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The Impact of Tourism on Ring-Tailed Lemur (*Lemur catta*) Behaviour, Home Range Size and Habitat Use at Berenty Reserve, Madagascar

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ABSTRACT

The ring-tailed lemur (Lemur catta), endemic to Madagascar, is considered 'Near Threatened' by the International Union of Conservation of Nature. The limited numbers are the result of anthropogenic activities. No previous research has specifically investigated the possible impact of primate tourism on free-ranging ring-tailed lemurs; which is imperative to understanding future conservation measures that need to be enforced. This study was carried out between February and April at Berenty Reserve in Madagascar, and investigated the impact of tourist pressure on the behaviour, home range size and habitat usage of two troops of ring-tailed lemur subjected to different intensities of tourism. Tourist presence was found to negatively influence the activity budget behaviour of resting, and positively influence intra-troop aggression. Furthermore, increasing tourist density was found to negatively influence feeding on human food resources. Greater rates of scent-marking (both a hypothesised self-directed behaviour indicative of anxiety, as well as an activity of 'tradition' in ring-tailed lemurs) were apparent when tourists were present. Increased inter-troop aggression was found to be positively related to greater rates of scent-marking, tourist feeding interactions, and feeding on human food resources. Minimum Convex Polygons and Kernel Density Estimators were used to analyse the home ranges, revealing that food resource distribution influenced home range size and usage. This research suggested that highly clumped and nutritious provisioned foods (including introduced tree species), resulted in greater rates of intra-troop and inter-troop aggression (most notably amongst females) and scent-marking behaviours. It was concluded that overcrowding, and smaller home ranges of troops found at the tourist front are indirectly due to tourist pressure. This study therefore highlights the need for improved monitoring of food provisioning and ways to control and mitigate the overcrowding lemur populations.

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CHAPTER 1: *INTRODUCTION*

'Primate tourism', where humans seek out free-ranging primates in their natural environment, is a recent and growing phenomenon. Past research investigating the effects of visitors on non-human primates has primarily focused on captive species (Hosey, 2005; Wells, 2005; Mallapur *et al.*, 2005). Recently however, with the growth of primate tourism there has been an increase in research conducted on free-ranging primates; most notably behavioural studies, as these are invaluable when assessing short-term impacts (Hodgeson *et al.*, 2004; Borg 2011). Nevertheless, the primary focus of this literature regards haplorhine primates, particularly the great apes (mountain gorilla, *Gorilla beringei beringei*: Muyambi, 2005; common chimpanzee, *Pan troglodytes*: Johns, 1996) and macaques (Barbary macaque, *Macaca sylvanus*: O'Leary and Fa, 1993; Marechal *et al.*, 2011; Sulawesi black macaque, *M. nigra*: Kinnaird and O'Brien, 1996; Tibetan macaque, *M. thibetana*: Matheson *et al.*, 2007; McCarthy *et al.*, 2009; Formosan macaque, *M. cyclopis*: Hsu *et al.*, 2009). To my knowledge, there is no specific research looking at the impact on strepsirrhine behaviours (Berman *et al.*, 2007).

Previous haplorhine studies found that tourism was related to behaviour alterations seen amongst non-human primates. Although the findings suggest that different species have varying interspecific sensitivities to tourism (Marechal, 2010), often these behaviour changes were associated with increased anxiety and/or physiological stress (Matheson *et al.*, 2007; Marechal *et al.*, 2011). Consequently, this could have adverse, long-term effects on primate health and welfare (Berman *et al.*, 2007). Therefore, research investigating the impacts of tourism on primates is essential for examining and mitigating tourism practices which could be detrimental to primate conservation.

The aim of this study was to determine the effect of tourism on ring-tailed lemur (*Lemur catta*) behaviour, particularly looking at anxiety levels and home range size, in two troops of free-ranging lemurs subjected to different intensities of tourism. The tourism impact was analysed through behavioural data collection on human/ring-tailed lemur interactions, activity budgets, intra-troop and inter-troop aggression, self-directed behaviours (SDB), aggressive vocalisations and home range use. Anxiety levels were analysed through the rates of self-directed behaviours; only few studies to my knowledge, have investigated this relationship between tourism and primates' anxiety levels (Matheson *et al.*, 2007; Marechal *et al.*, 2011).

This chapter introduces the broad concept of wildlife tourism, including a short description of primate tourism, most notably in Madagascar. Types of tourist/wildlife interactions and animal responses to these interactions are briefly presented before looking at the importance of captive versus free-ranging tourism/wildlife relationship studies. The main impacts of wildlife tourism on animals are then discussed, followed by a summary of the literature and the rationale behind this research. The chapter closes with a description of the study species, followed by the aims and hypotheses of the study.

1.1 WILDLIFE TOURISM

The tourist industry generates greater than 9% of global gross domestic product (Muehlenbein and Ancrenaz 2009), with wildlife tourism being the fastest growing sector within the industry (Balmford *et al.*, 2009; Higginbottom, 2004; Giannecchini, 1993). Wildlife tourism involves humans paying to encounter non-domesticated animals, predominantly in their natural habitat (Higginbottom *et al.*, 2001; Higginbottom, 2004) and is often associated with a range of diverse activities including whale-watching and bird-watching, visiting zoological gardens and aquaria, recreational fishing and hunting (Sinha, 2001).

Wildlife tourism became popular in the 18th century with the creation of the first zoological garden in 1752 in Schonbrunn, Austria (Higginbottom, 2004; Marechal, 2010). Technological advancements in transportation in the 20th century witnessed the growth of the tourism sector, resulting in tourism extending to the far corners of the world (Higginbottom, 2004). Much of the wildlife tourism today is found in developing countries with biodiversity-rich areas offering 'immeasurable' opportunities for wildlife viewing (Akama, 1996; Muehlenbein and Ancrenaz, 2009).

Wildlife tourism is often considered a form of 'ecotourism' – tourism adopting environmentally-friendly and sustainable practices for both local people and wildlife (Higginbottom, 2004); which is essential for the management and protection of species (Cunha, 2010). Nevertheless, "true" ecotourism is often hard to define, manage, and achieve; resulting in unsuccessful projects, most notably those focused on wildlife such as primates (Cunha, 2010; Fuentes *et al.*, 2007; Nakamura and Nishida, 2009). Primate tourism is considered a 'special interest tourism', whereby tourists have travelled to a particular location primarily for the purpose of viewing a particular non-human primate species (Higginbottom, 2004).

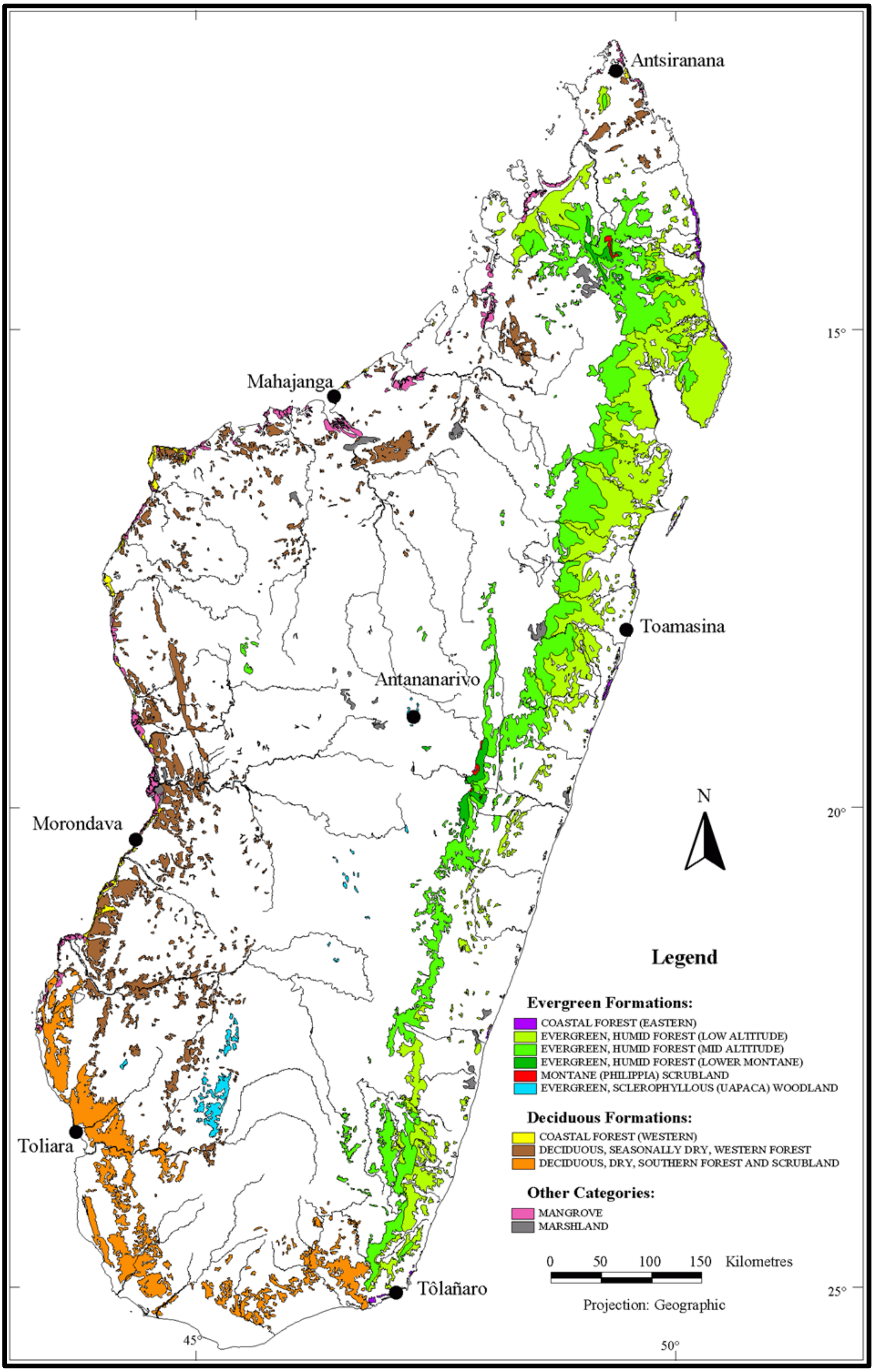
1.1.1 Primate Tourism

Primate species are often considered charismatic; this bodes well for their conservation through the protection and awareness enforced by ecotourism projects (Cunha, 2010). Conversely, primate species are therefore more exposed to the impacts of wildlife tourism (Cowlishaw and Dunbar, 2000). Primate tourism is a fairly recent phenomenon, which took off in the early 1960's when humans had the opportunity to view the great apes in Malaysia, Rwanda and Uganda (Muehlenbein and Ancrenaz, 2009). Nowadays, tourists can easily trek across the globe to view many different primate species in their natural surroundings. In addition, they also have the opportunity to encounter many 'threatened' and 'endangered' species; such as the bonobo (*Pan paniscus*) in the Democratic Republic of Congo, Barbary macaques in Morocco, slender loris (*Loris tardigradus*) in Sri Lanka, and the red ruffed lemur (*Varecia rubrai*) in Madagascar. This threat classification of the primate makes the "nature experience" even more special compared to viewing non-threatened wildlife (Fuentes *et al.*, 2007). For this special interest tourism to be successful, it is thought that primates should be approachable, diurnal, easily identified in predictable locations, and habituated to tourist presence (Reynolds and Braithwaite, 2001). Although primate tourism serves valuable conservation and educational goals, more research is needed to investigate the possible impacts on primate species (Berman and Li, 2002).

1.1.2 Primate Tourism in Madagascar

Madagascar, considered one of the most important 'biodiversity hotspots' in the world by the Conservation International, is the only known habitat of many endemic species, including the lemurs (Mittermeier *et al.*, 2004; 2005). As a result of being isolated for approximately 165 million years; about 93% of the flora and fauna species on the island are endemic, with 100% of the primate species being endemic (Valentine and Birtles, 2004; Bradt, 2011). Consequently, this makes Madagascar a highly desirable primate tourism destination.

The first humans arrived on the island about 2000 years ago, and since this time Madagascar has been subjected to increased habitat alteration through various agricultural clearing practices (Burney *et al.*, 2004; Cameron, 2007). Additionally, the growth in human population, tourism, logging, and mining, has resulted in further forest destruction and subsequent habitat loss for the approximately 101 lemur species on the 587,045 km^2 island (Mittermeier *et al.*, 1999; 2005; 2008; Markolf *et al.*, 2011). Since the arrival of the first humans, at least 14 lemur species have become extinct and more than half of the remaining species are classified as 'threatened' or 'endangered' (Smith *et al.*, 2002; Mittermeier et al., 1999). It is thought that only 50 – 60,000 km^2 of available land mass is capable of supporting existing lemur populations (Figure 1.1) (Mittermeier *et al.*, 2005; 2008; Burney, 2003), so efforts to conserve the biodiversity in Madagascar has focused on establishing and managing nature reserves (i.e. protected areas), which gain revenue through primate tourism (Axel and Maurer, 2011; Smith *et al.*, 2002).



<u>FIGURE 1.1</u> Remaining Primary Vegetation in Madagascar (*Source*: Du Puy and Moat, 1998).

The government of Madagascar is promoting tourism as an 'economic development strategy' to bring the country out of poverty; this saw the industry generating approximately $50 million per annum in the mid-1990's (Buckley, 2003). Regardless of the underdeveloped tourist regions, primate tourism is therefore becoming increasingly popular in Madagascar, thus highlighting the urgency for research to be conducted investigating the impact of human/lemur interactions.

1.2 TYPES OF TOURIST/WILDLIFE INTERACTIONS

"Rogue baboon executed after terrorising South African residents" (The Telegraph, 2010) and *"2 dingoes maul 3-year-old girl on Australia beach"* (The Guardian, 2011), are two news story examples of where the most common tourist/wildlife interaction of 'feeding' (Orams, 2002), often initiated by tourists (Berman *et al.*, 2007; O'Leary and Fa, 1993), has spiralled out of control, thus provoking additional agonistic behaviours in animals and resulting in a disastrous outcome (Orams, 2002; Burns and Howard, 2003). Although extreme cases, these news stories highlight why tourist/wildlife interactions may not always be positive for the wildlife and/or the humans involved.

Sinha (2001) suggests tourist/wildlife interactions can be categorised into 'consumptive' and 'non-consumptive'. Consumptive wildlife tourism, although not the type of interactions being investigated in this study, is briefly described as the interaction of wildlife and tourists through recreational hunting, fishing, or trophy hunting and fishing. Conversely, non-consumptive wildlife tourism does not involve the capture and killing of animals, but wildlife and tourists interact through activities of wildlife viewing, neutral interactions (i.e. waving and photo-taking), and often feeding and touching (Sinha, 2001; Higginbottom *et al.*, 2001). These non-consumptive interactions affect animals differently due to their varying interspecific sensitivities to humans (Marechal, 2010). Nonetheless, these types of tourist/wildlife interactions can lead to possible behavioural changes, disease transmission, and an increase in anxiety and physiological stress (*Section 1.4*).

1.2.1 Animal Responses

Wildlife reactions to tourists can be determined through the analysis of animal responses towards tourist/wildlife interactions (Marechal, 2010). These immediate responses are categorised into ‘avoidance’, ‘attraction’ and ‘acceptance’ which correspond to the animal’s perception of the external tourist stimuli being aversive, reinforcing or neutral, respectively (Whittaker and Knight, 1998). The ‘avoidance response’ describes when animals flee from humans, hide, or actively/passively defend themselves (Knight, 2009; Borg, 2011). This response was observed in golden eagles (*Aquila chrysaetos*), whom abandoned their nests on perceiving human presence, regardless if the humans were far away and unaware of the eagles’ existence (Huxley, 1994). Similarly, killer whales (*Orcinus orca*) were shown to display avoidance tactics (i.e. similar to those seen when prey escapes a predator) when approached by a boat (Williams *et al.*, 2002; Constantine *et al.*, 2004).

Conversely the ‘attraction response’ is often seen when animals overcome their fear and approach tourists – usually with the expectation of food rewards (Orams, 2002; Knight, 2009). Wildlife-watching tourism may depend on this response for regular, reliable sightings; resulting in increased tourist satisfaction (Orams, 2002). Finally, the ‘acceptance response’ occurs when animals become habituated to tourist presence, whereby the recurring stimulus of tourist pressure leads to the reduction of a response (Knight, 2009). For example, magellanic penguins (*Spheniscus magellanicus*) prone to high levels of visitors were found to have lower physiological stress levels at nesting sites than penguins who were non-habituated (Fowler, 1999) (*Section 1.4.1*).

Tourist pressure can be measured through tourist presence, density of tourists, noise levels, and proximity towards the animals (Hosey and Druck, 1987; Birke, 2002; Ruesto *et al.*, 2010). Nevertheless, animals appear to display different sensitivities to tourist pressure, which are also affected by individual characteristics (i.e. species, age, health and rank) and external factors (i.e. habitat type, season and tourist activity) (Mullner *et al.*, 2004; Sinha, 2001). Studies have shown that tourist density can have an effect on activity budget behaviour and physiological stress levels. For example, bottlenose dolphins (*Tursiops truncatus*) displayed decreased amounts of resting time as the number of tourist boats increased (Constantine *et al.*, 2004). With regards to physiological stress; yellow-eyed penguins (*Megadyptes antipodes*) showed a positive correlation between increased tourist number and physiological stress levels (Ellenberg *et al.*, 2007). Such behavioural and physiological changes could have adverse impacts on long-term health and survival (*Sections 1.4.3.3 and 1.4.3.5*).

Tourist pressure can also be measured through noise disturbance. For example, Ruesto *et al.* (2010) found that the rate of aggressive threats seen in Tibetan macaques, were positively related to an increase in tourist decibel levels. Finally, although limited research has been conducted looking at the effect of tourist proximity on animal behaviour and anxiety levels (Tibetan macaques, *M. thibetana*: Matheson *et al.,* 2007; Barbary macaques, *M. sylvanus*: Marechal *et al.*, 2011), these studies demonstrated that animals increased self-directed behaviours when tourists were in close proximity. To confirm, there is a need for more research to be conducted on the tourist/wildlife interactions with regard to the impact of tourist pressure on animal behaviours.

1.3 CAPTIVE VERSUS FREE-RANGING STUDIES

The impact of tourist pressure and wildlife/tourism interactions have been documented in free-ranging animal species (European pine marten, *Martes martes*: Barja *et al*., 2007; Tibetan macaques, *M. thibetana*: Berman *et al.*, 2007; pygmy marmosets, *Cebuella pygmaea*: De la Torre *et al.*, 2000; Barbary macaques, *M. sylvanus*: Marechal *et al.*, 2011), and even more so in captive species (western lowland gorilla, *G. gorilla gorilla:* Carder and Semple, 2008; common chimpanzee, *P. troglodytes*: Cook and Hosey, 1995; long-tailed macaques, *M. silenus*: Mallapur *et al.*, 2005). Captive animal studies of this kind have been well researched for the past 25 years, with free-ranging studies being a more recent area of exploration (Hosey, 2005).

Captive studies benefit from the obvious advantage that animals in captivity are easier to identify and research (Mulcahy, 2003). However, captive studies regarding animal behaviour have been open to criticism when applying these findings to wild or free-ranging populations; it is thought that the captive environment encourages abnormal behaviours which cannot be applied to such populations (Hutchins *et al.*, 1984). Such behavioural examples include body rocking in chimpanzees (Pazol and Bloomsmith, 1993) and regurgitation in gorilla species (Lukas, 1999). Nevertheless, it has been discovered that certain behaviours were found to differ between zoo-environments but were not significantly different when compared with the wild (i.e. activity budgets of Sulawesi macaques, *M. nigra*: Melfi and Feistner, 2002). This suggests that captive and free-ranging studies are of equal importance and act as a means of comparison to each other when conducting research on any species, most notably studies examining animal behaviour (Hosey, 1997; 2005).

Free-ranging ring-tailed lemurs were researched in this study because, although zoos play an important role in the protection and conservation of many species, a primary focus should look at those species currently existing in their natural environment. With numbers of lemurs decreasing due to anthropological impacts, it is important to research human/lemur interactions in their natural environment to find ways of mitigating these impacts (Smith *et al.*, 2002; Mittermeier et al., 1999). The ring-tailed lemur is seen as a 'flagship species' of Madagascar, thus studies on them in their natural environment can also increase awareness and be applied to more engendered lemur species on the island (Mittermeier *et al.*, 1999; 2008; Jolly *et al.*, 2002).

1.4 THE MAIN IMPACTS OF WILDLIFE TOURISM ON ANIMALS

Although wildlife tourism can have a positive influence on animal species, the majority of research suggests the impact is negative; ranging from short-term behaviour changes to long-term physiological changes in life history patterns (Figure 1.2) (Matheson *et al.*, 2006; Ellenberg *et al.*, 2007; Marechal, 2010). It is therefore imperative to examine a wide range of literature, across a variety of different taxa to fully understand the impacts of tourist/wildlife interactions (Higginbottom, 2004; Borg, 2011). This understanding is important for the future conservation of animal species subjected to wildlife tourism, because impacts on an individual scale can affect whole communities (Tapper, 2006).

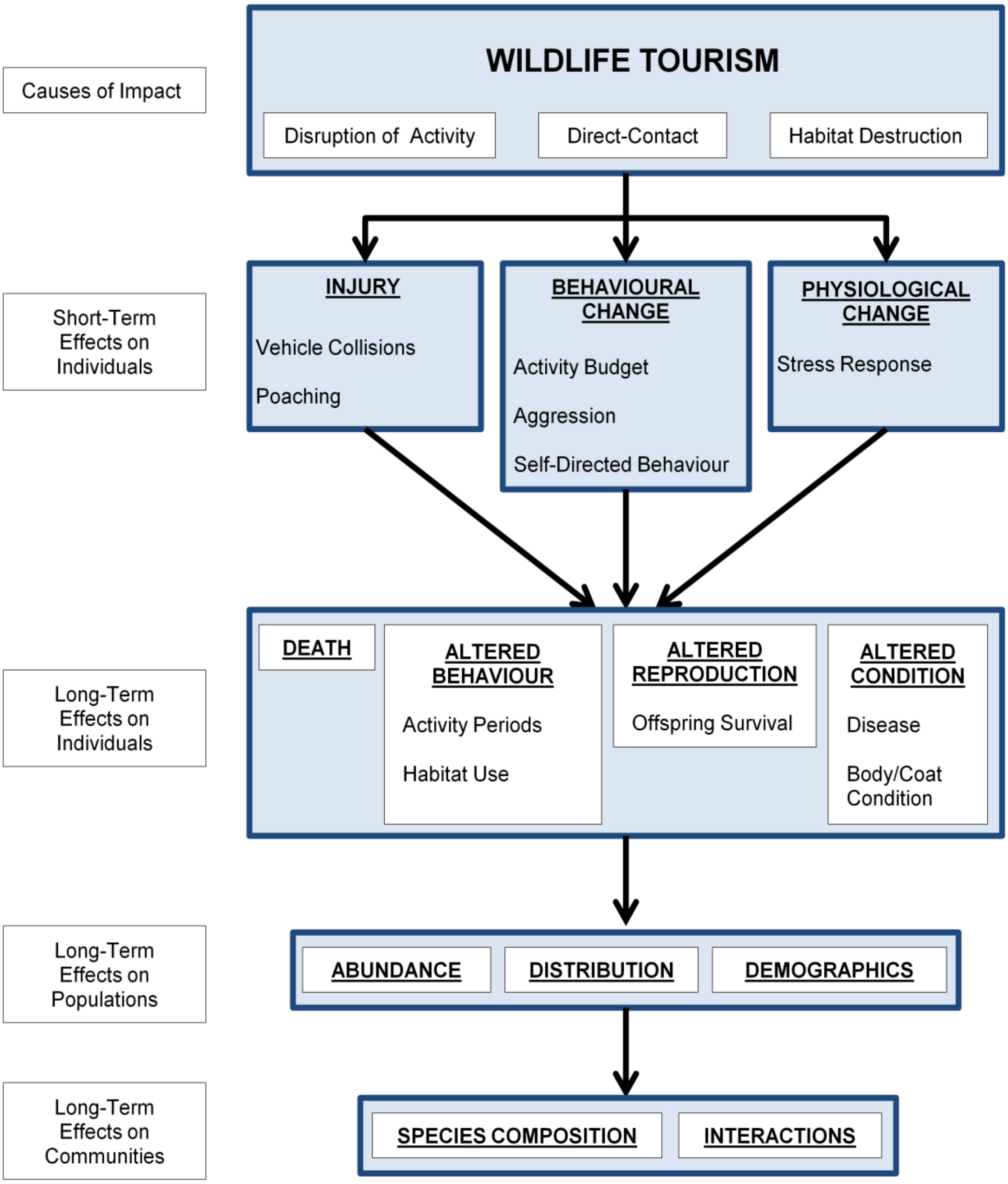


FIGURE 1.2 A Conceptual Model of the Impacts of Wildlife Tourism on Animals *(Sourced and adapted from Green and Higginbottom (2001); Borg (2011); Knight and Cole (1995).*

This section will examine the following impacts of wildlife tourism on animals: habituation, disease transmission, behaviour and demography.

