered to be lower, so to reach the same protein requirements, individuals in this area need to spend more time feeding on them. Females in the undisturbed forest need to spend more time feeding on low quality leaves than their counterparts in the disturbed forest in order to reach the same nutritional level. With female nutritional requirements being the same in the two studied areas, this difference in their feeding behavior may evidence the differences in the quality of leaves in one habitat and in the other. However, no conclusions can be made due to the lack of data on food quality and availability. During the study period, there were two lactating females in each study site sample. Lactation has been previously described as a high energetic demanding phase in reproduction for mammal females in general, allocating 80% of the total energy (Gittleman & Thompson, 1988). Females during this phase, may need to increase energetic intake, feeding more than nonlactating females, in order to maintain normal their metabolic balance (Barrett *et al.*, 2006; Dias *et al.*, 2011). There's a possible increase in about 30% in feeding bout lengths, as well as an increase in feeding frequency and selection (Gittleman & Thompson, 1988). They have been estimated to increase caloric intake by 66-188% during lactation, with peak levels of energy use approaching 2.5-5 times non-reproductive females (Dias *et al.*, 2011; Gittleman & Thompson, 1988). Other strategies may be adopted, such as the allocation of energy from activity to lactation by reducing some behaviors, minimizing additional energy requirements (Dias *et al.*, 2011; Gittleman & Thompson, 1988). Thus, females may present more significant differences between sites than males due to their higher reproduction costs and nutritional requirements.

Irwin (2008) showed some interesting results about food preference among sifakas in continuous and fragmented forests. He suggested that “leaves are the least preferred food”, despite sifakas predisposition to folivory. Norscia *et al.* (2006) observed sifakas feeding on fruits and immature leaves, until such food items were available, leading sometimes to their total consumption on the tree. Although no food data related to availability and taxonomy was collected in the present study, the high levels of fruits, seeds and flowers consumption suggest that sifakas eat those foods items whenever they are available, showing preference for fruits. Arrigo-Nelson (2006) had already suggested that these sifakas are not obligate folivores, supporting this evidence with her own study. Wright *et al.* (2005) results suggested that sifakas are

opportunistic frugivores that track the overall fruit richness in the forest, although they spend the majority of time eating leaves.

Sifakas digestive adaptations do not show themselves so efficient extracting nutrients, when compared to other folivores primates, such as the *Indri indri*. Powsyk & Mowry (2003) found that Indri's digestive tract presents advantages that made them more efficient folivores than *Propithecus diadema diadema*. Sifakas have showed a richer diet in fats and water-soluble carbohydrates than the Indri, which reflects their preference for seeds, fruits and flowers. Thus, they are more dependent on those food items, result of their faster gut passage, better nutrient absorption and less limitation of digestive constrains on activity, than the Indri. Also, fruits represent a food resource with readily available nutrients, which make them more easily to be digested, decreasing the digestion time. If their digestion time is lower, they need to spend more time feeding on those foods, than others who spend more time feeding on leaves and have longer digestion periods. Leaves on the other hand, take more time to digest and extract the nutrients, and their digestion takes longer, what causes the increase in energy cost (Powsyk & Mowry, 2003). This may explain why in the disturbed site, sifakas spent more time feeding, once they eat more readily available nutrients present in fruits and flowers, while in the pristine forest, they eat more leaves with more longer digestion periods. Hanya & Chapman (2013) showed evidences that large body size primates with digestive adaptations to folivory, are able to gain sufficient protein from leaves, so they prioritize non-protein energy intake.

Energy intake during cool/dry season, it's especially important for *P. edwardsi* because it's their birth season. Foods, such as fruits and seeds, are specially nutritional because of their high rates of sugar and fats, and are usually consumed during this season (Arrigo-Nelson, 2006). Females should be expected to feed more on those food items, once they spend more energy related to reproduction and parental care costs than males. No differences between males and females were found in each study site, but the differences between females in the two sites may result from differences in food availability which leads to different diets that may have negative impacts on reproductive success of this species. In the undisturbed site, females spent less time feeding on fruits and seeds, and thus, do not store as much sugar and fats that their counterparts in the disturbed site. Female sifakas at RNP, give to birth during June, lactating for the two first months without fruits and seeds. However, newborns are very

small, weighting around 100g (less than 2% of the mother's weight), which allows the reduction of initial costs of lactation (Wright, 1999). It's during the peak fruiting season that infants start to increase their nutritional requirements, associated to an increase in biomass. Thus, Wright *et al.* (2005) suggested that, "even sifakas, while relatively opportunistic fruit eaters, may rely on fruit as key resources for reproductive success". Although fruits may be important for reproductive success and represent a great part of their diet, they are not decisive in animal's survival. During lean season, sifakas drop fruit consumption and increase leave consumption, and appear to adopt a conservancy energy strategy. However, these strategies seem not to be compensating the energy loss, in terms of low fruit consumption, once sifakas may lose up to 20% of their weight during winter (Wright *et al.*, 2005). During this period, individuals only rely on leaves as are presumed to be nutrient-limited during some times of the year (Hemingway, 1998).

More results on our study also showed differences in time spent feeding on other food items, such as flowers, and fruits and seeds; individuals in the disturbed forest spent more time feeding on flowers (only males), and fruits and seed (only females). During the cool/dry season, flowers are predicted to be more available than fruits, however the levels of fruits and seeds consumption were always higher than the levels of flower consumption. The fact that, in the disturbed forest, females spent more time feeding on fruits and seeds and males spent more time feeding on flowers, and that, according to the bibliography, females are dominant over males, their feeding priority gives females the priority over males to choose fruits and seeds over flowers. Irwin (2008) showed several evidences that sifakas may have preference for fruits over flowers; he found that fruit/ seed consumption was positively correlated with fruit availability, while bud/ flower consumption was negatively correlated with fruit availability. Hemingway (1998) also found preference over seeds during sifakas' feeding periods. *P. diadema edwardsi*, had shown dramatic interannual switch to leaf eating, when occurs the decrease of preferred seed sources. Altitude differences between the two study sites may also have repercussions on food availability, once altitude can influence the micro climate of each site, including precipitation. Rainfall has been previously related to patterns of new leaves and flower production, but not with fruiting patterning (Hemingway, 1998).

However, most studies on selective logging mention the removal of larger trees, which have the greatest economic value and are also responsible for an important part of fruit production within the forest (Wright *et al.*, 2005). Timber extraction leads to a decrease in fruit production and their availability as a food resource (Arrigo-Nelson, 2006; Herrera *et al.*, 2011). The fruit patterning in Malagasy forest has been described as a peculiar process due to many canopy species which produce flowers and fruits on very irregular cycles, becoming food availability highly seasonal. During winter, fruit production is not only characterized by a drop in the number of producing trees but also in the number of producing species. Thus, the seasonal cycling of fruit diversity was found to be strongly reflected in the diet of *P. edwardsi* (Wright *et al.*, 2005). After logging, tree species diversity in the forest changes, and the new gaps created by the removal of large trees allow other small, medium trees to grow, as well as invasive species (Brown & Gurevitch, 2004; Ganzhorn, 1995). Ganzhorn (1995) observed in his study that some tree species may increase their production of biomass when subjected to low, moderated levels of anthropogenic disturbance. He didn't find differences in fruit fall between logged and unlogged areas, however, along logging trails it was higher. Along forest edge, the exposure to sunlight by the remaining trees can induce a higher production of flowers and fruits, increasing their availability. Even without having any information about species richness and availability in our two study sites, selective logging at RNP occurred about 30 years ago, which may represent a significant amount of time to create changes in the remaining forest previously disturbed. We then suggest, the disturbed forest may have a higher composition in species flowering and fructifying, leading to an increase in high energetic food items availability during the cold/ dry season. Thus, time spent feeding may be related with the type of food ingested. In the disturbed forest, it looks like there are enough fruits and flowers availability to let sifakas choose them those foods over leaves. The relation between food choice and availability, can be very variable leading to differences in selectivity and preference. Hemingway (1998) found no correlation between food availability and diet choice in *P. diadema edwardsi*, which she interpreted "as highly monthly selectivity and feeding in accordance with the availability of certain foods". Dietary choices of some species may be more related to availability, which can result in nonsignificant differences, explaining those results.