1.4.1 Habituation

The ethological definition of ‘habituation’, states that with increased exposure, an animal learns that the stimulus has neither adverse nor beneficial effects, thus the animal’s responsiveness to that stimulus wanes (Thorpe, 1963 in Bedjer *et al.*, 2009). Therefore, by constantly being exposed to tourists, wild animals eventually learn to accept the human observers as a neutral element in their environment and no longer flee from their presence (McLennan and Hill 2010); as seen in chimpanzees (Johns, 1996) and grey whales, *Eschrichtius robustus* (Swartz *et al.*, 2006). This was also demonstrated in wintering bald eagles (*Haliaeetus leucocephalus*), which became habituated to tourist boats along a stretch of heavily travelled water in America, and as a result flushed from trees less than non-habituated eagles (Knight and Knight, 1984). This acceptance behaviour can lead to alterations in animals’ stress responses by reducing the instinctive, evolutionary classic ‘fight or flight’ reaction (Higham and Shelton, 2011; Knight, 2009). This resultant loss of fear and increase in tolerance to human contact, proximity and interaction, has made animals more susceptible to capture and poaching (Orams, 2002). For example, habituated eastern lowland gorillas (*Gorilla beringei graueri*) in Kahuzi-Biega National Park in the Democratic Republic of Congo were found to be 1.6 times more susceptible to poaching compared to their non-habituated counterparts (Kasereka *et al.*, 2006). Additionally, habituated animals can also lose fear of vehicles and boats, which saw a whole population of eastern quoll (*Dasyurus viverrinus*) being killed by motor vehicles in Tasmania (Jones, 2000), and numerous tourist-exposed stingrays (*Dasyatis americana*) sporting boat propeller injuries in Grand Cayman (Semeniuk and Rothley, 2008).

The problem is exacerbated by tourists' expectations of wildlife tourism. For example, some Japanese tourists were found to believe that animals should be habituated so that they were easily accessible, visible and could interact with the tourists (Knight, 2010). Thus to keep tourists satisfied, animals can undergo the stressful process of purposeful habituation (McLennan and Hill, 2010). It can provoke aggression, fear, and disrupted ranging and activity patterns (i.e. grizzly bears, *Ursus arctos horribili*, foraging in urban areas: Gunther, 1992), exacerbation of crop-raiding behaviour, and increased risk of physical attacks on people (Madden, 2006; Hocking *et al.*, 2010). For example, in Bulindi in Uganda, chimpanzees have been known to attack young children (McLennan, 2008; McLennan and Hill, 2010). This increase in aggression is often observed in primates (e.g. some baboon, Barbary macaque and chimpanzee populations) whose curious nature and opportunistic diet make them very susceptible to provisioning effects (Wrangham, 1974; Goodall, 1986; O'Leary and Fa, 1993; Borg, 2011). In Indonesia, lion-tailed macaque species were shown to display more aggressive behaviours towards tourists who possessed food (Wheatley and Harya Putra, 1994). This redirection of aggression towards tourists is an increasing problem, often with severe outcomes of injury or death (e.g. Tibetan macaques, *Macaca thibetana*: Zhao, 2005; Matheson *et al.*, 2007). Tourists who displayed aggression (i.e. throwing objects) towards animal culprits who stole their food, were often physically attacked (i.e. grabbed and bitten) (Long-tailed macaques, *Macaca fascicularis*: Fuentes *et al*., 2008).

In addition to increased aggression and reduced 'fight or flight' responses, habituation can also cause immunosuppression, thus resulting in increased susceptibility to infectious diseases and even decreasing fecundity (Muehlenbein and Ancrenaz, 2009). In contrast, artificial provisioning has also been linked to improved health and nutrition, enhanced survival and fertility, and increased population and group sizes (Barbary macaques, *Macaca sylvanus*: Marechal, 2011; ring-tailed lemur, *Lemur catta*, and Verreauxi sifaka, *Propithecus verreauxi*: Axel and Maurer, 2011; ring-tailed lemur, *Lemur catta*: Mertl-Millhollen, 2000).

The ring-tailed lemur population in Berenty increased threefold between 1985 to 1997 due to tourist provisioning and an increase in available food resources from introduced tree species (Soma, 2006). However, introduced vegetation can sometimes be dangerous. For example in 1998 symptoms of alopecia were apparent amongst the ring-tailed lemur troops due to *Leucaena leucocephala* – a plant species containing the toxic compound mimosine, which is thought to cause weight loss, infertility, cataracts, goitre and paralysis of the limbs (Soma, 2006).

1.4.2 Disease Transmission

Increased susceptibility to disease is one of the most serious impacts of human/wildlife interactions on animal species (Cowlishaw and Dunbar, 2000). Wildlife tourism has been implicated as the main cause of pathogen transmission seen between humans and animals (Muehlenbein *et al.*, 2008). This is due to the diverse backgrounds of foreign visitors potentially introducing new strains of diseases to which native animals have no immunity (Wallis and Lee, 1999; Muehlenbein *et al.*, 2010; Woodford *et al.*, 2002). The animals in wildlife tourism destinations are often habituated and therefore more at risk to disease transmission through close contact and repeated exposure (Muehlenbein and Ancrenaz, 2009). This can have devastating effects on endangered wildlife and small populations (Borg, 2011).

The problem is exacerbated by tourists not respecting the rules and regulations of responsible travel. It is common for tourists to not consult travel clinics for health advice prior to departure, thus human respiratory and gastrointestinal travel illnesses are very common (Muehlenbein *et al.,* 2008). A study at Sepilok Orangutan Rehabilitation Centre in Borneo demonstrated that tourists did not know of the high risks of transmission between humans and animals, and most had not been properly immunised before travelling to Malaysia (Muehlenbein and Ancrenaz, 2009). Additionally, despite awareness of possible transmission risks, tourists still do not obey human-wildlife regulations. This was seen in Uganda where tourists approached mountain gorilla closer than the 7 metre distance guideline, therefore increasing the risk of disease transmission (i.e. via air-borne respiratory droplets) (Sandbrook and Semple, 2006). Disease transmission can pose serious consequences on wildlife fertility and survivorship (Goldberg *et al.*, 2007). For example, within four years of exposure to an unidentified pathogen in Venezuela, a population of red howler monkeys (*Alouatta seniculus*) decreased by 85% (Pope, 1998).

The spread of viral and bacterial diseases are primarily through direct contact, air-borne or habitat contamination (i.e. urinating, defecating and littering) (Muehlenbein *et al.*, 2010; Wallis and Lee, 1999). Although not as severe, parasitic ectoparasites and endoparasites also pose a risk to wildlife. The avoidance response seen in animals reacting to tourist stimuli can actually cause higher rates of susceptibility to parasitic infections. When animals move to a new habitat as a consequence of tourist pressure, they are often exposed to new, unknown parasites in which they have no immunity (Borg, 2011). Additionally, stress from tourism can decrease immunity, thus increasing susceptibility to infections (Apanius, 1998).

1.4.2.1 Disease Transmission in Primate Species

Research on human-wildlife disease transmission has been investigated widely in non-human primate species. This is because non-human primates share similar physiologic and genetic characteristics with that of humans, thus making them more susceptible to infection (Wolfe *et al*., 1998). *Escherichia coli* bacteria harboured by chimpanzees, was genetically similar to that of local primatologist researchers and tourists (Goldberg *et al.*, 2007). Additionally, Williams *et al.* (2008) found that 49% of chimpanzee deaths during a 47-year period in Tanzania were caused by a respiratory disease originating from humans. Similar case studies have also been seen in gorilla populations (Graczyk *et al.*, 2002) and macaque species (Jones-Engel *et al.*, 2001).

Human to non-human primate routes of transmission can occur through shared water resources (e.g. guinea worm disease, *Dracunculus medinensis*), vector-borne (e.g. malaria, *Plasmodium*), fecal-oral (e.g. polio-virus, *Picornaviridae*) or respiratory droplets (e.g. tuberculosis, *Mycobacterium tuberculosis*) (CDC, 2011). Conversely, humans are also at risk from exposure to a number of simian viruses: herpes B virus (*Herpesvirus simiae*), Ebola virus, and simian retrovirus (SRV) (Fuentes, 2006).

1.4.3 Behavioural Changes

Wildlife tourism can cause behavioural changes in animal species. Such behaviour changes include: increased aggression, anxiety and self-directed behaviours, physiological stress, altered reproduction, activity budgets, ranging behaviour and habitat use.

1.4.3.1 Aggression

High rates of aggression (i.e. within and between species) are often seen in animal species subjected to wildlife tourism (Reynolds and Braithwaite, 2001; Klailova *et al.*, 2010). Aggression is a normal response which can be initiated to intimidate other animals and thus may be elevated in stressful situations (McFarland, 2006). This hyperaggression can be linked with changes in the animals' habitat activity patterns, physiological stress levels, and reduce immunity to infectious diseases (Reynolds and Braithwaite, 2001). Increased aggression can also have an effect on communicative behaviours within groups; thus affecting predator-prey relationships, inter-group relationships (i.e. group fissioning: Berman and Li, 2002), diet and social development (Muehlenbein and Ancrenaz, 2009).

These agonistic encounters are often caused by the provisioning of food by tourists (Fuentes *et al.*, 2008). Food provisioning at tourist sites increases the local density of animals, and therefore the intra-group and inter-group competition for food resources. This has been seen in many animal species including sting rays, *Myliobatiformes* (Newsome *et al*., 2004); rock-wallabies, *Petrogale mareeba* (Hodgeson *et al.*, 2004); and Rhesus macaques, *M. mulatta* (Hill, 1994). This increased competition for provisioned resources is very common in many primate species (lion-tailed macaques, *M. silenus*: Wheatley and Harya Putra, 1994; Formosan rock macaques, *M. cyclopis*: Hsu *et al.*, 2009; Japanese macaques, *M. fuscata*: Hill, 1999). For example, Berman *et al.* (2007) showed that adult male Tibetan macaques that were highly dependent on provisioned food resources had correlated increased rates of aggression with provisioning and range restriction, compared to periods of no provisioning. Additionally, this aggression was redirected towards infants, thus resulting in high infant mortality at the tourist site. Redirection of aggression can be towards conspecifics, and often towards tourists, resulting in serious injury and even death (i.e. southern cassowaries, *Casuarius casuarius johnsonii*: Kofron, 1999; Barbary macaques, *M. sylvanus*: Fa, 1992; and dingoes, *Canis lupus dingo*: Thompson *et al.*, 2003).

Nevertheless, through behavioural and physiological studies examining corticosteroid levels, it has been demonstrated that various species of macaque respond to tourist stressors in different ways (Clarke *et al.*,1988). The findings showed that crab-eating macaques (*M. fascicularis*) had the highest corticosteroid levels and behaviourally were seen to be reactive and fearful, whilst Rhesus macaques had the lowest corticosteroid levels but were seen as the most aggressive. This suggests there is no uniform response of aggression due to tourist/wildlife interactions, thus further research is needed investigating this in a variety of different taxa (Hosey, 2005), including improved monitoring of food provisioning and its effects at tourist sites (McCarthy *et al.*, 2009; O'Leary and Fa, 1993).

1.4.3.2 Anxiety and Self-Directed Behaviours (SDB)

Self-directed behaviours (SDB), also known as displacement activities, form part of an animal's behaviour repertoire, but are observed in situations when they are deemed irrelevant (Maestripieri *et al.*, 1992). SDB include self-scratching, yawning, body shaking and self-grooming; however some of these behaviours are also associated with hygienic maintenance in birds (Clayton *et al.*, 2010) and non-human primates (Maestripieri *et al.*, 1992; Mooring *et al.*, 2000). Additionally, even scent-marking is considered a displacement activity in some primate species (Garnett's small-eared bushbaby, *Otolemur garnettii*: Watson *et al.,* 1999; Black-tufted marmoset, *Callithrix penicillata*: Barros *et al.*, 2004).

Research began in 1952 with Tinbergen who discovered that SDB were potentially for mitigating stress in post-conflict situations. SDB rates were also found to increase during uncertain (Maestripieri *et al.*, 1992) and frustrating situations (i.e. limited access to food resources: Diezinger and Anderson, 1986). Furthermore, SDB were linked to anxiety levels through pharmacological studies, whereby Rhesus macaques were given anxiolytic (anxiety reducing) and anxiogenic (anxiety inducing) drugs; the rate of SDB were found to increase post-consumption of the anxiogenic drug (Schino *et al.*, 1996).

It is thought that SDB are an indicator of anxiety, a subset of stress, in animals (Higham *et al.,* 2009; Carder and Semple, 2008; Reamer *et al.*, 2010). However, the majority of the literature has only focused on non-human primate species, most notably macaque species (Barbary macaques, *M. sylvanus*: Marechal *et al.*, 2011; lion-tailed macaques, *M. silenus*: Maestripieri *et al.*, 1992; Japanese macaques, *M. mulatta*: Diezinger and Anderson, 1986; Schino *et al.*, 1996; Tibetan macaques, *M. thibetana*: Matheson *et al.*, 2006; 2007) and baboon species (olive baboons, *Papio Anubis*: Higham *et al.*, 2009; Castles *et al.*, 1999; Castles and Whiten, 2010). It was previously thought that SDB could directly assess stress levels in non-human primates (Troisi, 2002; Matheson *et al.*, 2007; Muyambi *et al.*, 2005). However, Higham *et al.* (2009) showed that SDB and glucocorticoid concentrations (stress hormone) were not linked in olive baboons and therefore hypothesised that SDB may only depict short-term anxiety levels and behavioural coping mechanisms, but not stress levels.

Limited research has investigated the effect of tourists acting as anxiety-inducing stressors (Borg, 2011; McFarland, 2006). Nevertheless, it has been seen that Adelie penguins (*Pygoscelis adeliae*) had increased rates of bill-shaking when tourists were within a 3 metre proximity (Giese, 1998), and Royal penguins (*Eudyptes* *schlegeli*) demonstrated greater maintenance activities (i.e. possible SDB) during and post-tourist presence (Holmes *et al.*, 2005). Furthermore, tourism has been associated with increased rates of aggression in animal species (*Section 1.4.3.1*), which has also been linked to anxiety levels. For example, it has been shown that lion-tailed macaques had higher rates of self-scratching after receiving and giving aggression (Aureli *et al.*, 1989). This was also seen in Barbary macaques (Aureli, 1997). Nevertheless, few animal studies have investigated the link between tourism, rates of aggression and SDB.

The occurrence of SDB in relation to primate tourism has not been well researched, and different studies have used different measures of tourism, and therefore cannot be easily compared (Tibetan macaques, *M. thibetana*: Matheson *et al.*, 2007; Mack *et al.*, 2008; Barbary macaques, *M. sylvanus*: Marechal *et al.*, 2011;; mountain gorillas, *G. beringei beringei*: Muyumbi, 2005). In Tibetan macaques, SDB rates were shown to be higher in relation to closer proximity to tourists and increased tourist density (Matheson *et al.,* 2007). Furthermore, increased rates of self-scratching in Barbary macaques have also been associated with aggressive, feeding and neutral interactions (Marechal *et al.*, 2011). Therefore it was hypothesised that tourism has an effect on anxiety levels in non-human primates. Nevertheless, quantifying anxiety levels in different taxa is extremely difficult as it appears that the type and rate of occurrence of SDB differ according to the species (Honess and Marin, 2006).

1.4.3.3 Physiological Stress

According to avoidance behavioural responses, tourism can be perceived by animals as an external stressor (*Section 1.2.1*); suggesting that physiological stress levels could be affected by tourism. Marechal describes stress as ‘a physiological response due to a physical or psychological stimulus (i.e. pain or fear), resulting in modification of the homeostasis of an individual' (2010, p. 15). Two main hormones are secreted during the stress response: catecholamines and glucocorticoids (Sheriff *et al.*, 2011). Released within seconds of experiencing a stressor, catecholamines are associated with the immediate 'fight or flight' response (Sapolsky, 1992). Glucocorticoids however, are secreted within minutes of experiencing the stressor, and are involved in the restoration of homeostasis by releasing stored energy for quick muscle delivery, thus aiding in the adaptation and coping of the life-threatening situation (Sapolsky *et al.*, 2000; Sheriff *et al.*, 2011). Physiological stress estimates are therefore generally measured using glucocorticoid metabolite levels; as they provide a good measure of animal health and welfare (Marechal, 2010). Additionally, recent advancements in hormone extraction research, means that glucocorticoids can be extracted non-invasively from animal faecal samples (Hodges and Heistermann, 2003).

Stress responses can be extremely harmful when a stressor is prolonged or when the stress response is continually activated; referred to as 'chronic stress' (Wielebnowski, 2003). Chronic stress can affect animal welfare and health by causing brain dysfunctions, gastrointestinal dysfunctions, suppression of growth, and fertility problems (Sapolsky, 1992). For example, chronic stress in birds was shown to make them more vulnerable to disease due to immune suppression and metabolism alterations (Siegel, 1980). It has been hypothesised that tourism can cause chronic stress in animals (Davis *et al.*, 2005; Marechal *et al.*, 2011). However, there are limited studies investigating this relationship, especially in non-human primate species.

Visitor effects on urinary cortisol levels in the Colombian spider monkey (*Ateles geoffroyii rufiventris*) were investigated, finding a significant relationship between cortisol concentrations and visitor number; thus suggesting that tourists were a potential stressor (Davis *et al.*, 2005). Additionally, elevated glucocorticoid levels in response to prolonged tourism have been witnessed in black howler monkeys (*Alouatta pigra:* Behie *et al.*, 2010), neotropical hoatzin chicks (*Opisthocomus hoazin*: Mullner *et al.*, 2004), European pine marten (*Martes* martes: Barja *et al.*, 2007), yellow-eyed penguins (*Megadyptes antipodes*: Ellenberg *et al.*, 2007) and magellanic penguins (*Spheniscus magellanicus*: Fowler, 1999). Marechal *et al.* (2011) also found a positive correlation between faecal glucocorticoids and rates of human/Barbary macaque aggressive interactions, but interestingly, no significance with other measures of tourist activity. Conversely, it was found that marine iguanas (*Amblyrhynchus cristatus*) exposed to prolonged tourism displayed reduced stress responses than those that were less exposed (Romero and Wikelski, 2002). This can be explained in terms of an acceptance response, whereby habituation caused the dulling of stress response senses, which could pose serious risk to the animal's future survival if presented with a life-threatening situation where a rapid 'fight or flight' response was needed (Romero, 2004).

1.4.3.4 Altered Reproduction and Infant Mortality

The alteration of animal behaviour, physiology, and/or available energy can have detrimental effects on reproductive fitness; affecting breeding success, offspring survival and even population size (French *et al.*, 2011; Gerrodette and Gilmartin, 1990). Tourism can have an effect on all these reproductive fitness factors. For example, yellow-eyed penguins exposed to unregulated tourism were found to have lower breeding success compared to nesting sites with less tourist exposure (Ellenberg *et al.*, 2007). Similar findings were seen in neotropical hoatzin birds (Mullner *et al.*, 2004). Tourism has also shown to affect certain behaviours in animal species, resulting in infanticide or affecting general infant survival (O'Leary and Fa, 1993). This was seen in Tibetan macaques where increased rates of aggression in adult males, due to tourist exposure, led to an increase in infant mortality rates. The male macaques redirected their aggression towards infants (Berman *et al.*, 2007). Additionally, cheetahs (*Acinonyxjubatus*) in Amosele National Park committed infanticide when surrounded by tourist minibuses (Mather, 1989 in Johns, 1996), and brown pelicans (*Pelecanus occidentalis californicus*) abandoned their nests due to ecotourist disturbances, thus leaving their eggs and chicks open to predation or crushing them upon departure (Anderson and Keith, 1980).

Nevertheless, tourism can have a positive influence on reproduction fitness. Food provisioning increases energy stores, thus improving reproductive success by decreasing weaning time and interbirth intervals (Di Bitetti and Janson, 2001). This has been seen in ring-tailed lemurs in Madagascar (Axel and Maurer, 2011).

1.4.3.5 Altered Activity Budget

An 'activity budget' includes the duration of an animal's main behaviour repertoire (e.g. feeding, resting, moving, and social interactions). Behaviours such as resting and social interactions are important for thermoregulatory purposes, digestion, and maintaining social bonds (Dunbar 1996; Fedurek and Dunbar, 2009). Therefore, any alterations to these behaviours can have adverse effects on animals, thus reflecting short-term impacts of human disturbance (Green and Giese, 2004).

Feeding and predator avoidance behaviours are the two main activities where an animal invests most of its time (Reynolds and Braithwaite, 2001), therefore if these are disrupted it could have negative implications to the animal's survival. Tourists can be perceived as food providers and as a predator threat, thus are likely to influence animals' activity budgets (Borg, 2011; Menard, 2004). For example, the Asian rhinoceros (*Rhinoceros unicornis*) reduced feeding duration and invested more time in vigilance when exposed to high numbers of tourists (Lott and McCoy, 1995). This was also seen in woodland caribou (*Rangifer tarandus caribou*) (Duchesne *et al*., 2000). Additionally, animal resting behaviours are reduced when high numbers of tourists are present (humpback whales, *Megaptera novaeangliae*: Corkeron, 1995; elephants, *Loxodonta Africana*: Anderson and Eltringham, 1997; chimpanzees, *P. troglodytes*: Johns, 1996; Mareeba rock-wallaby, *P. mareeba*: Hodgeson *et al.*, 2004). It was shown that during periods of low visitor density, gorilla species spent a greater portion of time resting, in comparison to periods of high visitor density where increased autogrooming and aggressive behaviours were witnessed (Wells 2005).

Provisioning by tourists influences food distribution, quality and availability, which can also affect an animal's daily activity budget (Adeyemo, 1997; Orams, 2002). It was demonstrated that Barbary macaques in Gibraltar spent less time feeding due to the greater nutritional value found in provisioned foods, whereas those that were non-provisioned had to travel greater distances for scattered resources (Fa, 1986). A similar finding was seen in Hamadryas baboons (*Papio hamadryas*: Boug *et al.*, 1994). Therefore, non-provisioned animals appear to spend more time feeding and foraging than investing in resting and social interactions (Menard, 2004). Provisioning may increase the time available for affiliative social behaviour but, due to increased provisioning, animals may also be involved in more aggressive interactions (Hamadryas baboons, *Papio hamadryas*: Kamal *et al.*, 1997).

1.4.3.6 Ranging Behaviour and Use of Environment

The short-term behavioural avoidance strategies discussed above (i.e. where animals flee to avoid tourists), can eventually lead to long-term displacement which can have devastating effects on animal populations (Constantine, *et al.*, 2004). Many studies have shown that tourist presence, most notably large numbers, can cause animal species to venture out of their home ranges, thus avoiding tourist areas (Boinski and Sirot, 1997; Kinnaird and O'Brien, 1996: de la Torre *et al*., 2000; Griffiths and van Schaik, 1993; O'leary and Fa, 1993). This has resulted in animals abandoning high quality habitats (i.e. good for raising offspring and sufficient with resources) due to human disturbance. Northern Royal Albatrosses (*Diomedea sanfordi*) in New Zealand shifted their habitat from a tourist-exposed observational site, to a quieter area, but which had poorer environmental conditions (e.g. intense sun exposure, limited nesting sites, and dry terrain) (Higham, 1998). Relocating to a different habitat may result in increased risk of infant mortality and reduced reproductive success (e.g. southern fur seals, *Arctocephalus australis*: Stevens and Boness, 2003).

Human disturbance can also affect how an animal utilises its habitat (Griffiths and van Schaik, 1993). It was shown that wild black howler monkeys and pygmy marmosets moved higher into tree canopies, avoiding the lower strata of the forest because of tourist presence (Treves and Brandon, 2005; De la Torre *et al.*, 2000). This also resulted in animals engaging in less social play compared to those groups that had less exposure to tourism. Social interactions are important for maintaining relationships within groups, thus could affect whole communities (e.g. abnormal behaviours) (Tibetan macaques, *M. thibetana*: Berman *et al.*, 2007).

Consequently, these changes in habitat use and home range size can alter long-term behaviours. Animals in Sumatra including sun bears (*Helarctos malayanus*), tigers (*Panthera tigri*), and barking deer (*Muntiacus muntjak*), not only moved away from tourist-prone regions, but some even shifted from diurnal to nocturnal activity patterns (Griffiths and van Schaik, 1993). Interestingly, Sumatran primates such as pigtailed macaques (*M. nemestrina*) and orangutans (*Pongo pygmaeus*), were less affected. It is therefore assumed that some primate species are perhaps more adaptable and prone to habituation effects than other taxa (Borg, 2011).

These studies have predominantly investigated tourism impacts on relatively unhabituated wild populations. Conversely, habituated wildlife can behave differently. Provisioned Japanese macaques permanently relocated to a new habitat due to food encouragement, however even though there was insufficient food during the tourist low season, they did not extend their home range to find additional resources (Koganezawa and Imaki, 1999). This type of habitat and behavioural shift could affect foraging abilities and survival for future generations (Orams, 2002). Although not as severe, a similar scenario is beginning to emerge at Berenty Reserve in Madagascar, whereby many ring-tailed lemur troops have adapted to small, overlapping home ranges, with increasing competition for resources (Gould, 2006).