Arrigo-Nelson (2006) showed different results from the ones of this study. On an annual scale, *P. edwardsi* showed differences in their diet when comparing it in disturbed and undisturbed forests, and a major dietary imbalance during the austral winter. During this season, individuals dwelling in the pristine forest spent less time feeding on leaves and more time feeding on fruits than their counterparts in the disturbed forest, getting a more energetic diet which decreases the time spent feeding. Her data then suggests that the diet of sifakas dwelling in the disturbed forest, contains smaller quantities of sugar and fats found in fruits and seeds. Although our study was carried out in a short period of time (only during the cool/dry season), our results are not supported by Arrigo-Nelson (2006), who concluded that in selective logged habitat, sifakas consume less fruit resources and more leaf resources than their counterparts living in the pristine forest. Related to tree-species dominance, she observed that by decreasing the dominance of the larger fruit producing trees through disturbance, there are limitations imposed to flower and fruit consumption by sifakas living in logged habitats. Those animals experienced a decrease in the consumption of these foods and increase the consumption of leaves in their diets. She also found (Arrigo-Nelson 2006) that on those habitats, animals use non-tree plant species as fallback foods, which were found more available in the disturbed forest. When compared the food quality of each food type between sites, she only found differences in the macronutrient content of mature leaves, suggesting that selective logging at RNP have little long-term impact on food quality. However, this do not have influence on the nutrient intake of individuals on each study site. During the cool/ dry season, her results corroborate ours when looking at time spent feeding. In the disturbed habitat, sifakas spent more time feeding than their counterparts in the undisturbed habitat and she explained it by invoking the differences in food availability between the two habitats. In this case, selective logging was responsible for the removal of major fruit trees and the new ones that replace them may be immature to produce flowers and fruits.

Soil consumption was also found to have differences between females in the two habitats, with females in Mangevo spending more time feeding on this food item than their counterparts in Vohiparara. Krishnamani & Mahaney (2000) formulated several hypotheses for the role of geophagy, some that may help to explain our results. First, geophagy may be related to detoxification of deleterious plant compounds, as observed in sifakas by Powsyk & Mowry (2003). Due to soil poor nutritional levels in rain

forests, plants developed high concentrations of defensive secondary compounds in their leaves, in order to avoid possible predators. Folivores primates have symbiotic bacteria dwelling in their foregut, that not only detoxify, but also feed deterrents avoiding possible gastrointestinal upsets. Soil consumption can lead to a microbiome enrichment (Norscia *et al.*, 2006). Other strategies may be used in order to dodge those compounds, such as avoiding mature leaves, which are richer in toxins, and eating more seeds (Krishnamani & Mahaney, 2000). Second, soil consumption may be related with acids production during fermentation. During this process, there's a production of volatile fatty acids that decrease stomach pH. Symbiotic bacteria found its optimal pH at high values, which is not favored by acids production. The ingestion of clay was found to enhance the buffering action of stomach secretions, as well as counteract the effects of acid food, by the absorption of organic molecules such as the fatty acids (Krishnamani & Mahaney, 2000). These hypotheses may explain the major consumption of soil in the undisturbed forest, relating them to the other types of food ingested. To finish, geophagy may also have no understanding meaning, as it is found in *Macaca fuscata*, but its practice is also known to an increase in nutrient and minerals in diet, which minimize most bowel and gastric disorders (Krishnamani & Mahaney, 2000). In the disturbed habitat, it is expected diet richness to be lower than in the undisturbed habitat. In this sense, individuals in the disturbed forest needed to spend more time feeding on soil to obtain more minerals and nutrients. However, these differences are only for females which can be explain by the higher nutritional requirements that they have when compared to males.

We found correlations between forest type and the time sifakas spent feeding, dependent and independently of food type. The main differences considered between the two study sites are the history of selective logging in the disturbed forest, and the differences in altitude that may influence climacteric events, such as precipitation, and influence plant productivity. Food availability was proved to change in the presence of human activities, such as selective logging, as previously referenced. Although our study lack in food availability information, the differences in their diet are clear, suggesting alterations in forest composition which result in differences in different food types availability and consumption.

Habitat disturbance was already found to change food resources and with it species diet, affecting other biological aspects of species behavior and ecology. In

folivores, biomass was previously found to be related with this and can increase with the ingestion of higher quality leaves in habitats previously affected by selective logging. The increased light penetration in the disturbed forest, increases the protein/fiber ratio in leaves, increasing their quality. Therefore, the abundance of some folivores species can also increase on those habitats, as it was described by Herrera *et al.* (2011). However, for *P. edwardsi* no differences in abundance were found between logged and unlogged habitats. Group size has also been described as affected by disturbance; resource patches become smaller and patchier distributed after a perturbation, reducing the habitat support capacity for individuals, than larger and denser patches, which are capable of support more individuals (Herrera *et al.*, 2011). Nevertheless, Chapman *et al.* (2000) in their study found differences in group size between logged and unlogged areas for a study species; group size was higher in the logged area and these differences were attributed either to reproductive rates that may be higher in the logged area or to movements of individuals from the unlogged to the logged area that may be considered by the species has a preferred habitat. In the present study, it was observed that groups in the pristine forest were smaller than groups found in the disturbed forest; in Vohiparara, group size ranges from three to seven individuals (Group 3 with seven individuals was not used as study sample due to the larger size), while in Mangevo the two habituated groups only have three individuals, besides other observed groups that were not followed or habituated with also three individuals (but no information was collected).

The fact sifakas spent more time in one activity, influences the time they spent in other activities. Richer habitats are usually associated to high food nutritional levels, allowing animals to reach their energetic needs quicker, leaving more time for other behaviors, such as social behaviors (Arrigo-Nelson, 2006). Our results showed that social grooming within each sex presents significant differences only for females, between sites. In the undisturbed habitat, females from *P. edwardsi* spent more time engaged in this activity than their counterparts in the disturbed habitat. Social interactions entail energetic costs, which can relate to the limitation of food resources in a negative way. In the undisturbed habitat, individuals spent less time feeding, so they have more time to spend in social behaviors (Lehmann *et al.*, 2007; Negrín *et al.*, 2016). However, because social interactions entail energetic costs, it would be expected that individuals who feed more on high energetic food items spend more time in these

activities, even without more free time. Yet, our results showed that they spent more time engaged in this activity in the pristine forest, where they feed more on leaves and less on fruits, and differences are only for females. This activity was observed between individuals from the same gender and from different ones. Because social groups in the undisturbed site were found to be smaller than in the disturbed site and the more followed group only had one female, males may need to spend more time grooming or mutual grooming the female to secure a reproductive pair for the mating season. Nevertheless, it would be expected that individuals belonging to larger groups spent less time resting and more time socializing in order to increase and to maintain their social network (Lehmann *et al.*, 2007; Majolo *et al.*, 2008). The increase in time spent grooming, leave sifakas less time to rest during daylight, as well as to other activities, such as foraging and infant care, which may affect negatively their fitness. In this case, individuals in larger groups are found in the disturbed habitat, where sifakas have their time budget limited by feeding behaviors. When individuals spend a great part of their day feeding, the remaining hours must be split by the other behaviors. However, in our results no correlation was found between the time spent feeding and the time spent in social grooming. This lack of correlation may result from the time these specimens also spent in other activities. For example, resting is the most common behavior found in the two study sites regardless their gender. The lack of high energetic foods during the cool/dry season, make them decrease their activity to preserve energy, explaining the high frequency of this behavior (Norscia *et al.*, 2006).