1.5 LITERATURE SUMMARY AND STUDY RATIONALE

The literature presented and discussed in this introductory chapter investigated the many possible impacts wildlife tourism has had on a wide variety of different taxa. All studies indicated that tourism was somehow related to behaviour alterations, most notably seen amongst non-human primate species. Nevertheless, the findings suggested that different species have varying interspecific sensitivities to tourism, thus no uniform explanations can be made across taxa. It is therefore important for further studies to be conducted on new and different primate species to have a better understanding of tourist-primate relationships and to act as a means of comparison to past literature.

The rationale behind this study was to investigate the impacts of primate tourism on free-ranging ring-tailed lemur behaviour because, to my knowledge, there appears to be no research investigating the link between tourism, rates of aggression and SDB in Lemuriformes, Strepsirrhine primates. With Madagascar's growing tourist industry coupled with its high percentage of endemic and threatened species, I believe it is imperative to fully understand the potentially irreversible impacts on Madagascar's primate wildlife.

1.6 STUDY SUBJECT

1.6.1 Lemuriformes Infraorder

The Lemuriformes Infraorder comprises about 101 lemur species, all of which are endemic to Madagascar (Mittermeier *et al.*, 1999; 2008; Markolf *et al.*, 2011). These species are split into five families including, Cheirogaleidae, Lemuridae, Lepilemuridae, Indriidae, and Daubentoniidae (Mittermeier *et al.*, 2008). Considering the limited area of land mass that is capable of supporting these existing lemur populations, this is an extraordinary level of diversity (Mittermeier *et al.* 2005; 2008; Burney, 2003).

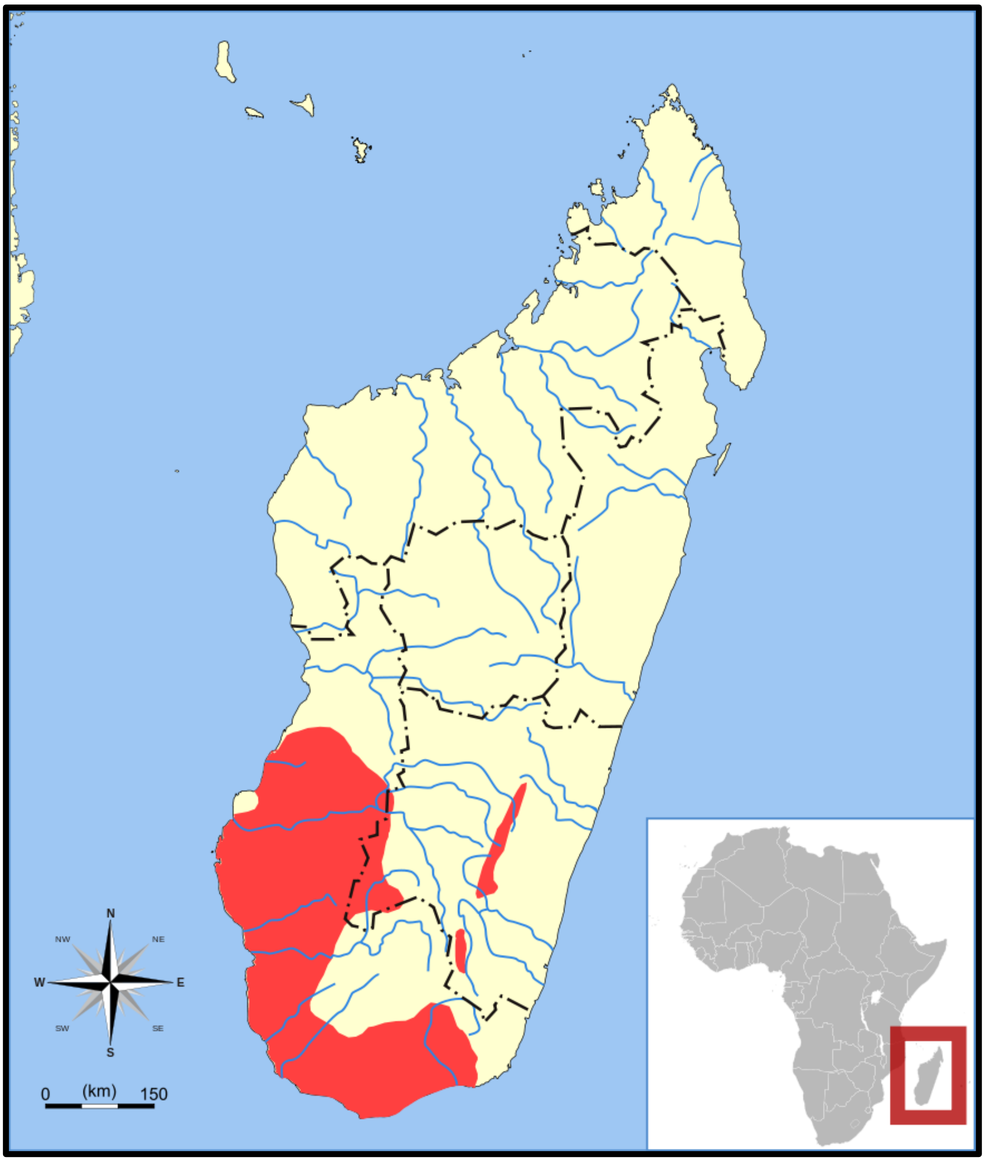
Strepsirhines are more similar to those of ancestral primates found in the fossil record, and differ from those of Haplorhine primates by possessing a range of different morphological characteristics. These include: a tapetum lucidum (i.e. a layer in retina that reflects light to enhance night-vision), sinuous nostril openings, moist rhinarium, bicornuate uterus and epithelichorial placenta, smaller brain case, unfused metopic suture, postorbital bar, unfused mandibular symphysis, grooming claws, toothcomb and sublingual (although this is absent in the aye-aye, *Daubentonia madagascariensis*), ectotympanic ring, and a larger olfactory bulb (Fleagle, 1999; Soligo and Martin, 2006).

Madagascar is considered one of the world's highest primate conservation priorities; not only are approximately 13% of the world's primate species inhabitants, but also a large majority of these are considered 'critically endangered' (e.g. hairy-eared dwarf lemur, *Allocebus trichotis*; golden bamboo lemur, *Hapalemur aureus*) (Mittermeier *et al.*, 1999). Furthermore, the entire Family of Daubentonidae which consists of one remaining living lemur species is also considered endangered. This lemur species, the aye-aye, is unique in that it possesses specialised dentition, large ears and an elongated middle digit on both hands (Mittermeier *et al.*, 1999). The main threat to future lemur survival is from deforestation to make way for tourism, agricultural land, logging and mining (Mittermeier *et al.*, 2005; Sussman *et al.*, 2003). The high numbers of endemic and endangered species means more research on the ecological, behaviour and genetics of this Infraorder is needed to fully understand the basic requirements for the lemurs' future survival.

1.6.2 Ring-Tailed lemur, *Lemur catta*

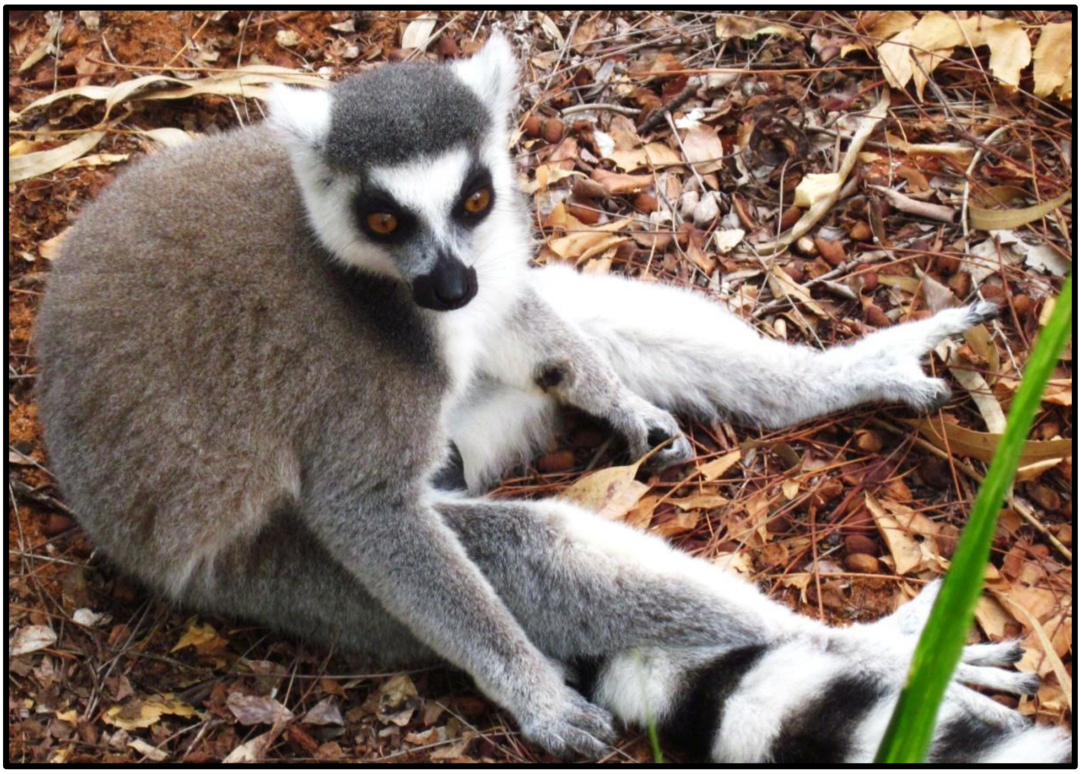
The ring-tailed lemur is a monotypic taxon, thus is the only member of the genus Lemur, and the only semi-terrestrial, diurnal lemur in Madagascar (Mittermeier *et al.*, 2008). Easily identifiable by its black-and-white tail bands, the ring-tailed lemur is often considered the “flagship species” of Madagascar (Mittermeier *et al.*, 1999; 2008; Jolly *et al.*, 2002). Nevertheless, with a declining population primarily due to habitat loss from deforestation, it is considered ‘near threatened’ by the International Union for Conservation of Nature (Andrainarivo *et al.,* 2008; Sussman *et al.*, 2003).

The ring-tailed lemur have a patchy distribution in the south and southwest of Madagascar (Figure 1.3), and are often referred to as a highly adaptable ‘edge’ or ‘weed’ species (Goodman *et al.*, 2006), whereby they are found in a range of different habitats (i.e. spiny, dry deciduous forest, brush and scrub forest, gallery forest, anthropogenic savannah, and high-altitude mountain regions) (Andrainarivo *et al.*, 2008; Gould 2006). Even though gallery forest is thought to be the preferred habitat (Axel and Maurer, 2011), the ring-tailed lemur are the least forest dwelling of all the lemur species (Goodman *et al.*, 2006). They send majority of their time on the ground travelling and foraging; thus their average degree of terrestriality is approximately 30% (Jolly, 1966). Population densities can vary between these habitats from approximately 100 lemurs/ km^2 in scrub and spiny forest to about 250 – 500 lemurs/ km^2 in gallery and secondary forest (Jolly *et al.*, 2002; 2006; Gould, 2006).



<u>FIGURE 1.3</u> Ring-Tailed Lemur (*Lemur catta*) Distribution in Madagascar (*Source:* Andrainarivo *et al.*, 2008).

Ring-tailed lemurs are medium sized, weighing approximately 2.3 – 3.5 kg (Sussman 1991; Gould *et al.*, 2003), and lack sexual size dimorphism (Bayart and Simmen, 2005; Kappeler, 1990; Sauther *et al.*, 1999). Besides their black-and-white tails bands, they are also distinguishable by their black muzzles and eye patches, and have longer limbs relative to their body size than other lemur species (Figure 1.4) (Cameron, 2007).



<u>FIGURE 1.4</u> Physical Characteristics of the Ring-Tailed Lemur (*Lemur catta*) (*Photograph*: C. Thompson).

Ring-tailed lemurs are a female-bonded species, where they live in a matrilineal society consisting of close kin females and non-kin mature males (Jolly and Pride, 1999; Ichino and Koyama, 2006). Females are socially dominant over males, and are central in resource and space defence (Rasamimanana *et al.*, 2006; Jolly and Pride, 1999). It is thought that this dominance evolved due to the erratic climate and highly seasonal reproduction period (Wright 1999). Additionally, there are separate hierarchies amongst males and females (Sussman, 1992). Troops consist of approximately 13-15 individuals, with an adult sex ratio of about 1:1, thus are a generally balanced multimale/multifemale troop (Sussman 1992). The social group structure is similar to that seen in *Cercopithecine* species, however the strongest relationships are between mother and daughter in ring-tailed lemurs, and occasionally sisters, but they have no close affiliative with more distant kin (i.e. granddaughters) (Jolly and Pride, 1999).

Being largely opportunistic frugivorous-folivorous foragers, the ring-tailed lemur diet consists of approximately 70% fruit, 25% leaves, and 5% herbs and flowers (Soma, 2006; Hohmann, 2009). Nevertheless, they are also known to consume introduced plant species, crop plants and tourist food and waste (Jolly *et al.*, 2002; Cameron, 2007). The kily tree, *Tamarindus indica*, is an important food source throughout the year, and often sees ring-tailed lemur troops maintaining home ranges around this resource (Simmen *et al.*, 2006; Axel and Maurer, 2011). However, as well as resource distribution, home ranges also depend on troop size (Jolly *et al.*, 2002). Ring-tailed lemurs are not necessarily described as 'territorial', as troops are often found timesharing at resting and feeding sites, especially during seasons with limited resources (Cameron, 2007).

Past research predominantly focused on free-ranging ring-tailed lemurs in confined gallery and deciduous forests in Berenty Private Reserve (i.e. Jolly, Koyama), Anja Private Reserve, and Beza Mahafaly Special Reserve (i.e. Sussman, Sauther and Gould). The majority of studies have looked at the effect of forest fragmentation and drought (Gould *et al.*, 1999), patterns of resource use (Blumenfeld-Jones *et al.*, 2006), feeding competition (Gemmill and Gould, 2008; Kappeler, 1990), and life history patterns and demography (Gould *et al.*, 2003; Jolly *et al.*, 2002). There appears to be no research, to my knowledge, investigating the effects of tourism on free-ranging ring-tailed lemurs in Madagascar.

1.7 AIMS AND HYPOTHESES

This study looked at adult male and female ring-tailed lemurs in Berenty Reserve. Two troops exposed to different intensities of tourism were studied; one found predominantly in an area frequently visited by tourists (the 'tourist front'), the other in a relatively undisturbed area of gallery forest (the 'forest troop'). The overall aim of the study was to investigate the relationship between tourism and animal behaviour in the two troops; specifically looking at how tourism may impact anxiety levels, aggression, activity budgets, home range size and use of habitat. Tourist pressure was measured by the number of tourists present and proximity to the ring-tailed lemur troop.

Four specific aims with seven corresponding hypotheses were investigated.

AIM 1: To determine whether tourism has an effect on activity budgets.

Tourism has been shown to affect animal activity behaviours by reducing feeding and resting time (Lott and McCoy, 1995; Constantine *et al.,* 2004), and increasing autogrooming and aggressive interactions (Kamal *et al.*, 1997; Wells, 2005). Therefore the following hypothesis was tested:

Hypothesis 1: Tourist pressure influences activity budgets, and is negatively related to feeding and resting time, but positively related to self-grooming.

AIM 2: To determine whether tourism has an effect on aggression.

The past literature showed that tourist presence can increase aggression in non-human primate species (Klailova *et al.*, 2010). Furthermore, tourist pressure can increase rates of competition and aggression in non-human primates, most notably when food provisioning is involved (Fuentes *et al.*, 2008; Berman *et al*., 2007). Therefore the following hypotheses were tested:

Hypothesis 2: The frequency of inter-troop and intra-troop aggression, aggressive tourist/lemur interactions and aggressive vocalisations are positively related to tourist pressure.

Hypothesis 3: Intra-troop aggression rates are significantly higher during bouts of tourist-feeding interactions, and specifically when eating human provided foods.

AIM 3: To determine whether tourism has an effect on displacement activities (self-directed behaviour).

Tourist pressure is positively correlated with SDB rate in non-human primates. Rates of SDB are especially high during aggressive encounters (between conspecifics and tourist/wildlife) and food provisioning (Diezinger and Anderson, 1986; Aureli *et al.*, 1989). SDB include self-scratching, yawning, self-grooming, and scent-marking. Scent-marking is of particular interest in this study as ring-tailed lemurs are known to engage in this activity often, and it could represent an indicator of anxiety in this species (Black-tufted marmoset, *Callithrix penicillata:* Barros *et al,* 2004; Small-eared bushbaby, *Otolemur garnettii* Watson *et al.*, 1999).

Therefore the following hypotheses were tested:

Hypothesis 4: Rates of self-directed behaviours are positively related to tourist pressure.

Hypothesis 5: Rates of SDB are positively related to inter- and intra-troop aggression and aggressive tourist/lemur interactions.

AIM 4: To determine whether tourism has an effect on home range size and habitat use.

Research on unhabituated animals showed that tourist pressure resulted in animals escaping to higher canopies (De la Torre *et al.*, 2000) and avoiding tourist areas (Boinski and Sirot, 1997; Kinnaird and O'Brien, 1996). Conversely, other studies have indicated that non-human primates have remained in provisioned areas, thus their home range size decreased (Koganezawa and Imaki, 1999). It is predicted that the effect of habituation on the ring-tailed lemur troop exposed to higher intensities of tourism will show a larger percentage of terrestriality, smaller home range and restricted habitat zone use (predominantly to degraded environments). The following hypotheses were investigated:

Hypothesis 6: Home range size and habitat zones are affected by tourist pressure.

Hypothesis 7: Terrestriality and troop elevation are affected by tourist pressure.

CHAPTER 2: *METHODS*

This chapter provides an overview of the study site, the two study troops, and study period; including an account of the pilot week involving individual identification and method-testing. The final methodology used to collect the data are then discussed, followed by the data, statistical and Geographical Information Systems analyses that were performed. All methods were approved by the Roehampton University Ethics Committee prior to carrying out this study (Appendix 23).

2.1 STUDY SITE

The research was carried out in a private reserve, Berenty Reserve, in southeast Madagascar (25°0.5' E and 46°18.5' S) (Figure 2.1).

FIGURE 2.1 Map of Madagascar in Relation to Eastern Africa, Showing the Location of Berenty Reserve (*Source:* Adapted from Google Maps).

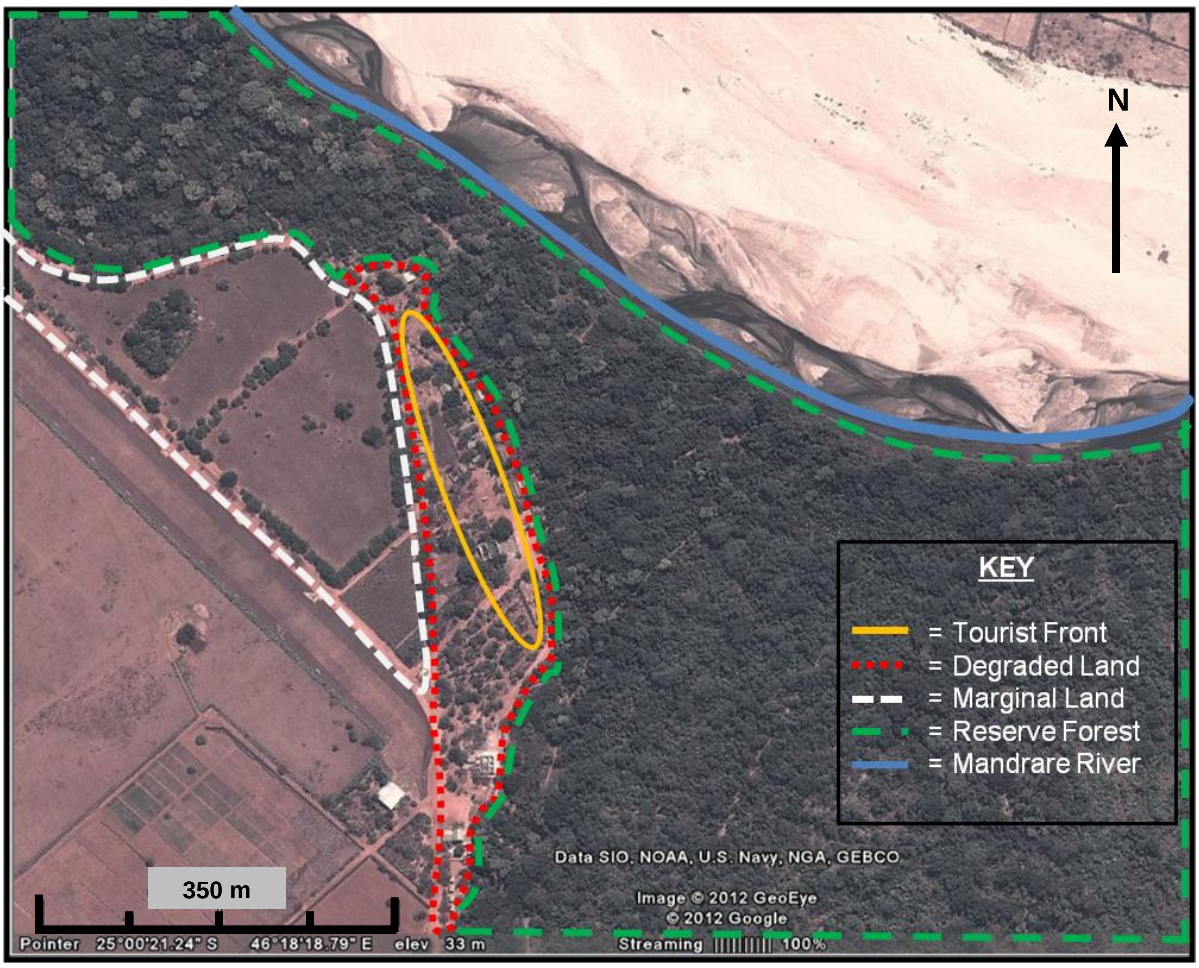
2.1.1 Berenty Reserve

Established in 1936 by the de Heaulme Family, Berenty Reserve is an approximately 2km² forest fragment made up of four distinct habitats: spiny forest, xerophytic scrub forest, second-growth deciduous forest, and riverine gallery forest (Gould, 2006; Soma, 2006). Although the reserve is now protected, it is nestled in between agricultural land to the south, the Mandrare River to the north and degraded forest to the east and west (Crawford *et al.*, 2006). Four fragments of gallery forest – natural forest where the canopy covers more than 50% of the sky – can be found along the Mandrare River, one of which is the Malaza Forest and was the focus area of the study (Jolly *et al.*, 2002).

2.1.1.1 Malaza Study Area

The 1km² Malaza Forest has been a study site since 1963, and is the habitat of six species of lemur: ring-tailed lemur (*Lemur catta*), Verreaux's sifaka (*Propithecus verreauxi verreauxi*), gray mouse lemur (*Microcebus murinus*), reddish-gray mouse lemur (*Microcebus griseorufus*), white-footed sportive lemur (*Lepilemur leucopus*) and the introduced hybrid brown lemur (*Eulemur fulvus rufus x Eulemur fulvus collaris*) (Soma, 2006; Blumenfeld-Jones *et al.*, 2006; Jolly and Pride, 1999). The region comprises a 'tourist front' as well as gallery forest and scrub/spiny forests. The tourist front is the area where the tourists are predominantly found (i.e. around the restaurant and bungalows). Ring-tailed lemur densities vary within the different habitats; approximately 500/km² at the tourist front, 250/km² in the gallery forest, and 150/km² in transitional scrub and spiny forest (Jolly and Pride, 1999; Jolly *et al.*, 2002; Crawford *et al.*, 2006). Artificial water troughs are available throughout the area, including in the gallery forest.

For the purpose of researching the ring-tailed lemurs' use of habitat zones, the area has previously been divided into 'degraded' land, 'marginal' land, 'reserve forest', and 'other' (Sauther *et al.*, 2006) (Figure 2.2 and Table 2.1).



<u>FIGURE 2.2</u> Map of the Malaza Study Area, Showing the Different Habitat Zones, Including the 'Tourist Front' in the Degraded Land Region (*Source:* Adapted from Google Maps).

HABITAT ZONE	DESCRIPTION
Degraded Land	Human inhabited/altered land. Includes the tourist front.
Marginal Land	Land subjected to heavy grazing and/or tree cutting.
Reserve Forest	Intact gallery forest.
Other	None of the habitat classes above.

<u>TABLE 2.1</u> Habitat Class Descriptions for the Malaza Study Area (*Source:* Adapted from Sauther *et al.*, 2006).

The ‘degraded’ habitat class included all the tourist facilities: bungalows, restaurant, and introduced vegetation flowerbeds (Figure 2.3).

FIGURE 2.3 Example of a ‘Degraded’ Habitat Class (*Photograph: C. Thompson*).

The ‘marginal’ habitat class included all agricultural land and any area that had been felled or cleared. This also included main paths found in the gallery reserve forest (Figure 2.4 and Figure 2.5).

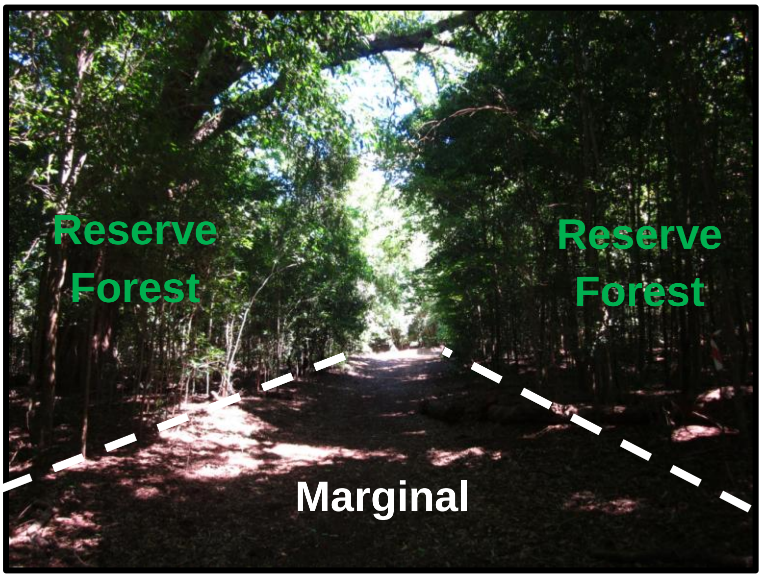


FIGURE 2.4 Example of a ‘Marginal’ Habitat Class in Reserve Forest (*Photograph: C. Thompson*).

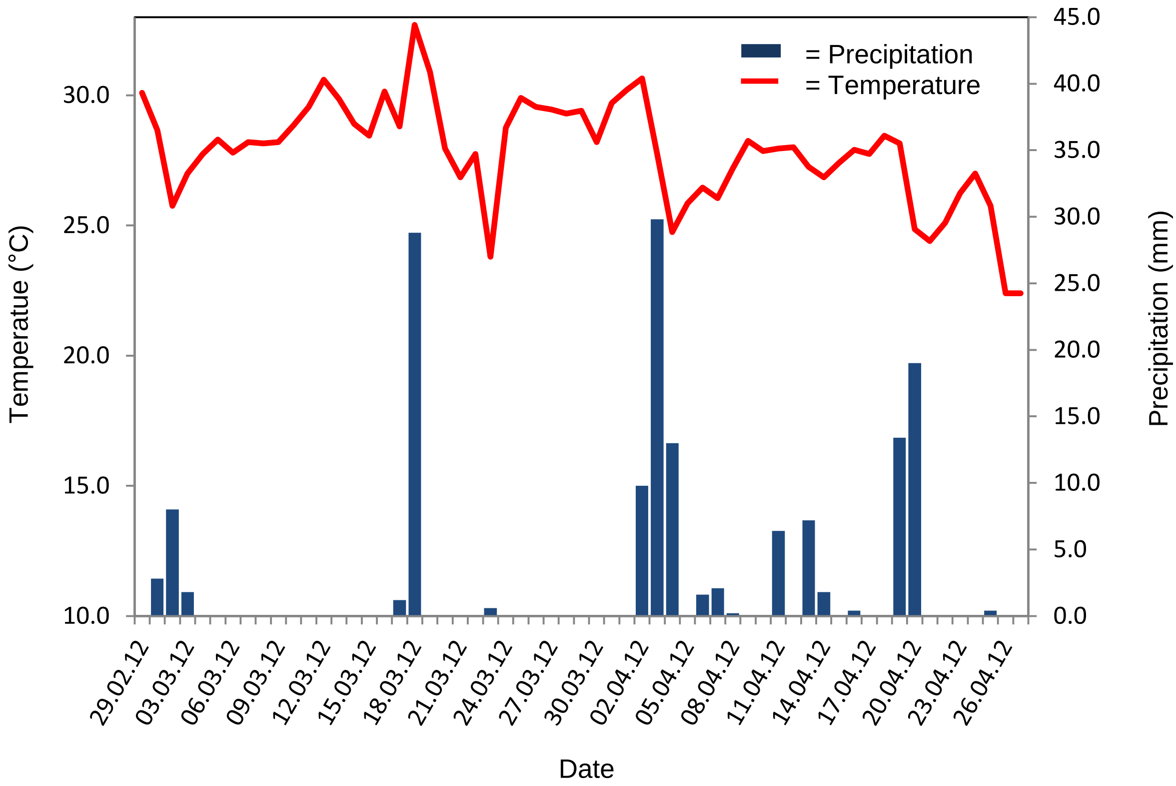
<u>FIGURE 2.5</u> Example of a 'Marginal' Habitat Class (*Photograph: C. Thompson*).

The 'reserve' habitat class included all intact gallery forest (Figure 2.6).

<u>FIGURE 2.6</u> Example of a 'Reserve' Habitat Class (*Photograph: C. Thompson*).

2.1.1.2 Climate

Although the climate is unpredictable, southern Madagascar generally experiences alternate dry and cold, and hot and wet seasons. The dry season is approximately from May to October, and the wet season from November to April (Soma, 2006). The hot, wet summers can experience temperatures as high as 40°C, whilst the dry, cold winters can have temperatures less than 10°C (Jolly *et al.*, 2006). The majority of rainfall occurs between November to February, with little rain falling between July to September. Annual rainfall varies from 300 to 900mm; during 1989 to 1998 the mean annual rainfall was 580.6mm (Koyama *et al.,* 2002; Koyama *et al.*, 2006; Jolly *et al.*, 2006). During the study period climate data were recorded (Figure 2.7).



<u>FIGURE 2.7</u> Precipitation and Temperature Data Recorded During the Study Period: 29/02/12 to 27/04/12 (*Source:* Data collected by Iris Dröscher, PhD student, University of Göttingen).

The overall arid climate, results in the soil having fewer nutrients (due to leaching), thus the vegetation experiences strict fruit seasonality. The adaptable lemur species have adopted their own feeding strategies to cope with these harsh conditions (Soma, 2006; Wright, 1999).

2.1.1.3 Vegetation

One of the dominant tree species in the gallery forest, the tamarind or kily tree (*Tamarindus indica*), is an important nesting and food resource for the ring-tailed lemur. This tamarind forest only survives along rivers with high water tables, thus fragments of this forest type are rare in Madagascar and are also highly threatened (Jolly *et al.*, 2006; Sussman *et al.*, 2006). Much of the region around Berenty Reserve has been deforested to make way for sisal plantations (*Agave rigida*) (Koyama *et al.*, 2006).

As well as native vegetation, many plant species are invasive (e.g. Veldt Grape or Devil's Backbone, *Cissus quadrangularis*) or introduced (e.g. *Azadirachta indica*) (Jolly *et al.*, 2002). The introduced species leaf and flower earlier in the spring season than most indigenous tree species (Jolly *et al.*, 2002). The ring-tailed lemurs feed on many native species (e.g. *T. Indica*, *Rinorea greveana*, *Cordia caffra*, *Alluaudia Procera*, *Maerua filiformis*, and Asclepiadaceae family) as well as introduced species (e.g. *Azadirachta indica*, *Cordia sinensis*, *Opuntia vulgaris* and *Leucaena leucocephala*) (Pers. Obs.).

2.1.1.4 Tourism

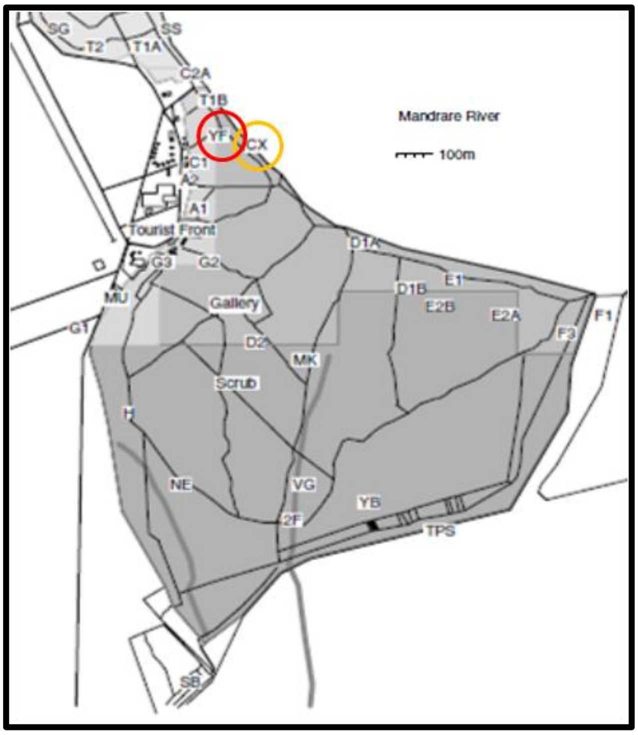
Tourism at Berenty Reserve was established in 1983 (Jolly and Pride, 1999). Visitors come to the area to view the Malagasy lemurs in their natural environment. As a consequence, the lemurs have become habituated to tourist presence; some populations more than others. Tourists can interact with the ring-tailed lemurs at the tourist front, most notably at the restaurant. Guided tours of the gallery forest are also available – although tourists strictly stay on the man-made paths, they can potentially come into contact with the ring-tailed lemur troops that inhabit the forest.

Berenty Reserve has seen deliberate human intervention in the last 30 years, including the improvement of the tourist infrastructure, water basins for the fauna in the reserve, planting of more introduced tree species, and increased provisioning of lemur troops (Jolly *et al.*, 2002). It has been hypothesised that this increased provisioning in the last 15 years has had a positive impact on the lemur species, resulting in a population boom in lemur troops at the tourist front (Crawford *et al.*, 2006; Jolly *et al.*, 2002; Mertl-Millhollen, 2000). Although feeding and touching the lemurs is now prohibited, tourists still engage in such activities (Pers. Obs.).

2.2 STUDY TROOPS

2.2.1 Selection

The ring-tailed lemur troops in Berenty Reserve have been well researched over the last 50 years. Two ring-tailed lemur troops were chosen for the study due to the different intensities of tourism that they were subjected to, the similarity of their habitats, and the similar balance of individuals in each troop; thus enabling easier intra-troop and inter-troop comparisons relating to tourist pressure (Figure 2.8).



<u>FIGURE 2.8</u> Map of the Previously Studied Ring-Tailed Lemur Troops in the Malaza Region, Berenty Reserve. The Location of the Two Study Troops – YF and CX – is Shown (*Source:* Adapted from Jolly *et al.*, 2006, p.38).

2.2.2 The Troops

Troops YF and CX are predominantly found at the tourist front and in the gallery forest, respectively. Nevertheless, both troops have been known to range into different habitat zones, including each other's (Soma 2006; Mertl-Millhollen *et al.*, 2006; Jolly *et al.*, 2006). This reduces possible confounding variables relating to their environment, thus making them more comparable when looking at the effects of tourism on their behaviour.

Only adult males, adult females and one sub-adult female were chosen for the study, giving a total of 14 study subjects (Table 2.2). All animals were greater than 2.5 years old, except for Avanana in Troop YF, who was 1.5 years old. Avanana was included in the study because she was classified as a well-developed sub-adult (*Section 2.2.2.1 Tourist Troop*).

TROOP	Individual ID (in order of dominance for each troop)*	Classification
YF	*Marika*	Adult Female
	Maso	Adult Female
	Avanana	Sub-Adult Female
	Sofina	Adult Female
	Kely	Adult Male
	Mainty	Adult Male
	Rambo	Adult Male
	Volo	Adult Male
CX	*Reny*	Adult Female
	Tsipika	Adult Female
	Tsia	Adult Female
	Mandidy	Adult Female
	Orona	Adult Male
	Pentina	Adult Male

**Dominance hierarchy (Pers. Obs.).*

TABLE 2.2 The 14 Study Subjects in Both the Tourist Troop (YF) and the Forest Troop (CX)

2.2.2.1 Tourist Troop

Troop YF was composed of 12 individuals: 4 adult males, 4 adult females, 2 juvenile males and 2 infant females. The adult male to adult female ratio was 1:1. The ages of the study subjects ranged from 5.5 to 8.5 years old, with the exception of Avanana who was 1.5 years old (Shinichiro Ichino, Pers. Comms., 2012). Avanana was included in the study for two reasons: 1) she was a well-developed female for her age (i.e. body size and well-developed genitalia) (Figure 2.9); 2) She was involved in many of the aggressive interactions, sometimes dominating older females; a behaviour seen in mature, well-established adult females (Pers. Obs.).

Juvenile Female **Sub-Adult Female: AVANANA** **Adult Female**

<u>FIGURE 2.9</u> Body Size and Genitalia Differences in Juvenile, Sub-Adult (Avanana) and Adult Female Ring-Tailed Lemurs (*Photographs*: C. Thompson).

Although sub-adults reach adult size between 1 to 1.5 years old, they supposedly still have genitalia that are half the size of that of an adult. Ring-tailed lemurs are normally considered an adult at 2.5 years of age, when they are sexually mature and ready to breed (Jolly, 2006). However, Avanana appears to have well-developed genitalia, similar to the size of an adult female. It is speculated that a possible reason for early maturity in some ring-tailed lemurs is due to the increased rich food resources from human provisioning and introduced vegetation (Drea, 2007; Gould, 2006). This has also been seen in captive ring-tailed lemurs (Sussman, 1991).

Troop YF has been documented to feed on introduced plant species, human garbage and man-made foods either given to them or stolen from the restaurant and bungalows. Nevertheless, the troop still ventures into the gallery forest to feed on native vegetation or for nesting (Jolly *et al.*, 2006).

2.2.2.2 Forest Troop

In 2002, Troop CX was documented to have 10 members, 7 of which were adults (Soma, 2006). However in 2012, Troop CX is now composed of 8 individuals: 2 adult males, 4 adult females, and 2 infants (one male, one female). The adult male to adult female ratio is 1:2. The known ages ranged from 6.5 to 12.5 years old (Shinichiro Ichino, Pers. Comms., 2012). The ages of the two adult males were unknown. Troops found in the gallery forest were hypothesised to have fewer members than the tourist troops because they are subjected to less provisioning and therefore have reduced, rich food resources. A smaller troop therefore has reduced competition for the available food resources (Erhart and Overdorff, 2008).

Previous studies have shown that CX generally ranges in the reserve gallery forest close to the Mandrare River; however they have also been documented to make excursions into neighbouring territories to feed on introduced species such as *A. indica*, *L. leucocephala*, and *C. sinensis*, especially during years of fruit failure (Soma 2006; Mertl-Millhollen *et al.*, 2006).

2.3 STUDY PERIOD

Data were collected between the 29th February to the 27th April 2012; a total of 42 days. This coincided with the mating season, and receptive females were first observed on the 7th April. This was taken into account during the data and statistical analyses (*Section 2.6 Data Analysis and Section 2.7 Statistical Analysis*). During the study period, Berenty Reserve was visited by 394 tourists: 149 in March, 245 in April.

2.4 FIRST WEEK: PREPARATION

The first week was treated as a pilot period to identify individuals, test the proposed methodology and train the research assistant. Three days were spent with the tourist troop, YF, and four days with the forest troop, CX.

2.4.1 Habituation and Identification

The ring-tailed lemur troops in Berenty Reserve are already habituated to human presence in the form of tourists and researchers. An extra day was allocated to the forest troop as they are less used to human presence in comparison to the tourist troop. Researcher/lemur interactions only occurred when the researchers had food in their possession, thus no food was carried during data collection.

A minimum distance of 7 to 10 metres was encouraged between the lemurs and the researcher throughout the study to avoid disturbing the focal or neighbouring lemurs. This is also the advised distance when viewing wildlife (most notably primates) to avoid provoking anxiety, stress or aggressive responses (Muehlenbein and Ancrenaz, 2009; Sandbrook and Semple, 2006). However, this was not always possible to maintain as the lemurs frequently approached the researcher's position, often with no visible intent of interaction. By relocating to a new position, the researcher would have disturbed the focal and its neighbours. Therefore once a focal had begun, the researcher tried to maintain the same position.

Individuals were identified by distinguishable physical characteristics such as facial markings, cuts and scars, ear marks, body and tail colouring and body shape/size (Appendix 1).

2.4.2 Method-Testing

A pilot study was carried out to verify the proposed data collection in field settings, and to test the configuration of the Psion WorkAbout handheld computer and corresponding software, Observer XT 8.0. This period was also used to identify the aggressive vocalisations in the field, and adjust and improve the ethogram (*Section 2.4.1.1 Ethogram*). After the pilot study, "self-groom < 10 seconds" (point behaviour) and "scent-mark" (state behaviour) were included in the ethogram and Psion WorkAbout configuration. Tests were also carried out to ensure that my and the research assistant's behavioural recordings were the same.

2.5 DATA COLLECTION

During the study period, the schedule involved working Monday to Friday, from approximately 6.30 a.m. to 6.00 p.m. on data collection days. The same routine was followed on each study day: the troop was found at approximately 6.30 a.m., continuous focal samples and scan samples were carried out on all individuals whilst waypoints were recorded using a Garmin ETREX Global Positioning Satellite (GPS). No data were collected between 12 p.m. and 2 p.m. as the lemurs mostly slept during that time interval (Rasamimanana *et al.*, 2006). Additionally, no data were collected on two days of extreme rainfall exceeding 20mm (18/03/12 and 03/04/12) (Figure 2.7) as the lemurs hid and no behavioural data could be recorded. Tourists often arrived at the beginning of the week and generally stayed one to two nights; hence the weekends were excluded from the study and used for data input. Data collection was alternated weekly between the troops.

2.5.1 Behavioural Data Collection

Behavioural observations were recorded for all 14 individuals in the form of 30-minute continuous focal samples and 3x 15-minute scan samples per focal sample (Altmann, 1974). Behaviours were defined using an ethogram.

2.5.1.1 Ethogram

The ethogram was divided into event and state behaviours, recorded in frequency and duration, respectively. The state behaviours included data collection on the activity budgets of the individual (i.e. feed, move, rest, grooming given and received, allo-groom, self-groom, scent-mark, out of sight, aggressive and non-aggressive tourist/lemur interaction, and other) (Table 2.3). These activities were defined as continuous and mutually exclusive of each other.

TYPE	BEHAVIOUR	DESCRIPTION	DIRECTION/ TYPE	ID
Activity Budgets	Feed	Focal animal is foraging for food, handling or consuming food.	Human, Natural	
	Move	Focal animal moves > 5 metres.		
	Rest	Focal animal is inactive: not vigilant, dozing or with eyes closed.		
	Groom	One lemur picks through the fur of another individual.	Give, Receive	Adult Male, Adult Female, Other, Unknown, Tourist
	Allo-Groom	Mutual grooming; focal and one or more individuals groom each other at the same time.		
	Self-Groom	Lemur grooms its own body. Not regarded as a displacement activity.		
	Scent-mark	Lemur rubs its anogenital, pubic, or back region along a surface. Occurs whilst travelling or whilst sitting.		
	Out of Sight	Focal animal is lost for > 3 minutes.		
	Aggressive Tourist/Lemur Interaction	Any form of aggressive interaction given/received from a tourist/lemur.	Give, Receive	Adult Male, Adult Female, Other, Unknown, Tourist
	Non-Aggressive Tourist/Lemur Interaction	Any form of non-aggressive interaction given/received from a tourist/lemur.	Give, Receive	Adult Male, Adult Female, Other, Unknown, Tourist
	Other	Any other state behaviour not listed above (e.g. play).		

TABLE 2.3 Ethogram and Psion Configuration of State Behaviour Data Collected.

The event behaviours were further separated into agonistic behaviours, non-agonistic tourist/lemur interactions, aggressive vocalisations, and displacement activities (Table 2.4).

TYPE	BEHAVIOUR	DESCRIPTION (Source where applicable)	DIRECTION	ID
Agonistic behaviour from ring-tailed lemur (1)	Aggression	*An aggression behaviour from a ring-tailed lemur includes any of the following:* Supplants: Aggressor enters an area and forces the target to leave. Lunge-and-cuff: Forward thrust of the head and trunk in direction of target; the aggressor extends one arm at shoulder level and cuffs the head of the target animal with a cross-wise slapping motion. Threat stare: Aggressor remains eye contact > 5 seconds. Chases: Aggressor chases target away. Bites: Aggressor physically bites target. Jump-fighting: Aggressor stands on hind legs with arms outspread and jumps around another individual. Stink-fight: Aggressor holds tail above its head and waves it back and forth. Other: Any other aggressive behaviour not listed above.	Give, Receive	Adult Male, Adult Female, Other, Unknown, Tourist
Agonistic behaviour from tourist (2)	Noise	Tourist stamps feet/kicks object, makes noise with hands (e.g. clapping, smack object), makes noise with mouth (e.g. scream, whistle).	Receive	Tourist
	Mimic	Tourist mimics ring-tailed lemur behaviour (e.g. threat stare).		
	Rock	Tourist pretends to throw object/rock.		
	Throw	Tourist physically throws object at ring-tailed lemur.		
	Other	Any aggressive behaviour which is not listed above.		
Aggressive vocalisations (3)	Yip	Short and high-pitched. Often expresses a willingness to defer to a dominant.		
	Squeal	Male "status assertion" vocalisation, or defensive display that may reflect a willingness to become aggressive if pressed.		
	Territorial Call	A continuous "yap".		
	Chutter	Low-to-moderate threat vocalization; may encourage subordinates to give way to dominants, thereby reaffirming dyadic dominance relationships.		
	Unknown Vocalisation	Any aggressive vocalisation not listed above.		
Non-agonistic tourist/lemur interaction (4)	Neutral	Tourist make no direct interaction or aggressive act towards ring-tailed lemurs (e.g. wave, take photograph, talk).	Receive	Tourist
	Stroke	Tourist physically touches lemur in a non-aggressive manner.		
	Play	Tourist runs with lemur, throws object to play with; not in an aggressive manner.		
	Feed	Tourist gives food directly or throws towards lemur; not in an aggressive manner.		
	Other	Any non-aggressive behaviour from a tourist not listed above.		
Displacement Activity	Self-Scratch	Individual movement of the hand or foot during which the fingertips are drawn across the fur or skin (usually repeated in quick succession).		
	Self-Groom < 10 Seconds	Individual picks through and/or brushed aside fur with one/both hands in less than 10 second bouts.		
	Yawn	Individual opens mouth briefly in a gaping movement. Canines not usually exposed. Not recorded as a SDB if accompanied by aggressive signals.		
Other	Startle	Lemur jumps as a response to tourist.		

TABLE 2.4 Ethogram and Psion Configuration of Event Behaviour Data Collected (*Source:* (1) Drea, 2007; (2) Ruesto *et al.*, 2010; (3) Macedonia, 1993; (4) Marechal *et al.*, 2011).

A new event was recorded when there was at least a 10 second interval between the behaviours.

2.5.1.2 Continuous Focal Samples

30-minute continuous focal samples were carried out on each individual in the troop every morning and afternoon (i.e. between 6.30 a.m. and 12 p.m., and again between 2.00 p.m. and 6.00 p.m.). Therefore a total of 16 and 12 focal samples were recorded per day for YF and CX, respectively. Individuals were chosen at random at the beginning of the study period using a random number generator, then were later reorganised every day to eliminate any influence of time of day on behaviours. State and event behaviours were recorded in duration and frequency, respectively, using the Psion WorkAbout Handheld Computer loaded with Observer XT 8.0 software. The complete lists of state and event behaviours are shown in the ethogram (Table 2.3 and Table 2.4). During the study period, a total of 336 and 252 focal samples were collected for YF and CX, respectively; a total of 42 focals (i.e. 21 hours) per individual in each troop.

2.5.1.3 15-Minute Scan Samples, including Tourist Pressure Measures

15-minute scan samples were carried out at 0, 15 and 30 minutes during each continuous focal sample, thus a total of 48 and 36 scan samples were recorded per day for YF and CX, respectively. The scan samples recorded the date, time, troop, focal ID, number of observers (i.e. tourists, researchers and other), number of lemurs engaging in certain activities (i.e. move, feed, rest, groom, self-groom, tourist interaction, SDB, other, and out of sight), proximity to the nearest observer, troop elevation, terrestriality and habitat zone (Table 2.5). Scan data were recorded on paper (Appendix 2).

CATEGORY	DESCRIPTION
Focal ID	Name of focal subject being followed.
Number of Observers	Tourist: Number of tourists. Researcher: Number of researchers. Other: Number of observers who are not a tourist/researcher.
Move	**See definitions in TABLE 2.3**
Feed	
Rest	
Groom	
Self-Groom	
Observer/Lemur Interaction	
Self-Directed Behaviours	
Other	
Out of Sight	
Proximity (1)	*Distance of nearest observer to centre of the troop - in category metres:*
	1 = 0 - ≤ 1 **2** = 1 - ≤ 2 **3** = 2 - ≤ 5 **4** = 5 - ≤ 10 **5** = 10 - ≤ 20 **6** = > 20 7 **=** Not visible.
Elevation	An estimation of the average height of the troop. In metres.
Terrestriality	A count of the number of lemurs on the ground.
Habitat Zone	**See definitions in TABLE 2.1** 1 = Reserve Forest 2 = Degraded Land 3 = Marginal Land 4 = Other

TABLE 2.5 Scan Sample Key (*Source:* (1) Adapted from Marechal *et al.*, 2011).

The scan samples were important because they recorded tourist pressure (i.e. whether tourists were present or absent, the density of the tourists, and the proximity of the nearest observer to the centre of the troop).