Sifakas spent more time resting in the undisturbed than in the disturbed forest. In the undisturbed habitat, their diet includes more leaves and less fruits which increase the digestion time, making animals spend more time resting. In the disturbed forest, even without data on food availability, sifakas ate other food than leaves more than their counterparts in the pristine forest which leads to a quicker digestion. Arrigo-Nelson (2006) used this explanation to support differences found in their behavior between seasons. In the pristine forest during this season, animals spent more time resting and socializing and less time traveling and feeding, due to the low availability of fruits and higher availability of leaves. Norscia *et al.* (2006) found that the dry season alone have influence in the behavior of *Propithecus verreauxi* in Kirindy. It's responsible for a reduction in home range, core area and daily path length, which may support our results. In our study, the behavior travel didn't have significant differences both for sexes in

each study site and for each sex between study sites. The fact that no differences were found in travel behavior between the two forests, may suggest that flower and fruit availability were more uniformly spread in the disturbed forest, once sifakas did not move more to reach these resources.

Group size can still be related with other behaviors. Majolo *et al.* (2008) found that groups with more individuals spend more time feeding, than groups with less individuals. They found that those differences are independent of species ecology and social system, and local climatic conditions, suggesting that those differences are not related with short-term habitat characteristics. However, food selection and distribution was found to play an important role in this context, supporting our results where individuals in the disturbed habitat, where group size is higher, did spend more time feeding than their counterparts in the undisturbed habitat. The increase in time feeding is possible to represent a cost for larger groups, once sifakas on those groups need to spend more time and energy foraging to fulfil their daily energetic requirements, than smaller groups. These groups may also struggle with high reproductive costs, once individuals dwelling on those groups experience greater foraging effort, causing detrimental effects on individual fitness. The capacity of individuals to adapt to changes that may occur on their physical or social environment, is considered a key factor on this issue. Larger groups may entail higher costs, preventing individuals from produce counter-strategies, such as the migration to smaller groups. When the habitat is saturated and/or fragmented, fission and dispersal strategies may be too costly, due to the lack of resources or suitable habitat and the presence of other groups in the surrounding areas (Majolo *et al.*, 2008).

5. Conclusions

Propithecus edwardsi have been described as obligate folivores but recent evidences may show the contrary. Leaves were found to be the most consumed food item by sifakas, but flowers and fruits/ seeds were eaten wherever they were available. Even without information either about quantity and quality of food resources, we believe that food availability is the main responsible for different diet profiles. Seasonal foods, such as flowers and fruits, were higher consumed in the disturbed forest, which may be due to differences provoked by selective logging in forest composition. Selective logging was found in many studies to change the diversity and quantity of tree species within the forest, which in turn have influence over food availability and diet.

Social groups dwelling in each forest adopt different strategies over food and energy consumption. In the pristine forest, sifakas ingested more leaves, spent more time resting and less time feeding. Leaves digestion takes more time and is not so nutritionally profitable than fruit ingestion. On this site, sifakas adopted an energy conservation strategy that allow them to feed on foods with lower nutritional value and preserve energy. In the disturbed forest, where flowers and fruits/ seeds availability is considered to be higher, sifakas eat them more than their counterparts in the pristine forest. Here, even without moving more along the forest, they spent more time feeding and less time resting. Those foods have a faster digestion, with the nutrients easier to reach, increasing the time animals need to spent feeding. Differences between the two adopted strategies are probably related with food availability with impacts in their diet.