To maintain inter-observer reliability, I carried out the continuous focal samples, and the research assistant carried out the 15-minute scan samples. 15 minute intervals were chosen because the scan samples often took up to 10 minutes to complete because each member of the troop had to be located. During the study period a total of 1008 and 756 scan samples were recorded for YF and CX, respectively.

2.5.1.4 Daily Scans and *Ad libitum* Data

Daily scans recorded the weather (e.g. clear, cloudy, rain etc.) and any unusual behaviours that were noticed within the troop. Any troop encounters or mating activities were also recorded when it was observed.

2.5.2 Home Range Data Collection

Whilst following the troops during the study period, waypoints were recorded approximately every 10 minutes using a Garmin ETREX GPS (programmed to collect XY coordinates corresponding to EASTING and SOUTHING fields). A total of 21 and 18 days worth of waypoints were recorded for YF and CX, respectively.

2.6 DATA ANALYSIS

The data were analysed by looking at the continuous focal observations and scan samples. The data collected were equally balanced between the troops and amongst individuals (Table 2.6). The tourist troop, YF, was in the nearby vicinity of tourists during 68 focal samples over the study period. As expected, the forest troop, CX, was only exposed to three tourists during the study period, thus no data is available to carry out an intra-troop comparison on tourist presence/absence. All analyses looking at the impact of tourist presence/absence on behaviours was done on YF, and CX was used as a means of inter-troop comparison.

Troop	Study Subject	Number of Continuous 30-Min Focal Observations	Total Number of Hours from Focal Observations	Total Number of Focals When Tourists were Present	Total Number of Focals When Tourists were Absent	Total Number of Scans per Individual
YF	*Avanana*	42	21	8	34	126
YF	*Kely*	42	21	9	33	126
YF	*Mainty*	42	21	7	35	126
YF	*Marika*	42	21	11	31	126
YF	*Maso*	42	21	10	32	126
YF	*Rambo*	42	21	7	35	126
YF	*Sofina*	42	21	10	32	126
YF	*Volo*	42	21	6	36	126
	TOTAL for YF	336	168	68	268	1008
CX	*Mandidy*	42	21			126
CX	*Orona*	42	21			126
CX	*Pentina*	42	21			126
CX	*Reny*	42	21	N/A	N/A	126
CX	*Tsia*	42	21			126
CX	*Tsipika*	42	21			126
	TOTAL for CX	252	126			756
	GRAND TOTAL*	**588**	**294**	**N/A**	**N/A**	**1764**

***** = *Grand Total for both troops. N/A = Not applicable as CX was only exposed to 3 tourists during the study period.*

TABLE 2.6 Summary of the Behavioural Data Collected Per Troop and Per Individual.

2.6.1 Preparation of Behavioural Data for Analysis

The original continuous focal observations, recorded event and state behaviours in counts per 30 minutes, and seconds per 30 minutes, respectively. The data were then transformed into counts per hour, and minutes per hour, respectively. Scan sample data were recorded in counts at 0, 15 and 30 minutes corresponding to each focal observation, thus three scan samples were taken during each individual 30-minute focal observation. The three scan samples were then averaged per focal and thus recorded in average counts per 30 minutes. ‘Habitat zone’, originally recorded as ‘D’, ‘R’ and ‘M’ (corresponding to the different habitat classes), were transformed into numerical values (Table 2.5). Terrestriality was transformed into a percentage per focal observation.

2.7 STATISTICAL ANALYSIS

Statistical analyses were performed using IBM SPSS Statistics Version 19. The normality of the data distribution was first analysed using the Kolmogorov-Smirnov test (Appendix 3). Data are considered normally distributed when $P > 0.05$, thus are parametric. All variables in this study however, except ‘rest’ (state behaviour and scan), were considered non-parametric as $P < 0.05$, thus did not follow a normal Gaussian curve distribution. ‘Rest’ (state) and ‘rest’ (scan) were considered parametric because $P = 0.146$ and $P = 0.092$, respectively. Nevertheless, as only two variables out of a possible 72 were parametric, only non-parametric tests were performed due to time constraints and to enable easier comparisons.

All statistical analyses were considered significant when $P < 0.05$. The Dunn-Šidák Correction was used on post-hoc Mann-Whitney U tests (Appendices 14 and 16): $P = 1 – (1 – \alpha)^{1/n}$. The Dunn-Šidák Correction was preferred over the Bonferroni Correction because it assumes individual tests are independent of each other, and is an improved method with a stronger bound (Ury, 1976). Macro computer programming was written to aid in performing the 28 and 14 post-hoc Mann-Whitney U tests on troops YF and CX, respectively (Appendices 15 and 17).

2.7.1 Inter-Troop and Combined Troop Comparisons

An inter-troop comparison of all behaviours was first made between YF ($n = 8$) and CX ($n = 6$) using a Mann-Whitney U test. Sex differences were then investigated in the combined males ($n = 6$) and females ($n = 8$) using a Mann-Whitney U test. To investigate whether time period had an effect on behaviours; morning and afternoon, and mating and non-mating periods were analysed in the combined average behaviours of the 14 study subjects using a Wilcoxon Matched-Pairs Signed-Rank test. The non-mating period was designated from the start of the study, to the day before the females became receptive (i.e. 29th February to 6th April 2012). The mating period started the day the females became receptive, to the end of the study (i.e. 7th April to 27th April 2012).

2.7.2 Intra-Troop and Individual Differences

A Kruskal-Wallis test was performed to investigate whether there were significant individual differences in the behaviours within each troop. Post-hoc Mann-Whitney U tests were then performed on any significant variables to compare each individual in the troop with each other.

A Wilcoxon Matched-Pairs Signed-Rank test was performed on all individual data (n = 14) to investigate whether there were any individual behavioural differences in the morning and afternoon.

A Wilcoxon Matched-Pairs Signed-Rank test was also performed on the combined averages in the tourist troop, YF, to investigate whether there were any behavioural differences when tourists were present (n = 68) or absent (n = 268). However, it was not possible to test individuals due to the limited data when tourists were present; the results all implied significance when tourists were absent (Appendix 20). Therefore these results were not reliable to make assumptions from, and this test was disregarded.

2.7.3 Testing the Aims and Hypotheses

The Wilcoxon Matched-Pairs Signed Rank test results regarding tourist presence (*Section 2.7.2*) were used to answer aims and hypotheses relating to tourist pressure. Additional Mann-Whitney U tests were performed to support findings. The influence of tourist proximity on behaviours was tested using a Kruskal-Wallis test. A Spearman's Correlation Coefficient tested the influence of tourist density on behaviours.

2.8 GEOGRAPHICAL INFORMATION SYSTEMS ANALYSIS

ESRI ArcGIS Version 9.2 (including the Home Range Extension, HRE Version 9) was used to investigate the impact of tourism on home range size. The GPS waypoints were first plotted on an imported map of Berenty Reserve sourced from Google Maps. The map was 'fixed' using known GPS coordinates corresponding to Berenty Reserve, with a technique known as 'rubber-sheeting'.

Minimum Convex Polygons (MCPs) taking into account 100% of data points were used to analyse the home range size and shape for both troops. An MCP is a convex polygon that has been created around the outer waypoints of a study area, thus creating the smallest polygon with interior angles not exceeding 180° degrees (Rodgers and Carr, 1998).

Kernel Density Estimators (KDE) taking into account 95% of data points were used to analyse use of home range space, examining regions of high activity. KDE are extremely useful in determining the utilization distribution of an animal by calculating the 'probability of occurrence at each point in space' (Blundell *et al.*, 2001, p.470). Thus isopleths of fixed percentage (i.e. 50, 90 and 95%) illustrate the main centres of activity, suggesting where the animal spends the majority of its time (Hemson *et al.*, 2005). KDE for troop CX had to be 'clipped' because they extended into the Mandrare River; inaccurately extending the troop's home range size.

2.8.1 Additional Mapping

Native and introduced plant species that the lemur troops were observed to regularly feed on in ‘degraded’, ‘marginal’, and ‘reserve forest’ zones, were plotted on a grid map of Berenty Reserve. This was used to aid in explanations for any differences found in home range size.

CHAPTER 3: *RESULTS*

The overall aim of the study was to determine whether tourism has an impact on adult ring-tailed lemurs' behaviour, most notably regarding aggression, activity budgets and displacement behaviours. This chapter will first focus on exploring and describing the data by comparing:

a) Inter-troop differences; including event behaviours, activity budgets, and scan sample results to investigate the behaviours between the two troops.

b) Combined adult male and adult female behaviour from both troops to investigate overall sex differences.

c) Average behaviours in the morning and afternoon, and on mating and non-mating days for the combined 14 study subjects to investigate whether time period had an influence on behaviours.

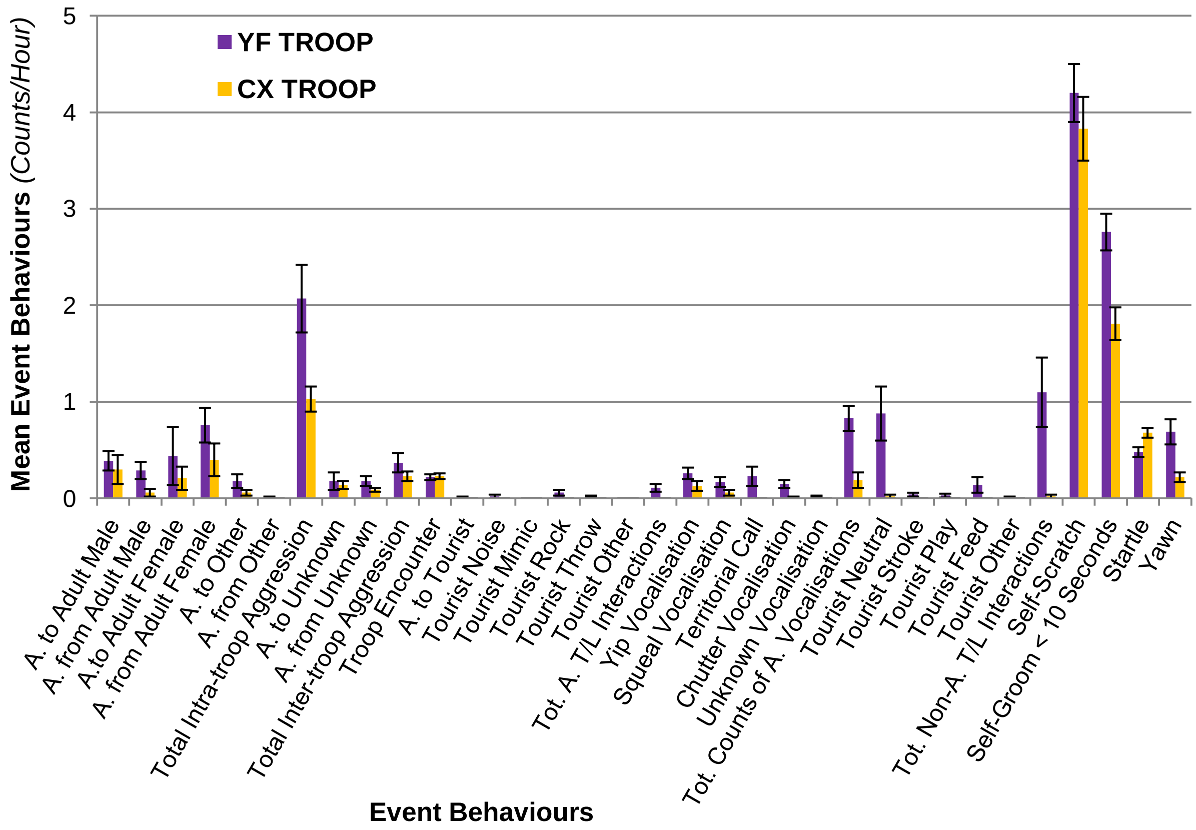
d) Intra-troop and individual behavioural differences; including the impact of morning and afternoon study periods, and the influence of tourist presence and absence.

Exploring the data in this way will aid in answering and supporting the individual aims and corresponding hypotheses relating to tourist pressure, by filtering out any external confounding variables. This chapter will then focus on addressing each individual aim and hypothesis (*Section 3.6*).

3.1 INTER-TROOP COMPARISON

3.1.1 Mean Event Behaviours

Troop YF appeared to have greater counts per hour of the majority of event behaviours in comparison to CX (Figure 3.1, Appendix 4). With regards to tourist interaction, this is not surprising, as YF is more exposed to tourism than CX.



A. = Aggression; Tot. = Total; T/L = Tourist/Lemur.

<u>FIGURE 3.1</u> Mean Event Behaviours for Troops YF (*n* = 8) and CX (*n* = 6) in Counts per Hour (APPENDIX 4).

The following agonistic and SDB behaviours were not only greater for YF compared to CX, but they were the greatest counts of event behaviours for both troops overall: ‘aggression from adult female’, ‘total intra-troop aggression’, ‘total aggressive vocalisations’, ‘self-scratch’ and ‘self-groom < 10 seconds’.

A Mann-Whitney U test revealed 10 significant inter-troop event behaviour differences out of a possible 34 (obvious significant results relating to tourist counts and tourist interactions are omitted from Table 3.1) (Appendix 5).

		YF TROOP (*n = 8*) Mean ± S.E.			CX TROOP (*n = 6*) Mean ± S.E.			Mann-Whitney U Test		
								U	Z	P
Event Behaviours *(Counts/Hour)*	Aggression from Adult Male	0.29	±	0.09	0.06	±	0.04	6.000	-2.350	0.020
	Total Intra-troop Aggression	2.07	±	0.35	1.03	±	0.13	3.500	-2.649	0.005
	Territorial Call	0.23	±	0.10	0.00	±	0.00	0.000	-3.236	0.001
	Chutter Vocalisation	0.15	±	0.04	0.01	±	0.01	7.000	-2.350	0.029
	Total Counts of Aggressive Voc.	0.83	±	0.13	0.19	±	0.08	1.500	-2.911	0.001
	Self-Groom < 10 Seconds	2.76	±	0.19	1.81	±	0.17	0.500	-3.041	0.001
	Startle	0.48	±	0.05	0.68	±	0.05	7.000	-2.212	0.029
	Yawn	0.69	±	0.13	0.22	±	0.05	2.000	-2.853	0.003

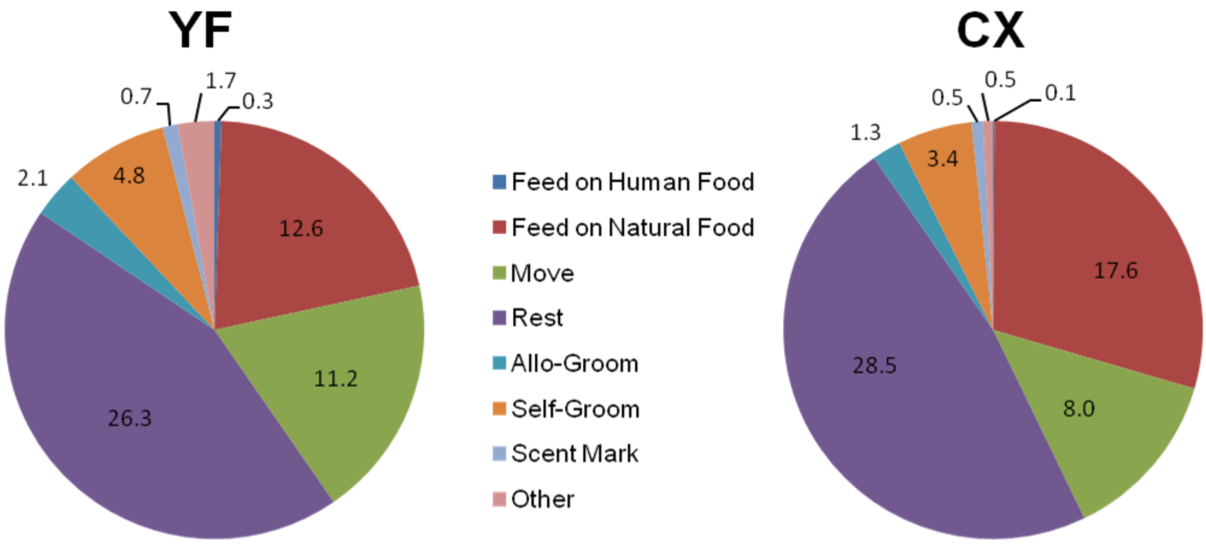
All data are significant when P < 0.05. Data coloured in blue indicates the higher value. Voc. = Vocalisation.

TABLE 3.1 Inter-Troop Comparison of Event Behaviours Using a Mann-Whitney U Test. Only Significant Results are Displayed (Omitting Obvious Significance in Tourist Interaction and Tourist Numbers) (APPENDIX 5).

Troop YF had significantly greater intra-troop aggression compared to CX; particularly ‘aggression from adult males’. YF also displayed a significantly greater count of total aggressive vocalisations; in particular the ‘territorial call’ and ‘chutter vocalisations’. In addition, YF had significantly greater rates of displacement behaviours, including ‘self-grooming [less than 10 seconds]’ and ‘yawn’.

3.1.2 Mean State Behaviours

CX spent a greater duration of minutes per hour feeding on natural food resources and resting compared to YF (Figure 3.2, Appendix 6). YF however, appeared to spend a greater proportion of time moving, general intra-troop grooming, allo-grooming, self-grooming, scent-marking, and feeding on human food resources.



'Groom' includes: groom adult male, groom adult female, groom other, receive grooming from adult male, receive grooming from adult female, and receive grooming from other. 'Other' includes: aggressive tourist/lemur interaction, non-aggressive tourist/lemur interaction, out of sight, and other behaviours.

<u>FIGURE 3.2</u> Mean State Behaviours for Troops YF (*n* = 8) and CX (*n* = 6) in Minutes per Hour (APPENDIX 6).

Nevertheless, only 5 out of a possible 21 inter-troop state behaviour differences were found to be significant (obvious significant results relating to tourist interactions are omitted from Table 3.2) (Appendix 7).

		YF TROOP (*n* = 8) Mean ± S.E.	CX TROOP (*n* = 6) Mean ± S.E.	Mann-Whitney U Test U	Z	P
State Behaviours *(Mins/Hour)*	Move	11.22 ± 0.44	7.98 ± 0.36	0.000	-3.098	0.001
	Receive Grooming from Adult Female	0.09 ± 0.05	0.01 ± 0.01	5.500	-2.486	0.013
	Receive Grooming from Other	0.08 ± 0.03	0.01 ± 0.00	7.000	-2.245	0.029
	Other	0.10 ± 0.03	0.00 ± 0.00	3.500	-2.755	0.005

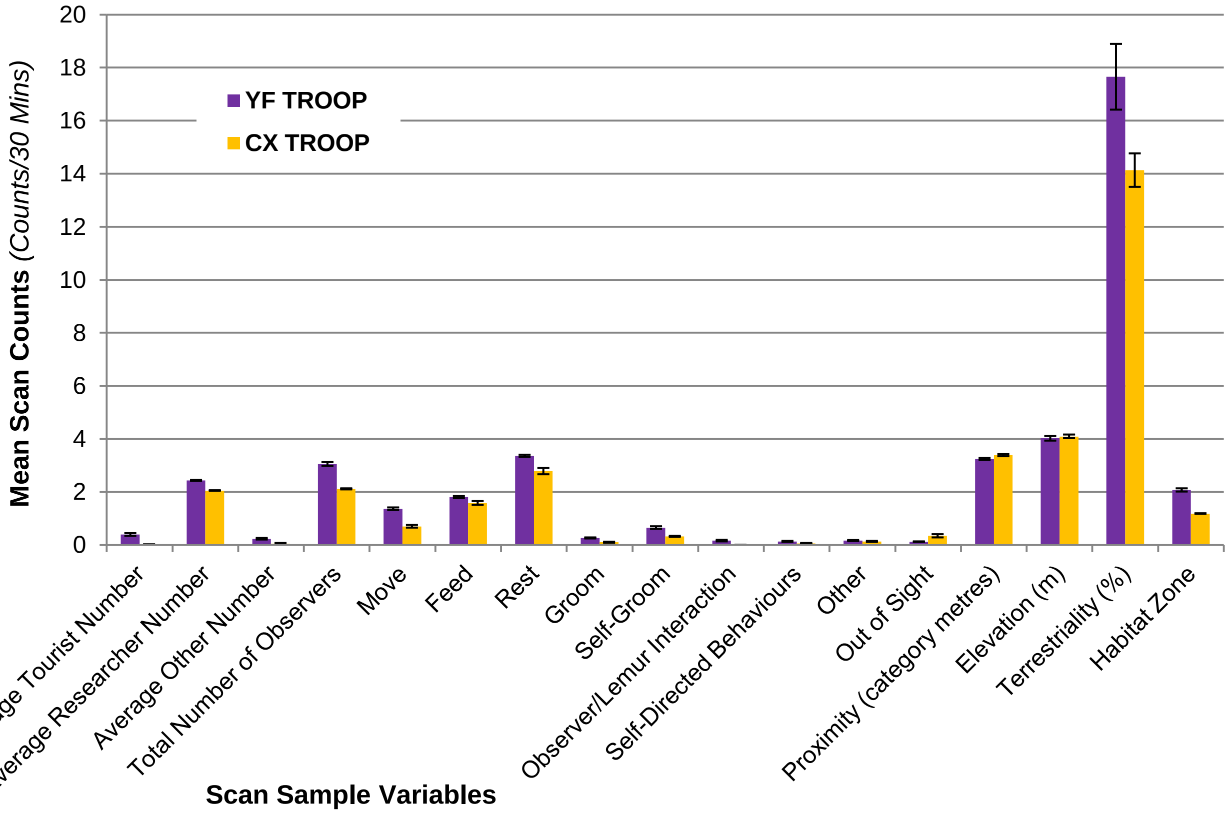
All data are significant when P < 0.05. Data coloured in blue indicates the higher value.

<u>TABLE 3.2</u> Inter-Troop Comparison of State Behaviours Using a Mann-Whitney U Test. Only Significant Results are Displayed (Omitting Obvious Significance in Tourist Interaction and Tourist Numbers) (APPENDIX 7).

YF spent a significantly greater proportion of time performing four of the activity budget behaviours compared to CX, where 'move' was of particular interest.

3.1.3 Scan Sample Results

YF and CX had a similar pattern in activity budget behaviours (i.e. counts of resting were greatest in both troops, followed by feeding, then moving etc.) (Figure 3.3, Appendix 8). Unsurprisingly, total number of observers was greatest in YF due to increased tourism exposure. Although the mean elevation was similar for both troops, the mean percentage of terrestriality was greater in YF compared to CX.



'Proximity' is in category metres, and 'Habitat Zone' is in categories (Section 2.5.1.3 15-Minute Scan Samples, including Tourist Pressure Measures).

FIGURE 3.3 Mean Scan Sample Results for Troops YF (*n* = 8) and CX (*n* = 6) in Counts per 30 Minutes (APPENDIX 8).

A Mann-Whitney U test revealed 14 significant inter-troop scan results out of a possible 17 (obvious significant results relating to tourist interactions are omitted from Table 3.3) (Appendix 9).

		YF TROOP (*n = 8*) Mean ± S.E.			CX TROOP (*n = 6*) Mean ± S.E.			Mann-Whitney U Test U	Z	P
Scan	Total Number of Observers	3.05	±	0.07	2.11	±	0.02	0.000	-3.105	0.001
(Counts/30 Mins)	Move	1.36	±	0.05	0.70	±	0.05	0.000	-3.102	0.001
	Feed	1.80	±	0.04	1.58	±	0.07	6.500	-2.262	0.020
	Rest	3.36	±	0.04	2.78	±	0.12	0.000	-3.098	0.001
	Groom	0.26	±	0.02	0.10	±	0.02	0.000	-3.098	0.001
	Self-Groom	0.65	±	0.05	0.32	±	0.02	0.000	-3.098	0.001
	Observer/Lemur Interaction	0.16	±	0.03	0.00	±	0.00	0.000	-3.172	0.001
	Self-Directed Behaviours	0.13	±	0.02	0.06	±	0.01	4.500	-2.523	0.008
	Out of Sight	0.12	±	0.01	0.34	±	0.06	8.000	-2.066	0.043
	Proximity (category metres)	3.24	±	0.04	3.38	±	0.04	6.000	-2.339	0.020
	Habitat Zone	2.07	±	0.06	1.18	±	0.01	0.000	-3.109	0.001

All data are significant when P < 0.05. Data coloured in blue indicates the higher value. 'Habitat Zone' is in categories, therefore has no direction of significance.

TABLE 3.3 Inter-Troop Comparison of Scan Sample Results Using a Mann-Whitney U Test. Only Significant Results are Displayed (Omitting Obvious Significance in Tourist Interaction and Tourist Numbers) (APPENDIX 9).

YF spent a significantly greater proportion of time performing each of the activity budget behaviours compared to CX; of particular interest includes: 'move', 'rest', and 'self-groom'. YF also demonstrated significantly greater counts of 'SDB'. Finally, it can be seen that YF and CX spent significantly more time in different habitat zones compared to each other; 'degraded land' (i.e. Zone 2) and 'reserve forest' (i.e. Zone 1), respectively.

3.2 SEX DIFFERENCES IN THE COMBINED TROOPS

The combined males and females from both troops revealed only 8 significant differences between the sexes (Table 3.4) out of a possible 72 variables (Appendix 10).