Long-term impacts of selective logging, were found to be responsible for changes in sifakas behavior and ecology. Effects on diet, caused by differences in food availability between disturbed and undisturbed forests, may lead to differences in the frequency of some daily activities, such as feeding, resting and grooming, being all related. This type of disturbance may also have an impact on social groups size and maybe on individuals' body mass, but no conclusions can be made with the collected data. In spite of selective logging changed habitat characteristics, sifakas dwelling on those areas showed very similar behavior patterns despite the differences in some frequencies. The new plant species that occupy the free spaces left by the removal of some major trees are probably affecting the food choices of sifakas but are not necessarily having a negative effect in their survival. Birth rates in the logged habitat seem to be stable, once in the last two years at least five infants were born.

In the continuation of the long-term study of this species, our results will improve it, exalting the importance of continuity in primatology studies. Our study may be important to understand in each way, anthropogenic activities such as selective logging, can influence the ecology of *P. edwardsi*. Further investigations, should be aware of the importance of information about food availability, both plants parts and taxonomic diversity, and the quality of those food items in feeding behavior studies. These data help to understand the results found in behavior with greater security, allowing to take more secure conclusions. Besides, it can also be important and help in future reforestation projects, taking into account the more consumed plant species and their presence in the forest.

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Annexes

Annex I

Table 5 Composition of social groups of *Propithecus edwardsi* used as study sample during the present study. Marked individuals represent the study subjects, individuals with ages up to 3 years old. (*Group 4 was followed during two weeks separated by a three weeks' period, in which a sub-adult male arrived into the group and killed the newborn. During the second week of observations, the adult female of the group was not lactating.)

Site	Group	ID	Sex	Age	
Mangevo	1	Mom1+ Infant	Female	> 4	Adult
		Mom2 + Infant	Female	> 4	Adult
		Tiel	Male	> 4	Adult
	2	Purple- Green	Female	> 4	Adult
		Yellow	Male	> 4	Adult
		Green	Male	3 – 4	Sub adult
Vohiparara	1	Mom + Infant	Female	> 4	Adult
		AM	Male	> 4	Adult
		SAF	Female	3 – 4	Sub adult
		SAM	Male	3 – 4	Sub adult
		JF	Female	1 – 2	Juvenile
	2	AF1	Female	> 4	Adult
		AF2	Female	> 4	Adult
		AM	Male	> 4	Adult
		EF	Female	≤1	Earlyling
	4	Mom* + Infant	Female	> 4	Adult
		Red	Male	> 4	Adult
		AM	Male	> 4	Adult
		Yellow- Orange	Female	1 – 2	Juvenile

Annex 2

Table 6 Comparison between sex in each study site, for feeding and grooming time values.

		P	
Site	Sex	Feeding time	Grooming time
Mangevo	Females	0,636	0,173
	Males		
Vohiparara	Females	0,278	0,275
	Males		

Table 7 Comparison between sex in each study site, for the time values spent feeding each food type.

		P			
Site	Sex	Leaves	Fruits and seeds	Flowers	Soil
Mangevo	Females	0,728	0,346	0,051	0,351
	Males				
Vohiparara	Females	0,185	0,058	0,510	0,170
	Males				

Field Technical Data Sheet

Project:

Site:

Researcher:

Group:

Date:

Individual:

Time	Activity	Food type/ Partners	Nearest neighbor	Height

Start time	End time	Activity	Food type/ Partners

Ethogram

Behaviors	Initials	Description
Rest	R	Animals are sitting or standing, in the trees or on the floor, without moving.
Self-groom	SG	Animals clean their own fur/skin, removing parasites and other materials.
Travel	T	Animals jump or move between trees or in the same tree.
Feed	F	Animals sniff or transport food, bite, gnaw or lick food, rip leaves or peels, picks up insects. It includes all foraging and eating behaviors.
Social activities	SA	Animals interact with each other's, including only affiliative interactions, e.g. allogrooming and play.
Scent mark	SM	Animals rub their chest (only males) or their genitals in the trunk of the trees.
Out of sight	OOS	Animal not in sight.