		Male *(n = 6)* Mean ± S.E.			Female *(n = 8)* Mean ± S.E.			Mann-Whitney U Test U	Z	P
Event Behaviours *(Counts/Hour)*	Aggression to Adult Male	0.14	±	0.07	0.51	±	0.11	6.000	-2.331	0.020
	Aggression to Adult Female	0.01	±	0.01	0.59	±	0.28	0.000	-3.176	0.001
	Aggression to Other	0.04	±	0.01	0.20	±	0.07	8.000	-2.103	0.043
	Aggression to Unknown	0.05	±	0.02	0.26	±	0.07	4.500	-2.569	0.008
State Behaviours *(Mins/Hour)*	Feed on Natural Food	12.22	±	0.98	16.63	±	1.64	8.000	-2.066	0.043
	Groom Adult Female	0.16	±	0.06	0.03	±	0.02	8.000	-2.113	0.043
	Groom Other	0.01	±	0.01	0.05	±	0.02	8.000	-2.206	0.043
	Scent-mark	0.96	±	0.21	0.37	±	0.10	6.000	-2.324	0.020

All data is significant when P < 0.05. Data coloured in blue indicates the higher value.

TABLE 3.4 Significant Sex Differences in the Combined Troops (YF and CX) Using a Mann-Whitney U Test (APPENDIX 10).

Females displayed significantly more intra-troop and inter-troop aggression. Interestingly, females had significantly greater rates of feeding on natural food resources, whilst males had significantly greater rates of grooming adult females and scent-marking.

3.3 MORNING AND AFTERNOON COMPARISON FOR THE COMBINED TROOPS

The results comparing the average behaviours for the 14 study subjects in the morning and afternoon revealed only 6 significant differences (Table 3.5) out of a possible 72 variables (Appendix 11). The limited significant results, suggests that the individual study subjects behaved in a similar way in both the morning and afternoon study periods.

		Morning (n = 14) Mean ± S.E.			Afternoon (n = 14) Mean ± S.E.			Wilcoxon M-P Test Z	P
Event Behaviours *(Counts/Hour)*	Aggression from Adult Female	0.72	±	0.05	0.49	±	0.03	-2.121	0.034
	Tourist Neutral	0.81	±	0.09	0.22	±	0.02	-2.264	0.024
	Total Non-Aggres. T/L Interactions	1.00	±	0.12	0.27	±	0.02	-2.032	0.042
State Behaviours	Move	10.98	±	0.15	8.68	±	0.22	-2.049	0.040
(Mins/Hour)	Rest	25.11	±	0.27	29.40	±	0.33	-2.390	0.017
Scan *(Counts/30 Mins)*	Terrestriality (%)	20.56	±	0.32	11.72	±	0.34	-3.109	0.002

All results are significant when P < 0.05. Non-Aggres. T/L = Non-Aggressive Tourist/Lemur. Data highlighted in blue indicates the higher value.

TABLE 3.5 Significant Average Behaviours for Morning and Afternoon for the 14 Study Subjects Using the Wilcoxon Matched-Pairs Signed-Rank Test (APPENDIX 11).

Five of these behaviours were significantly greater in the morning, including: counts of neutral tourist interaction and non-aggressive tourist/lemur interactions, aggression directed from adult females, moving and terrestriality. Only rates of resting were found to be significantly greater in the afternoon.

3.4 MATING AND NON-MATING PERIOD COMPARISON FOR THE COMBINED TROOPS

The results comparing the average behaviours for the 14 individuals in the mating and non-mating periods, revealed 8 significant differences (Table 3.6) out of a possible 72 variables (Appendix 12).

		Mating (n = 14) Mean ± S.E.			Non-Mating (n = 14) Mean ± S.E.			Wilcoxon M-P Test Z	P
Event Behaviours	Self-Scratch	3.26	±	0.08	4.50	±	0.06	-2.961	0.003
(Counts/Hour)	Startle	0.29	±	0.02	0.73	±	0.02	-2.828	0.005
State Behaviours	Move	7.51	±	0.12	11.18	±	0.16	-3.321	0.001
(Mins/Hour)	Out of Sight	0.07	±	0.01	0.71	±	0.03	-2.887	0.004
Scan *(Counts/30 Mins)*	Average Researcher No.	2.06	±	0.01	2.39	±	0.02	-2.449	0.014
	Average Other No.	0.22	±	0.02	0.11	±	0.01	-2.000	0.046
	Out of Sight	0.31	±	0.02	0.16	±	0.01	-2.236	0.025
	Elevation (m)	4.62	±	0.03	3.72	±	0.03	-2.739	0.006

All data are significant when P < 0.05. Data highlighted in blue indicates the higher value.

TABLE 3.6 Significant Average Behaviours for Mating and Non-Mating Periods for the 14 Study Subjects Using the Wilcoxon Matched-Pairs Signed-Rank Test (APPENDIX 12).

The displacement behaviour of ‘self-scratching’ was greater in the non-mating period. Other results of interest included ‘move’ and ‘elevation’ which were greater in the non-mating and mating period, respectively.

3.5 INTRA-TROOP AND INDIVIDUAL DIFFERENCES

3.5.1 Overall Individual Differences within Each Troop

To see if any individuals demonstrated behavioural differences in comparison to the rest of the troop, a Kruskal-Wallis test was performed on each troop. Post-hoc Mann-Whitney U tests were then performed to show which individual showed significance.

3.5.1.1 Troop YF

Troop YF was discovered to have 14 significant differences between individuals (Table 3.7) out of a possible 72 variables (Appendix 13). These significant differences were related to aggression, tourist interactions and grooming.

		YF TROOP (*n = 8, df = 7*)	
		X^2	P
Point Behaviours *(Counts/Hour)*	Aggression to Adult Male	27.173	< 0.001
	Aggression to Adult Female	88.643	< 0.001
	Aggression from Adult Female	22.538	0.002
	Aggression to Other	30.743	< 0.001
	Total Intra-troop Aggression	19.260	0.007
	Tourist Noise	16.145	0.024
	Tourist Rock	17.157	0.016
	Tourist Neutral	20.492	0.005
	Tourist Feed	24.229	0.001
	Total Non-Aggressive Tourist/Lemur Interactions	22.796	0.002
State Behaviours *(Mins/Hour)*	Feed on Human Food	16.142	0.024
	Receive Grooming from Adult Male	30.878	< 0.001
	Self-Groom	17.626	0.014
	Non-Aggressive Tourist/Lemur Interaction	24.333	0.001

All results are significant when P < 0.05. Df = Degrees of Freedom.

TABLE 3.7 Significant Individual Differences in the Behaviours of Troop YF Using a Kruskal-Wallis Test. *n* = 8. (APPENDIX 13).

A post-hoc Mann-Whitney U test, Appendix 14, revealed that all of the significant individual differences were due to two females, Maso and Marika. Once the Dunn-Šidák Correction had been applied to the original significant results, 15 behaviours were found to be significantly different between Maso and Marika, and the other individuals in YF when P < 0.00183. Both females displayed significantly greater intra-troop aggression and non-aggressive tourist/lemur interactions compared to the other individuals in the troop.

Marika accounted for 12 out of the 15 significant behavioural differences. These differences were predominantly found between Marika and three males, and one female (Volo, Rambo, Mainty and Sofina, respectively). She was found to be significantly more aggressive towards adult males than two other individuals in the troop, and more aggressive towards adult females than six other individuals in the troop. Both Marika and Maso were found to have significantly greater minutes per hour and counts per hour of non-aggressive tourist/lemur interactions than one male, Volo (all: U = 648.000, P = 0.001). The 3 remaining behavioural differences were found between Maso, and Volo and Rambo. Of interest, Maso was more aggressive towards adult males than Rambo (U = 630.000, P = < 0.001).

3.5.1.2 Troop CX

Troop CX was discovered to have 12 significant intra-troop differences (Table 3.8) out of a possible 72 variables (Appendix 13). Like YF, the significant differences in CX were found in intra-troop aggression and grooming, but also in feeding, resting and scent-marking behaviours.

		CX TROOP *(n = 6, df = 5)*	
		X^2	P
Point Behaviours *(Counts/Hour)*	Aggression to Adult Male	24.010	< 0.001
	Aggression from Adult Male	16.538	0.005
	Aggression to Adult Female	19.220	0.002
	Aggression from Adult Female	30.581	< 0.001
	Aggression to Other	11.830	0.037
	Total Counts of Aggressive Vocalisations	11.093	0.050
Event Behaviours *(Mins/Hour)*	Feed on Natural Food	15.836	0.007
	Rest	13.515	0.019
	Allo-Groom	14.272	0.014
	Self-Groom	14.195	0.014
	Scent-mark	64.645	< 0.001
Scan *(Counts/30Mins)*	Out of Sight	17.632	0.003

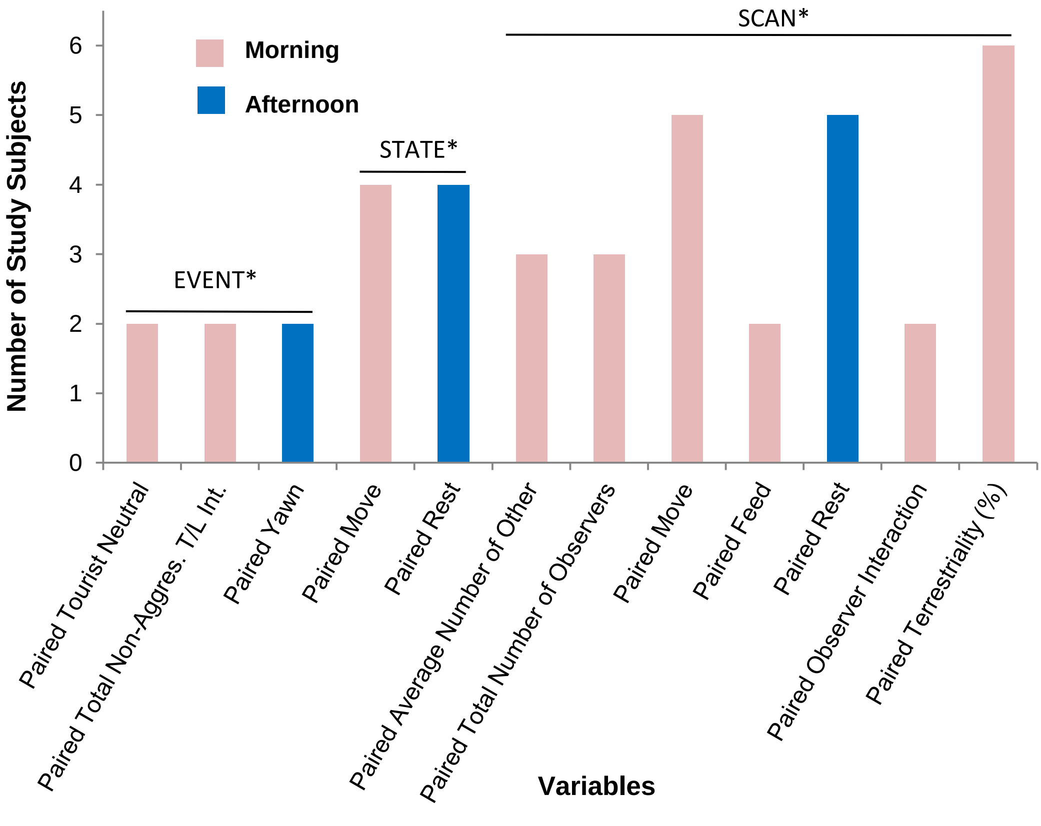
All results are significant when P < 0.05. Df = Degrees of Freedom.

TABLE 3.8 Significant Individual Differences in the Behaviours of Troop CX Using a Kruskal-Wallis Test. *n* = 6. (APPENDIX 13).

A post-hoc Mann-Whitney U test, Appendix 16, revealed that all six individuals had significant behavioural differences when compared to each other. Once the Dunn-Šidák Correction had been applied to the original significant results, 20 behaviours were found to be significantly different between individuals in CX when P < 0.0036571. Of interest, Orona had greater minutes per hour of scent-marking compared to the other individuals in the troop. He also had greater counts per hour of aggression directed towards him from all three of the adult females. Additionally, Tsipika had greater counts of aggression towards adult females compared to the two males, Orona and Pentina (both: U = 714.000, P = 0.003).

3.5.2 Morning and Afternoon Comparison in the 14 Individual Study Subjects

A Wilcoxon Matched-Pairs Signed-Rank test was performed to investigate morning and afternoon comparisons in the combined troops (i.e. 14 individual study subjects) (Appendix 18). The results revealed that differences were found between morning and afternoon for all individuals, except Kely and Avanana in Troop YF (Figure 3.4).



** Behaviours/Samples. Variables were paired for morning (n_1 = 294) and afternoon (n_2 = 294). Non-Aggres. T/L Int. = Non-Aggressive Tourist/Lemur Interaction.*

<u>FIGURE 3.4</u> The Number of Study Subjects with Significant Behavioural Differences Between Morning and Afternoon Using the Wilcoxon Matched-Pairs Signed-Rank Test (APPENDIX 18).

The representation of the significant findings in Figure 3.4 indicates that the strongest trends were seen in 'terrestriality', 'move' and 'rest'. Terrestriality and moving were significantly greater in the morning. 'Rest' and 'yawn' were the only behaviours that were more common in the afternoon.

3.5.3 Tourist Presence and Absence

A Wilcoxon Matched-Pairs Signed-Rank test was performed on all data for the combined individuals in the tourist troop, YF, to look for significant behaviours during tourist presence/absence. 6 and 7 behaviours/counts (omitting 'habitat zone' and obvious tourist/lemur interaction) out of a possible 72 variables were found to be significant in YF when tourists were present and absent, respectively (Table 3.9, Appendix 19).

		Absent *(n = 268)* Mean ± S.E.			**Present** *(n = 68)* Mean ± S.E.			Wilcoxon M-P Z	P
Event Behaviours	Total Intra-troop Aggression	1.63	±	0.19	3.79	±	0.70	-2.366	0.018
(Counts/Hour)	Troop Encounter	0.17	±	0.03	0.41	±	0.10	-2.380	0.017
State Behaviours	Rest	27.50	±	0.97	21.59	±	1.43	-2.100	0.036
(Mins/Hour)	Groom Other	0.04	±	0.02	0.00	±	0.00	-2.023	0.043
	Allo-Groom	2.48	±	0.27	0.66	±	0.22	-2.521	0.012
Scan	Average Other Number	0.11	±	0.03	0.59	±	0.10	-2.521	0.012
(Counts/30 Mins)	Total Number of Observers	2.56	±	0.04	4.96	±	0.41	-2.521	0.012
	Rest	3.48	±	0.11	2.94	±	0.18	-1.960	0.050
	Self-Groom	0.66	±	0.04	0.43	±	0.07	-2.103	0.035
	Observer/Lemur Interaction	0.04	±	0.01	0.62	±	0.09	-2.521	0.012
	Proximity (category metres)	3.28	±	0.04	3.12	±	0.07	-1.960	0.050
	Elevation (m)	4.13	±	0.08	3.56	±	0.15	-2.100	0.036
	Terrestriality (%)	14.04	±	1.19	31.69	±	2.83	-2.521	0.012
	Habitat Zone	1.85	±	0.06	2.91	±	0.04	-2.521	0.012

All data were significant when P < 0.05. Data coloured in blue indicates the higher value, thus the direction of significance. 'Habitat Zone' is in categories, therefore has no direction of significance. All obvious significance relating to tourist/lemur interaction has been omitted from this table.

TABLE 3.9 Significant Differences in the Mean Behaviours in Troop YF during Tourist Presence and Absence (Omitting Obvious Tourist/Lemur Interactions) Using the Wilcoxon Matched-Pairs Signed-Rank Test. (APPENDIX 19).

Of interest, resting (both state behaviour and scan sample count) was found to be more significant when tourists were absent. This was also found for 'self-groom' and ‘allo-groom’. Intra-troop aggression and troop encounters were significantly greater during tourist presence. Additionally, the troop had greater terrestriality during tourist presence, thus spent a mean of 4.13 metres elevated when tourists were absent. Interestingly, YF spent significantly more time in habitat zone 2 (i.e. ‘degraded land’) and habitat zone 3 (i.e. ‘marginal land’) when tourists were absent and present, respectively.

3.6 AIMS AND HYPOTHESES

3.6.1 AIM 1: To determine whether tourism has an effect on activity budgets.

Hypothesis 1: Tourist pressure influences activity budgets, and is negatively related to feeding and resting time, but positively related to self-grooming.

‘Tourist pressure’ is measured by looking at tourist presence, proximity and density. The Wilcoxon Matched-Pairs Signed-Rank test revealed 3 state behaviours to be significant when tourists were absent: ‘rest’, ‘groom other’ and ‘allo-groom’ (omitting obvious significant tourist/lemur interactions) (Table 3.9, Appendix 19). An additional Mann-Whitney U test revealed a further 4 significant activity budget behaviours (omitting obvious significant tourist/lemur interactions) (Table 3.10, Appendix 21). ‘Feed on human food’, ‘move’ and ‘scent-mark’ were all significant when tourists were present, and ‘self-groom’ was significant when tourists were absent.

		Absent (*n*=268) Mean ± S.E.			Present (*n*=68) Mean ± S.E.			Mann-Whitney U Test U	Z	P
State behaviours	Feed on Human Food	0.27	±	0.14	0.54	±	0.20	7956.000	-3.941	< 0.001
(Mins/Hour)	Move	10.76	±	0.52	13.09	±	0.83	7154.500	-2.739	0.006
	Rest	27.50	±	0.97	21.59	±	1.43	7362.500	-2.446	0.014
	Allo-Groom	2.48	±	0.27	0.66	±	0.22	6840.500	-3.630	< 0.001
	Self-Groom	4.96	±	0.29	4.00	±	0.58	7332.500	-2.501	0.012
	Scent-mark	0.55	±	0.07	1.01	±	0.23	7855.500	-2.165	0.030

All data were significant when P < 0.05. Data coloured in blue indicates the higher value, thus the direction of significance. All obvious significance relating to tourist/lemur interaction has been omitted from this table.

<u>TABLE 3.10</u> Significant Differences Found Between the Mean State Behaviours in Troop YF during Tourist Presence and Absence (Omitting Obvious Tourist/Lemur Interactions) Using the Mann-Whitney U Test. (APPENDIX 21).

A Kruskal-Wallis test revealed that tourist proximity had no significant difference on feed, rest, and self-groom behaviours (Table 3.11).

	X^2	*P*
Feed on Human Food	0.182	0.913
Feed on Natural Food	1.522	0.467
Rest	0.746	0.689
Self-Groom	1.931	0.381

Results are not significant when P < 0.05.
Degrees of Freedom = 2. n = 68.

<u>TABLE 3.11</u> Kruskal-Wallis Test Looking at the Effect of Tourist Proximity on the State Behaviours of Feeding, Resting and Self-Grooming in Troop YF.

A Spearman's Correlation Coefficient test revealed that only 'feed on human food' was correlated to the average tourist number (Table 3.12). When average tourist number increased, feeding on human food resources decreased (Figure 3.5).

		Feed on Human Food	**Feed on Natural Food**	**Rest**	**Self-Groom**
Average Tourist Number	*rs*	-0.256	-0.066	-0.152	0.190
	P	0.035	0.592	0.216	0.122

Highlighted data = significant when P < 0.05 (two-tailed). rs = Spearman's Correlation Coefficient. n = 68.

<u>TABLE 3.12</u> Spearman's Correlation Coefficient Test Looking at the Relationship between Average Tourist Number and Feeding, Resting and Self-Grooming in Troop YF.

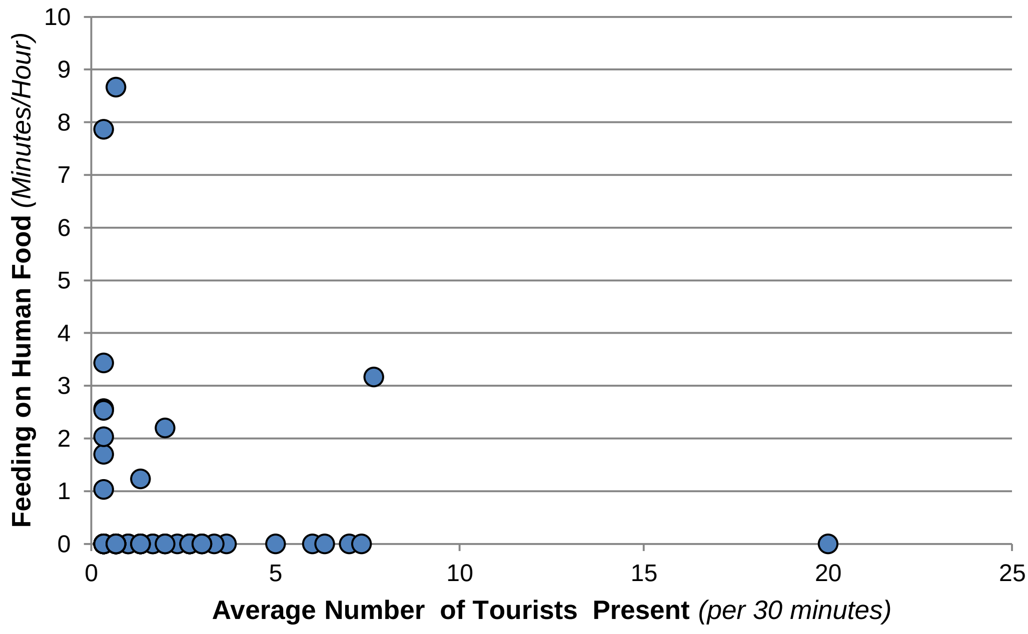


FIGURE 3.5 **The Relationship Between Average Tourist Number and Lemurs in Troop YF Feeding on Human Food**

3.6.2 AIM 2: To determine whether tourism has an effect on aggression.

Hypothesis 2: The frequency of inter-troop and intra-troop aggression, aggressive tourist/lemur interactions and aggressive vocalisations are positively related to tourist pressure.

The results of the Wilcoxon Matched-Pairs Signed-Rank test in Table 3.9 and Appendix 19 revealed that 'total intra-troop aggression', 'troop encounters', 'total aggressive tourist/lemur interactions' and 'total non-aggressive tourist/lemur interactions' were significantly greater during tourist presence. An additional Mann-Whitney U test revealed 19 significant event behaviour differences relating to aggression out of a possible 30, all of which were greater during tourist presence (Table 3.13, Appendix 22).

		Absent (*n*=268) Mean ± S.E.			Present (*n*=68) Mean ± S.E.			Mann-Whitney U Test		
								U	Z	P
Event behaviours	Aggression to Adult Male	0.31	±	0.05	0.74	±	0.22	8206.000	-2.085	0.037
(Counts/hour)	Aggression from Adult Male	0.17	±	0.04	0.76	±	0.34	8164.500	-2.603	0.009
	Aggression to Adult Female	0.31	±	0.09	0.94	±	0.44	8226.500	-2.366	0.018
	Aggression to Other	0.14	±	0.04	0.35	±	0.11	8315.000	-2.406	0.016
	Tot. Intra-troop Aggression	1.63	±	0.19	3.79	±	0.70	6524.500	-4.020	< 0.001
	Aggression from Unknown	0.11	±	0.05	0.47	±	0.21	8314.000	-3.023	0.003
	Tot. Inter-troop Aggression	0.28	±	0.11	0.74	±	0.28	8119.500	-3.050	0.002
	Troop Encounter	0.17	±	0.03	0.41	±	0.10	8018.000	-2.820	0.005
	Aggression to Tourist	0.00	±	0.00	0.03	±	0.03	8978.000	-1.985	0.047
	Tourist Noise	0.00	±	0.00	0.12	±	0.06	8576.000	-3.988	< 0.001
	Tourist Rock	0.00	±	0.00	0.29	±	0.12	8174.000	-5.300	< 0.001
	Tourist Throw	0.00	±	0.00	0.09	±	0.05	8710.000	-3.449	0.001
	Tot. Aggres. T/L Int.	0.00	±	0.00	0.53	±	0.15	7504.000	-6.992	< 0.001
	Tourist Neutral	0.03	±	0.02	4.24	±	0.59	2744.500	-14.261	< 0.001
	Tourist Stroke	0.01	±	0.01	0.15	±	0.09	8743.000	-2.746	0.006
	Tourist Play	0.00	±	0.00	0.15	±	0.08	8576.000	-3.988	< 0.001
	Tourist Feed	0.03	±	0.02	0.56	±	0.19	7870.000	-5.196	< 0.001
	Tourist Other	0.00	±	0.00	0.06	±	0.04	8844.000	-2.812	0.005
	Tot. Non-Aggres. T/L Int.	0.07	±	0.04	5.15	±	0.71	2788.500	-14.046	< 0.001

Highlighted data = Significant when P < 0.05.Tot. = Total. Aggres.T/L Int. = Aggressive Tourist/Lemur Interactions.

<u>TABLE 3.13</u> Significant Differences Found Between the Mean Event Behaviours Relating to Aggression in Troop YF during Tourist Presence and Absence Using the Mann-Whitney U Test. (APPENDIX 22).

Although tourist presence appeared to have an impact on aggression, tourist proximity (Table 3.14) and tourist density (Table 3.15) did not.

	X^2	P
Total Intra-troop Aggression	1.838	0.399
Total Inter-troop Aggression	0.303	0.859
Total Aggression Tourist/Lemur Interactions	1.783	0.410
Total Counts of Aggressive Vocalisations	0.172	0.917

Results are not significant when P < 0.05. Degrees of Freedom = 2. n = 68.

<u>TABLE 3.14</u> Kruskal-Wallis Test Looking at the Effect of Tourist Proximity on Measures of Aggression in Troop YF.

		Total Intra-troop Aggression	Total Inter-troop Aggression	Total Aggressive Tourist/Lemur Interactions	Total Counts of Aggressive Vocalisations
Average Tourist Number	*rs*	-0.075	-0.060	0.015	0.093
	P	0.544	0.625	0.904	0.453

Data is not significant when P < 0.05. rs = Spearman's Correlation Coefficient. n = 68.

TABLE 3.15 Spearman's Correlation Coefficient Test Looking at the Relationship between Average Tourist Number and Measures of Aggression in Troop YF.

Hypothesis 3: Intra-troop aggression rates are significantly higher during bouts of tourist-feeding interactions, and specifically when eating human provided foods.

A relationship was found between total-intra troop aggression and lemurs feeding on human food, as well as tourists feeding the lemurs (Table 3.16).

		Feed on Human Food	Tourist Feed Lemur
Total Intra-troop Aggression	*rs*	0.280	0.259
	P	0.021	0.033

Highlighted data = significant when P < 0.05. rs = Spearman's Correlation Coefficient. n = 68.

TABLE 3.16 Spearman's Correlation Coefficient Test Looking at the Relationship between Intra-Troop Aggression and 'Tourist Feed' and 'Feed on Human Food' in Troop YF.

A positive correlation was found for both relationships (i.e. total intra-troop aggression increased when the lemurs fed on human food or were fed by tourists) (Figure 3.6 and 3.7).

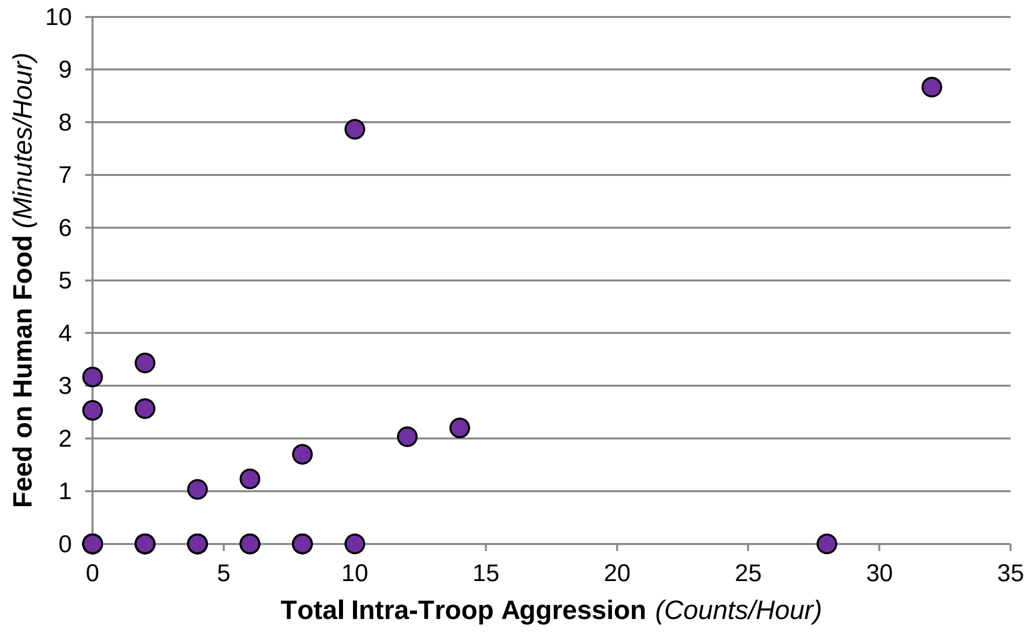


FIGURE 3.6 The Relationship Between Total Intra-Troop Aggression and Feeding on Human Food Resources in Troop YF.

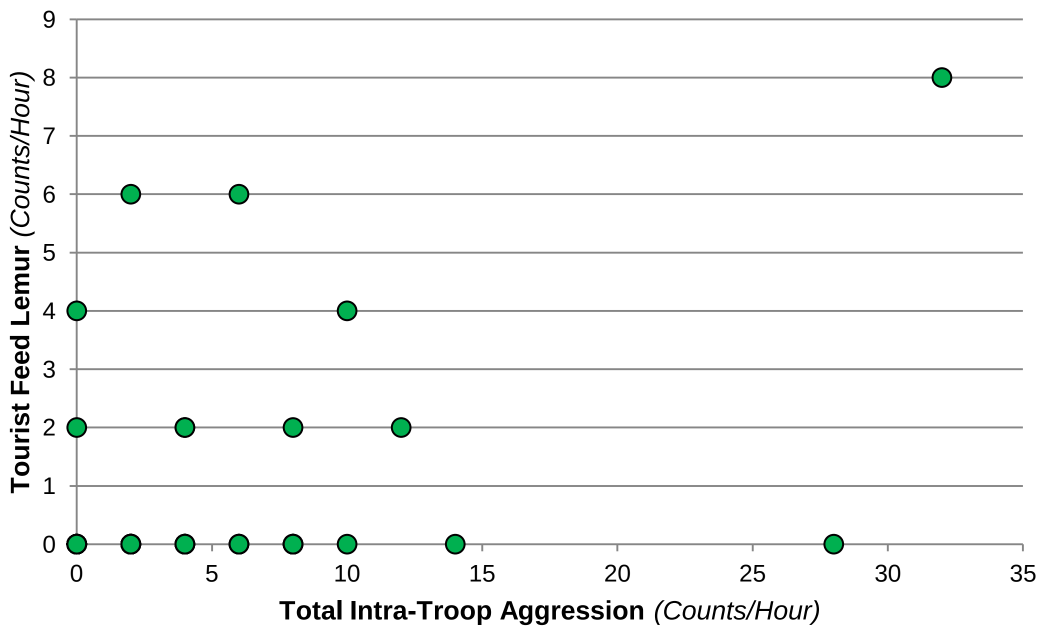


FIGURE 3.7 The Relationship Between Total Intra-Troop Aggression and Tourists Feeding the Lemurs in Troop YF.

3.6.3 AIM 3: To determine whether tourism has an effect on displacement activities (self-directed behaviour).

Hypothesis 4: Rates of SDB are positively related to tourist pressure.

The results of the Wilcoxon Matched-Pairs Signed-Rank test revealed no significant difference in displacement activities when tourists were present or absent (Appendix 19). Nevertheless, an additional Mann-Whitney U test found scent-marking to be more significant when tourists were present (Table 3.17).

		Absent (*n*=268) Mean ± S.E.	**Present** (*n*=68) Mean ± S.E.	Mann-Whitney U Test U	Z	P
Event behaviours *(Counts/Hour)*	Self-Scratch	4.24 ± 0.28	4.06 ± 0.49	8987.500	-0.177	0.859
	Self-Groom < 10 S	2.70 ± 0.21	2.97 ± 0.48	9048.500	-0.093	0.926
	Yawn	0.75 ± 0.11	0.44 ± 0.14	8500.000	-1.228	0.219
State Behaviour *(Mins/Hour)*	Scent-mark	0.55 ± 0.07	1.01 ± 0.23	7855.500	-2.165	0.030

Highlighted data = Significant when P < 0.05. Data coloured in blue indicates the higher value.

TABLE 3.17 Mann Whitney U Test Results Looking at the Impact of Tourist Presence on the Self-Directed Behaviours of Self-Scratch, Self-Groom Less Than 10 Seconds, Yawn and Scent-Mark in Troop YF.

Although tourist proximity appeared to have no impact on the frequency of SDB (Table 3.18), a relationship was found between 'average tourist number' and 'self-groom < 10 seconds' (Table 3.19).

	X^2	P
Self-Scratch	0.118	0.943
Self-Groom < 10 Seconds	2.088	0.352
Yawn	0.369	0.831
Scent-mark	0.799	0.671

Results are not significant when P < 0.05. Degrees of Freedom = 2. n = 68.

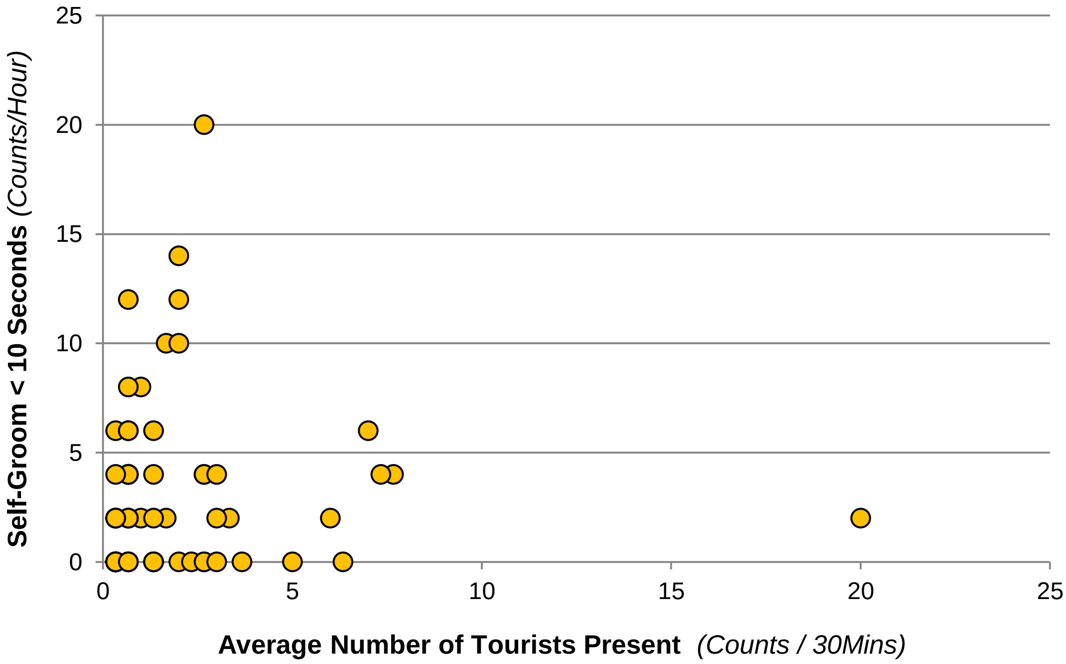
TABLE 3.18 Kruskal-Wallis Test Looking at the Effect of Tourist Proximity on Self-Directed Behaviours in Troop YF.

		Yawn	Self-Scratch	Self-Groom < 10 Seconds	Scent-mark
Average Tourist Number	*rs*	0.091	-0.202	0.258	0.220
	P	0.460	0.098	0.034	0.072

Highlighted data = significant when P < 0.05. rs = Spearman's Correlation Coefficient. n = 68.

<u>TABLE 3.19</u> Spearman's Correlation Coefficient Test Looking at the Relationship between Average Tourist Number and Yawn, Self-Scratch, Self-Groom < 10 Seconds and Scent-Mark in Troop YF.

As the average number of tourists increased, so did the frequency of self-grooming less than 10 seconds (Figure 3.8).



<u>FIGURE 3.8</u> The Relationship between Average Tourist Number and Self-Groom < 10 Seconds in Troop YF.

<u>Hypothesis 5</u>: Rates of SDB are positively related to inter-troop and intra-troop aggression and aggressive tourist/lemur interactions.

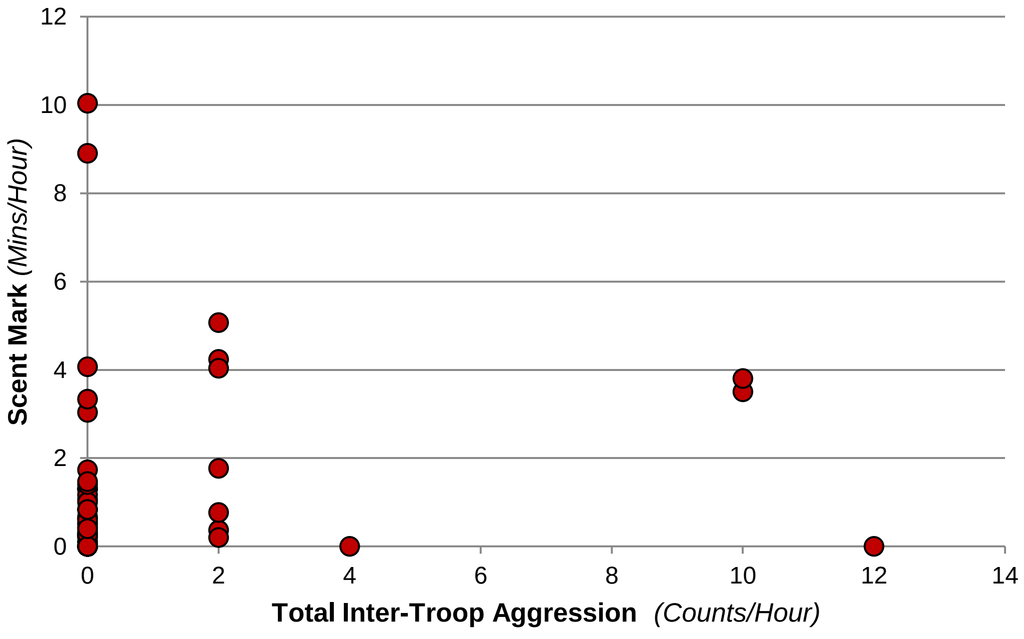
A Spearman's Correlation Coefficient test investigating SDB and aggressive interactions in Troop YF revealed only one significant relationship between total inter-troop aggression and scent-marking (Table 3.20).

		Total Intra-troop Aggression	Total Inter-troop Aggression	Total Aggressive Tourist/Lemur Interactions
Yawn	*rs*	-0.150	0.039	0.014
	P	0.222	0.753	0.908
Self-Scratch	*rs*	-0.006	-0.090	0.182
	P	0.964	0.467	0.138
Self-Groom < 10 seconds	*rs*	-0.076	-0.164	0.099
	P	0.537	0.180	0.422
Scent-mark	*rs*	-0.013	0.279	-0.159
	P	0.916	0.021	0.197

Highlighted data = significant when P < 0.05. rs = Spearman's Correlation Coefficient. n = 68.

<u>TABLE 3.20</u> Spearman's Correlation Coefficient Test Looking at the Relationship between Self-Directed Behaviours and Inter-Troop, Inter-Troop Aggression, and Aggressive Tourist/Lemur Interactions in Troop YF.

The relationship was a positive one; as the total inter-troop aggression increased, scent-marking within Troop YF also increased (Figure 3.9).



<u>FIGURE 3.9</u> The Relationship between Total Inter-Troop Aggression and Scent-Marking in Troop YF.

3.6.4 AIM 4: To determine whether tourism has an effect on home range size and habitat use.

Hypothesis 6: Home range size and habitat zones are affected by tourist pressure.

The tourist troop, YF, appeared to have a tighter cluster of GPS waypoints in comparison to the forest troop, CX (Figure 3.10). Both troops ventured into all three habitat zones: reserve forest, degraded land and marginal land.

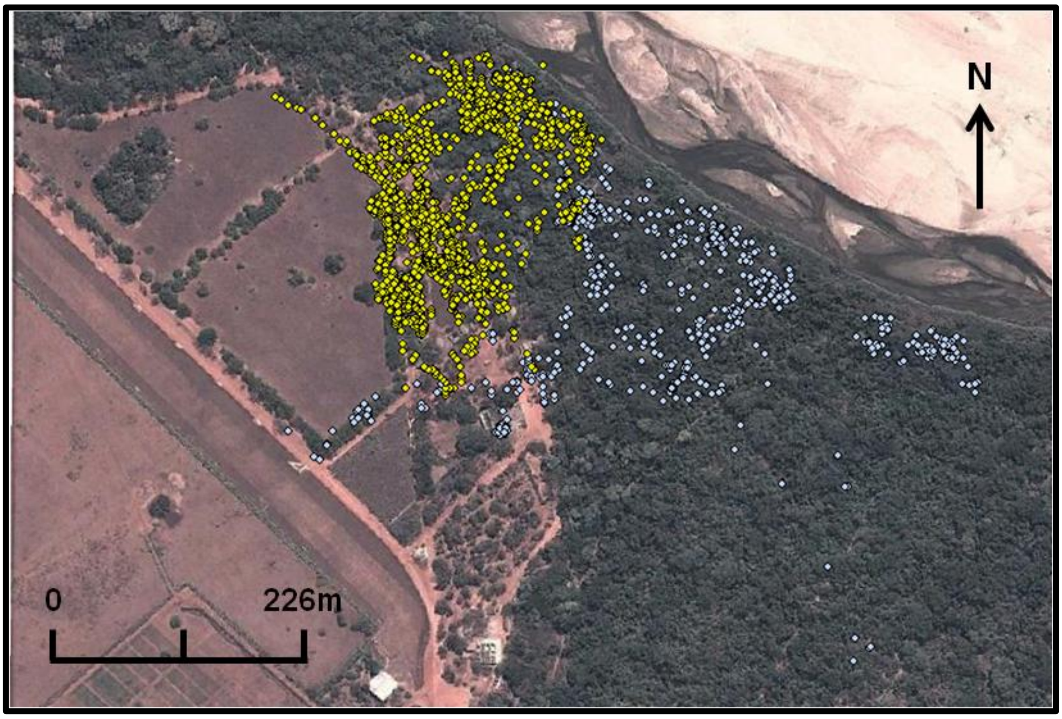


FIGURE 3.10 All GPS Waypoints Recorded during the Whole Study Period for Troops YF (yellow) and CX (blue).

Almost 50% of focals for Troop YF were found in 'marginal' land, followed closely by 'reserve forest' (Figure 3.11).

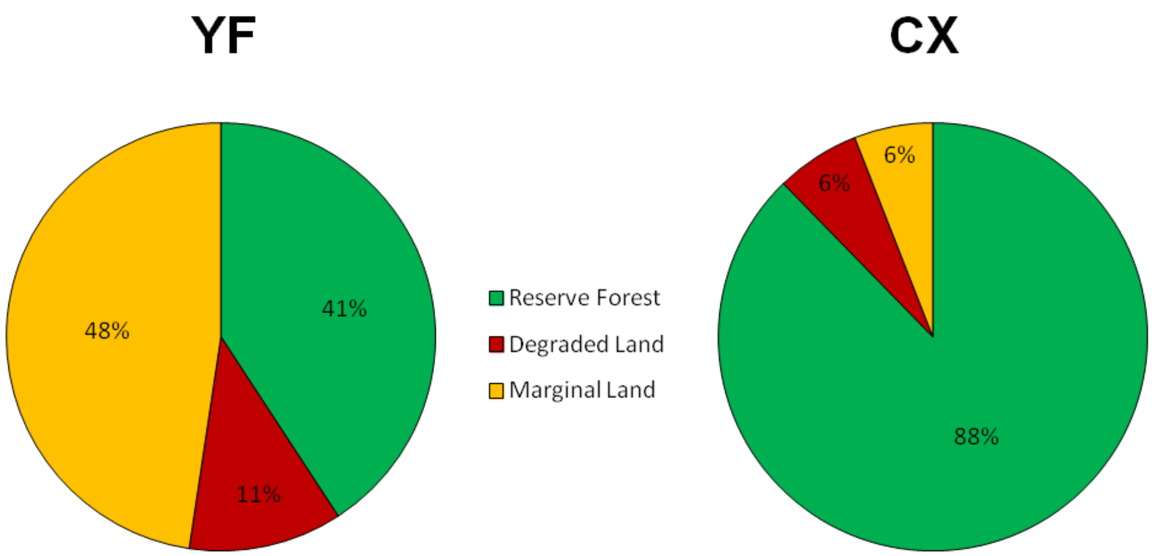
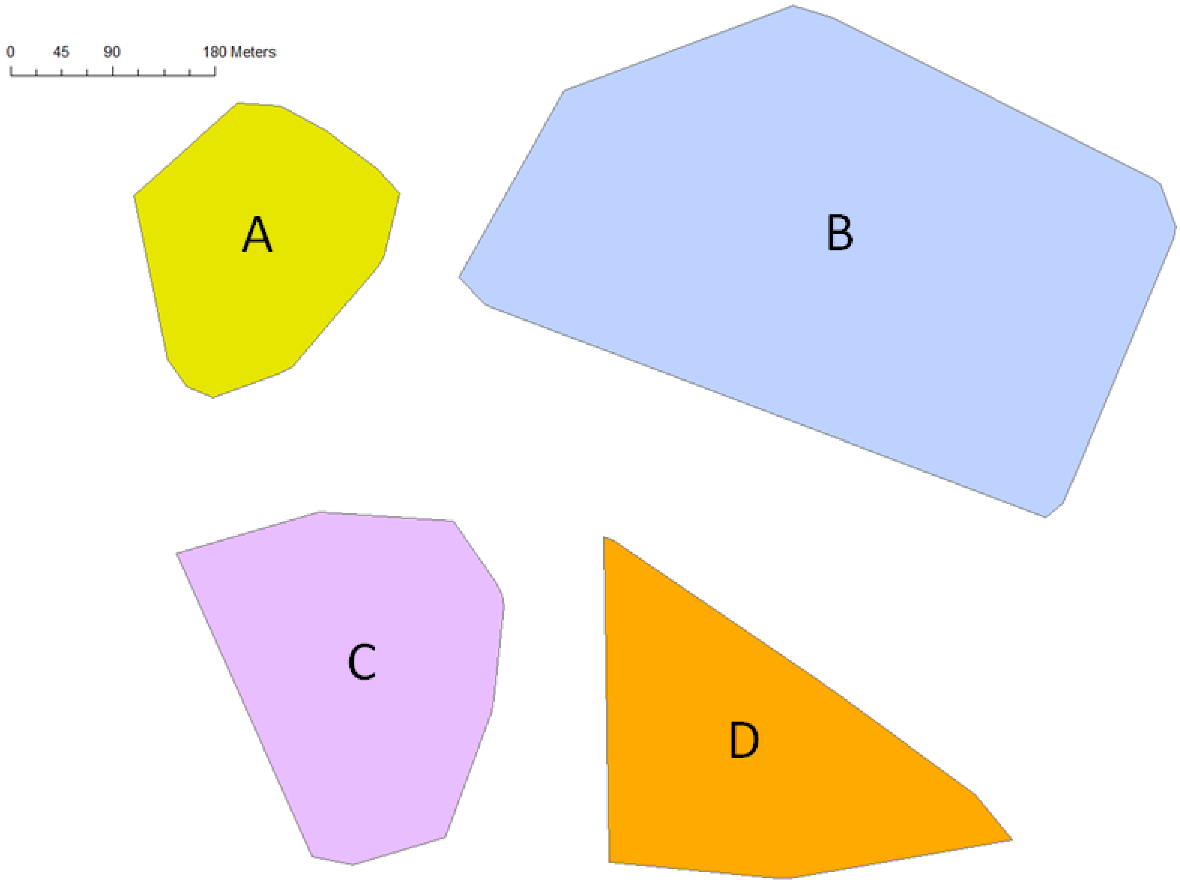


FIGURE 3.11 Average Number of Focals Spent in Each of the Three Habitat Zones for Troops YF (*n* = 336) and CX (*n* = 252).

Focals in Troop CX however, were predominantly found in 'reserve forest'; with approximately equal numbers of focals found in 'marginal' and 'degraded' land. The Mann-Whitney U test investigating inter-troop behavioural differences, confirmed that YF spent significantly more time in habitat zone 2 ('degraded') compared to CX, and CX spent significantly more time in habitat zone 1 ('reserve forest') compared to YF (U = 0.000, P = 0.001) (Appendix 9).

The MCPs depicting home range size for both troops over the study period showed that YF had a smaller home range in March compared to April, whilst CX had a larger home range in March compared to April (Figure 3.12).



A) YF in March, B) CX in March, C) YF in April, D) CX in April.

FIGURE 3.12 Minimum Convex Polygons (100%) Depicting Home Range Size in March and April for Troops YF and CX.

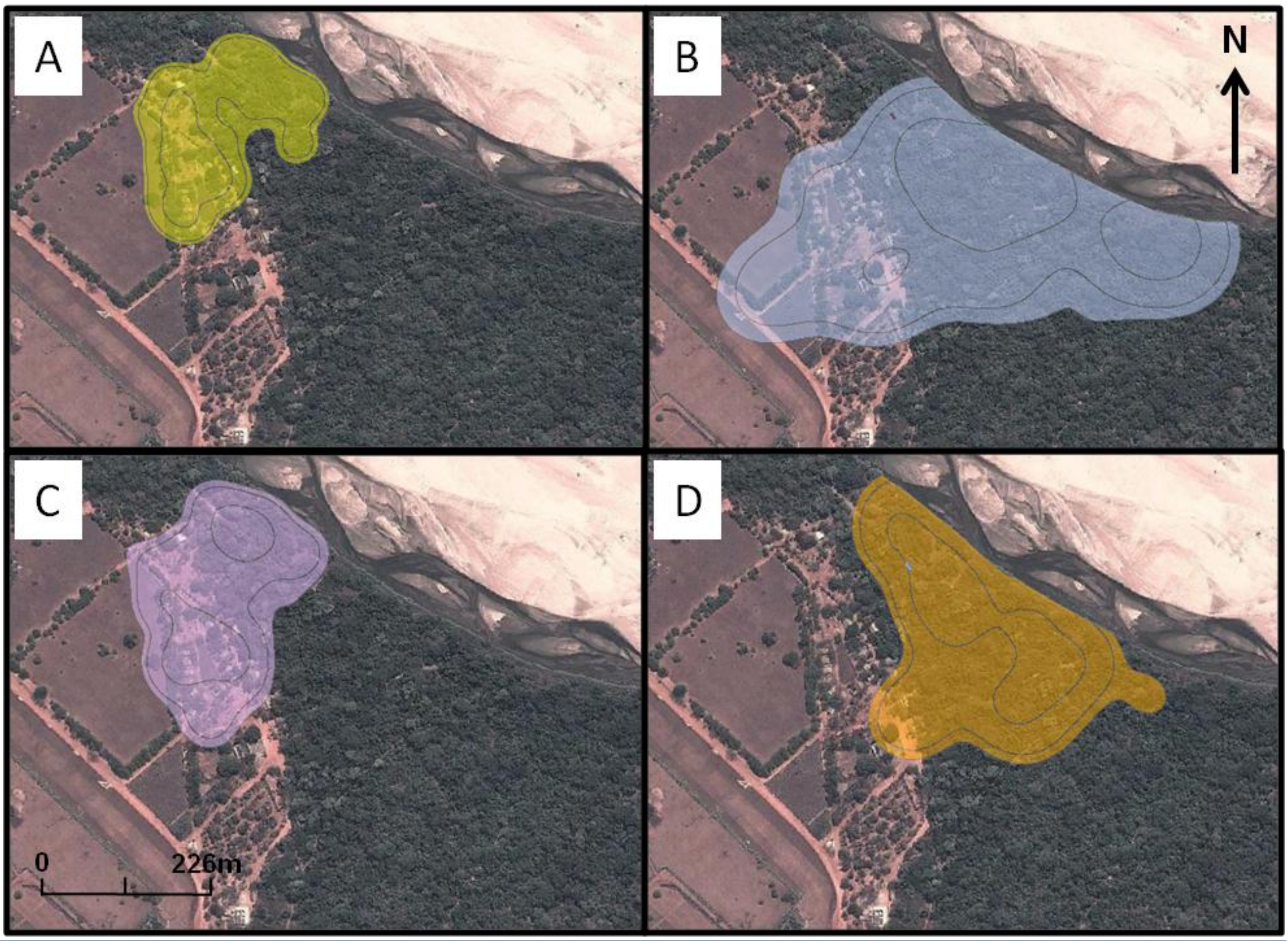
The MCP areas indicated that both troops had a similar home range size in April, whilst in March the MCP area for CX was greater than four times the size of the corresponding home range for YF (Table 3.21).

	MCP Area (100%)		KDE Area (95%)					
Troop	March	April	March* 50	March* 90	March* 95	April* 50	April* 90	April* 95
YF	4.09	6.24	1.12	3.81	4.64	1.38	4.59	5.76
CX	17.32	5.94	4.71	13.34	16.59	2.47	6.69	7.96

Data are in km² to 2 decimal places. = with corresponding isopleths of 50, 90 and 95%. KDEs for CX have been clipped.*

TABLE 3.21 Comparison of Home Range Size Areas for Troops YF and CX in March and April Using Minimum Convex Polygons (100%) and Kernel Density Estimators (95%).

The KDE areas for YF in March and April revealed that the troop's home range size did not really differ between these months. In March, YF had one main centre of activity where the troop spent the majority of its time (Figure 3.13). This was at the tourist front, predominantly on 'degraded' land.



A) YF in March, B) CX in March, C) YF in April, and D) CX in April. KDEs for CX have been clipped.

FIGURE 3.13 Kernel Density Estimators (95%) [With Corresponding Isopleths] Depicting Home Range Size and Space Usage in March and April for Troops YF and CX.

In April however, YF had two main centres of activity: the 'reserve forest', as well as 'degraded land'.

The KDE areas for CX revealed that the troop's home range was approximately doubled in March than in April (Table 3.21). In March, CX travelled out of the 'reserve forest' to the 'marginal' and 'degraded' land areas on the outskirts of the study site (Figure 3.13); to an area where there are clumped introduced plant species (Figure 3.14). CX had three main centres of activity: two in the 'reserve forest' by the Mandrare River and one on 'degraded' land at the tourist front. During March, the home ranges of both troops appeared to overlap. In April however, CX had one large centre of activity in the 'reserve forest'. Nevertheless, they still travelled to the outskirts of the gallery forest onto 'marginal' and 'degraded' land.

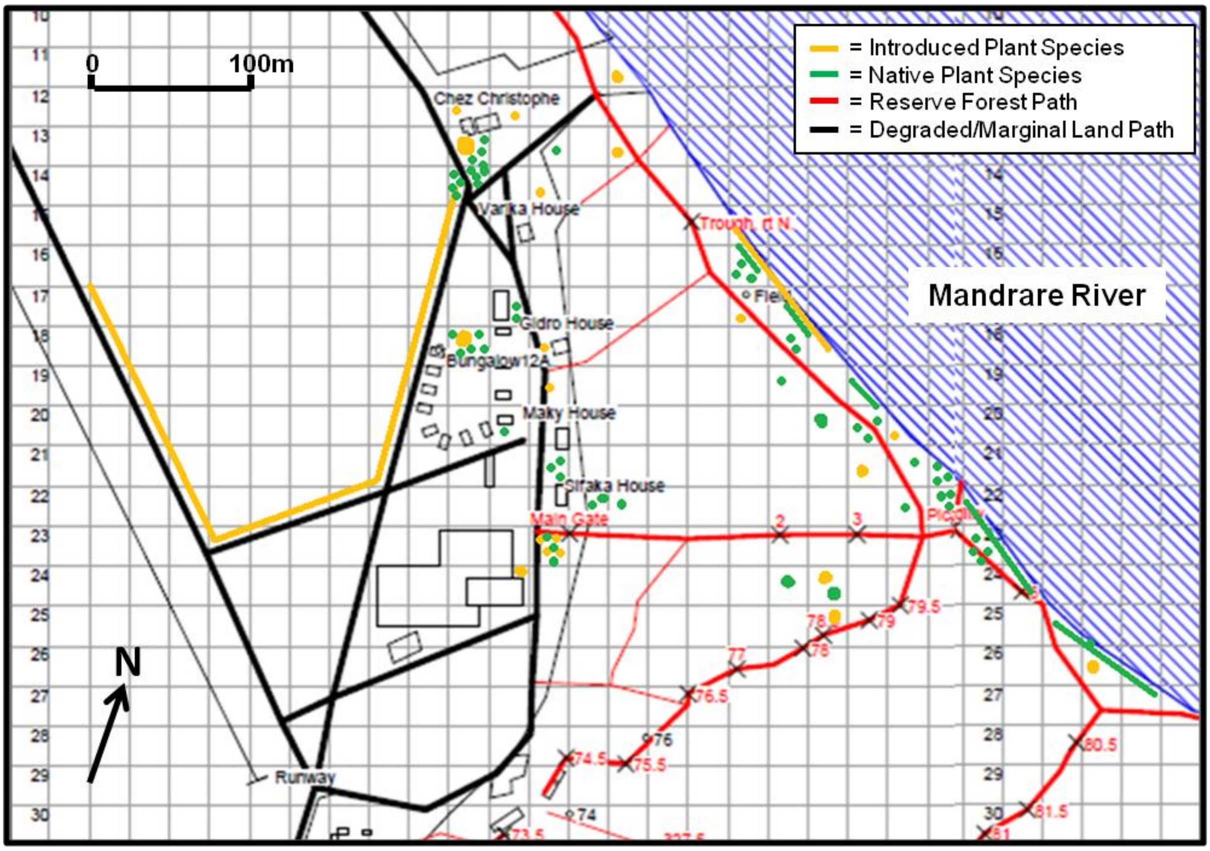


FIGURE 3.14 Location of Key Feeding Plants Observed and Grid-Mapped during the Study Period (*Map sourced and adapted from:* Josia Razafindramanana, Pers. Comm.).

Introduced plant species were predominantly found on 'degraded' and 'marginal' land zones adjacent to the tourist front (Figure 3.14). Native plant species, that the troops were regularly observed to feed on, were found by the Mandrare River in the reserve forest, and also clumps were found around the tourist front.

Hypothesis 7: Terrestriality and troop elevation are affected by tourist pressure.

The Wilcoxon Matched-Pairs Signed-Rank test revealed that terrestriality and troop elevation for YF were found to be significantly greater when tourists were present and absent, respectively (Table 3.9, Appendix 19). This significance was also confirmed using a Mann-Whitney U test, whereby the percentage of terrestriality was approximately doubled during tourist presence (Table 3.22).

		Absent (*n*=268) Mean ± S.E.			**Present** (*n*=68) Mean ± S.E.			Mann-Whitney U Test		
								U	Z	P
Scan Sample	Elevation (m)	4.13	±	0.08	3.56	±	0.15	6667.500	-3.534	< 0.001
(Counts/30Mins)	Terrestriality (%)	14.04	±	1.19	31.69	±	2.83	4630.000	-6.469	< 0.001

Highlighted data = Significant when P < 0.05. Data coloured in blue indicates the higher value, thus the direction of significance.

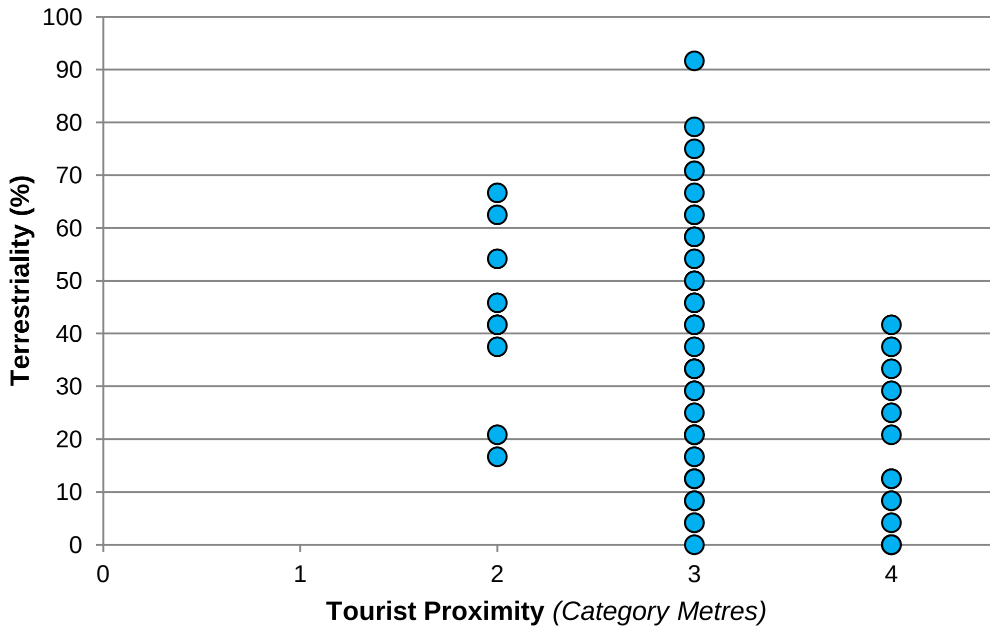
TABLE 3.22 Mann-Whitney U Test Results Comparing Terrestriality and Elevation for Troop YF during Tourist Presence and Absence.

Tourist proximity was found to have a significant impact on terrestriality and elevation in YF (Table 3.23). As tourist proximity increased, terrestriality in YF appeared to decrease (Figure 3.15). Contrastingly, as tourist proximity increased, troop elevation increased (Figure 3.16).

	X^2	P
Elevation	27.295	< 0.001
Terrestriality	14.790	0.001

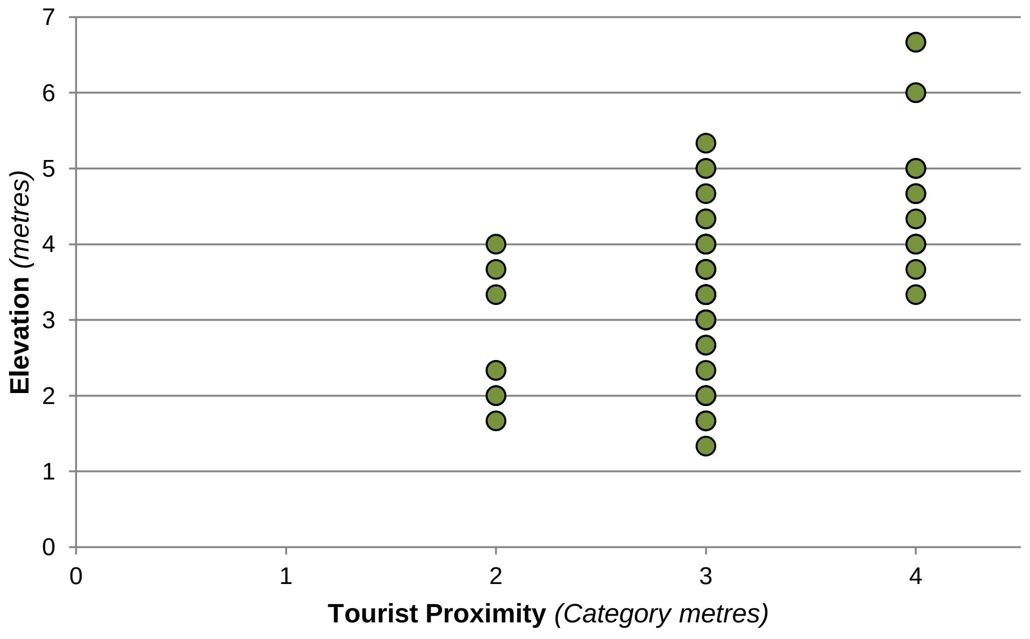
Highlighted data = Significant when P < 0.05. Degrees of Freedom = 2. n = 68.

TABLE 3.23 Kruskal-Wallis Test Looking at the Effect of Tourist Proximity on Elevation and Terrestriality in Troop YF.



Category metres: 1 = 0 - ≤ 1 m; 2 = 1 - ≤ 2 m; 3 = 2 - ≤ 5 m; 4 = 5 - ≤ 10 m.

<u>FIGURE 3.15</u> The Relationship between Tourist Proximity and Terrestriality in Troop YF.



Category metres: 1 = 0 - ≤ 1 m; 2 = 1 - ≤ 2 m; 3 = 2 - ≤ 5 m; 4 = 5 - ≤ 10 m.

<u>FIGURE 3.16</u> The Relationship between Tourist Proximity and Elevation in Troop YF.

Tourist density however, appeared to have no impact on terrestriality and elevation in the tourist troop, YF (Table 3.24).

		Terrestriality	Elevation
Average Tourist Number	*rs*	0.151	-0.129
	P	0.218	0.294

Data is not significant when P < 0.05. rs = Spearman's Correlation Coefficient. n = 68.

TABLE 3.24 Kruskal-Wallis Test Looking at the Effect of Tourist Density on Elevation and Terrestriality in Troop YF.

CHAPTER 4: *DISCUSSION*

The purpose of this study was to investigate whether tourism had an impact on the behaviour and ranging patterns of two populations of ring-tailed lemur. Confounding variables including environment and age were controlled throughout the study (*Chapter 2*). The climate was consistent throughout the study period, with an average temperature of 27.8 °C, and almost equal days of rain falling in CX and YF data collection periods (i.e. 6 and 7 days, respectively). Nevertheless, the data were first scrutinised for additional confounding variables that may affect the outcome of the results for the aims and hypotheses. These confounding variables included differences in behaviour between: the sexes, morning and afternoon, and mating and non-mating periods.

This chapter will first examine the results investigating these three confounding variables and discuss their potential impact on answering the aims and hypotheses of the study. Results for each individual aim and corresponding hypothesis will then be discussed, followed by short-comings of the study, and future areas of research. Finally, broader implications of the findings of the study will be discussed, and conclusions will be drawn.

4.1 DOES SEX EFFECT BEHAVIOUR?

Compared to males, females were revealed to have greater intra-troop and inter-troop aggression, and greater rates of feeding on natural food resources. When investigating individual differences within both troops, it was not only confirmed that females were more aggressive overall, but Maso and Marika accounted for all significant aggression directed towards other individuals in troop YF.

Female ring-tailed lemurs are known to be socially dominant over males and are in charge of resource and space defence (Jolly and Pride, 1999). Additionally, when food resources are limited, there is increased local resource competition among females, thus heightened inter-troop and intra-troop aggression (Silk, 1983; Isbell and Young, 2002). It has been hypothesised that in an attempt to reduce this local resource competition, closely related females form coalitions and direct their aggression towards other non-related females, with the hope of inevitably evicting them from within the troop (Sterck *et al*., 1997; Silk, 1983). This targeted aggression is seen in both captive and free-ranging ring-tailed lemurs (Palagi *et al.*, 2005). The strongest relationships are seen between mother and daughter, but also between sisters (Jolly and Pride, 1999). This helps explain the overall aggression directed from Maso and Marika towards the other members of YF (most notably the males, and one female, Sofina); they are both highly ranked and related maternal-sisters.

Many studies have examined this influence of resource distribution on group composition and behaviour in primates (Wrangham, 1980; Isbell and Young, 2002; Sterck *et al*., 1997; Janson and Goldsmith, 1995; Van Schaik, 1983; Hill and Lee, 1998; Vasudev *et al.*, 2008). As seen in this study, it is thought that resource distribution influences the behaviour and number of females in a group, but males are impacted by the ease of access to these females (Cowlishaw and Dunbar, 2000; Sterck *et al*., 1997).

Aggression directed from females and the activity of feeding, are closely associated. Females were found to spend significantly more time feeding compared to males, because in addition to females being socially dominant over males, they also have feeding priority. This is considered a unique behavioural trait in Lemuriformes, and classically seen in ring-tailed lemurs (White *et al.*, 2007). This feeding priority is thought to be due to two potential reproductive strategies. Firstly, by being more agonistically dominant over males, females not only mitigate male-female resource competition, but also maximise their high energy demands to compensate for highly seasonal breeding in an unpredictable climate. Secondly, it has been stated that males postpone time feeding on resources to allow females to feed first, thus improving male-female intra-troop relationships and maximising their future access to females during the mating season (White *et al.*, 2007; Sterck *et al*., 1997).

In addition to the sex differences seen in aggression and feeding, males were found to have greater rates of grooming females and scent-marking in comparison to females. The rate of scent-marking in adult males is known to differ according to reproductive season, with higher rates occurring during the mating and lactation periods (Gould and Overdorff, 2002). As this study coincided with the start of the mating season, this higher rate of scent-marking in males is therefore not surprising. Males scent-mark more than females due to reproductive competition during the mating season; the scent-mark acts as a means of communication to other males within and between troops in an attempt to mediate this male competition (Gould and Overdorff, 2002). Additionally, increased grooming of females by males is another potential reproductive strategy to maximise access to females during the mating season by reinforcing social bonds (Sauther, 1991). This chapter also discusses the possibility that scent-marking could be a self-directed behaviour (indicative of stress) in ring-tailed lemurs (*Section 4.6*).

4.1.1 Summary

Although there were only few significant sex differences, greater aggression seen in females and greater scent-marking seen in males, could potentially influence the results for those aims and hypotheses relating to these behaviours. This has greater implications for troop YF, who had the greater exposure to tourists, and the two dominant females (Maso and Marika), who were more aggressive compared to the other individuals within the troop. These findings were therefore taken into account when discussing the results for the associated aims and hypotheses (*Sections 4.5 and 4.6*).

4.2 DOES TIME OF DAY EFFECT BEHAVIOUR?

Aggression from adult females, tourist/lemur interactions, moving and terrestriality were all found to be significantly greater in the morning compared to the afternoon. Only resting was found to be greater in the afternoon. Nevertheless, no morning and afternoon behavioural differences were found for Avanana and Kely in troop YF. The few differences that were found can be explained in terms of tourist pressure. Greater numbers of tourists were always found during the morning data collection periods, therefore more tourist/lemur interactions occurred. These tourist/lemur interactions often included feeding, which could have increased intra-troop and inter-troop aggression from the adult females (*Sections 4.1 and 4.5.2*). The results comparing morning and afternoon behavioural differences coincided with those results investigating differences seen in YF during tourist presence and absence. When tourists were present there was significantly greater intra-troop aggression and terrestriality, and when tourists were absent there were significantly greater rates of resting. Therefore the behavioural differences seen in the morning and afternoon could be due to tourist pressure (*Sections 4.4, 4.5* and *4.7*).

4.2.1 Summary

Although behavioural differences were found between the morning and afternoon, the results imply that a strong assumption can be made that these are due to tourist pressure. Therefore it is assumed that there were no differences in behaviour in the morning and afternoon that would affect the outcome of the aims and hypotheses.

4.3 DOES THE MATING SEASON EFFECT BEHAVIOUR?

The non-mating and mating periods were estimated to be from 29/02/12 to 06/04/12, and 07/04/12 to 27/04/12, respectively. There appeared to be no important behavioural differences that would affect the outcome of the aims and hypotheses. Nevertheless, elevation (i.e. the height of the lemur off the ground) was found to be greater during the mating period, possibly because lemurs copulate in the trees to avoid predation and inter-troop and intra-troop competition for mates (Koyama, 1988).

4.3.1 Summary

Mating season appeared to have no major effect on behaviours that would influence the aims and hypotheses of the study. Nevertheless, the fact that the study coincided with the onset of the mating season has been taken into account.

4.4 AIM 1: TO DETERMINE WHETHER TOURISM HAS AN EFFECT ON ACTIVITY BUDGETS.

4.4.1 Hypothesis 1: Tourist pressure influences activity budgets, and is negatively related to feeding and resting time, but positively related to self-grooming.

Tourist pressure was measured by looking at tourist presence, density, and proximity of the nearest tourist to the centre of the troop. Resting and grooming behaviours (including allo-groom and self-groom) were significantly greater in YF when tourists were absent. Tourist proximity was found to have no effect on state behaviours. The rate of feeding on human food resources in YF was significantly greater when tourists were present, but was found to decrease when tourist density increased. There was no significant impact of tourist pressure on feeding on natural food resources.

Tourists are regarded as resource providers and as a predator threat, thus are likely to influence activity budget behaviours (Borg, 2011; Menard, 2004). Rates of resting in YF were found to be significantly increased when tourists were absent; which is supported by many studies looking at the effect of tourism on activity budget behaviours in a whole range of different taxa (humpback whales, *Megaptera novaeangliae*: Corkeron, 1995; elephants, *Loxodonta Africana*: Anderson and Eltringham, 1997; chimpanzees, *Pan troglodytes*: Johns, 1996; Mareeba rock-wallaby, *Petrogale mareeba*: Hodgeson *et al.*, 2004; bottlenosed dolphins (*Tursiops truncatus*: Constantine *et al.*, 2004; gorilla species, *Gorilla gorilla*: Wells, 2005; Wood, 1998). It is therefore suggested that there is a positive relationship between active-type behaviours (i.e. moving) and tourist presence (Mitchell *et al*., 1992). If this is the case, then the tourist troop (YF) should display significantly greater rates of moving in comparison to the forest troop (CX) due to the increased tourism exposure in YF. The results of this study confirmed this finding.

Furthermore, there is a clear difference between the immediate effects of tourists compared to access to provisioned foods on activity budget behaviours, thus highlighting the true cause of alterations in activities. As previously mentioned, tourism has shown to influence activity budget behaviours, resulting in increased travelling and decreased resting (Borg, 2011). Contrastingly, studies investigating the impact of provisioned food resources on activity budgets in a variety of different primate taxa, have shown increased rates of resting, but reduced amounts of time moving and feeding (Olive baboons, *Papio anubis*: Warren *et al.*, 2011; baboon species, *Papio*: Dunbar, 1992; Bronikowski and Altmann, 1996; savannah baboons, *Papio cynocephalus*: Altmann and Muruthi, 1988; Rhesus macaques, *Macaca rhesus*: Malik, 1986). This supports the findings of this study, highlighting the cause of activity budget behaviour change to be due to the immediate effects of tourist pressure and not from provisioned resources.

Nevertheless, it is thought that resting is important for thermoregulatory and digestion purposes (Dunbar, 1996; Fedurek and Dunbar, 2009). Therefore it can speculated that, as YF had significantly greater rates of feeding on human food resources when tourists were present in the morning, a possible explanation for increased resting when tourists were absent in the afternoon, could be due to digestion purpose. However, this theory is only speculative and cannot be proven in this study.

It has been hypothesised that increased tourist presence is negatively related to feeding in wild species (Asian rhinoceros, *Rhinoceros unicornis*: Lott and McCoy, 1995; woodland caribou, *Rangifer tarandus caribou*: Duchesne *et al.*, 2000). In habituated animals however, it has been suggested that there is a positive relationship, with more active-type behaviours, such as feeding, being more apparent (Todd *et al.*, 2007). This was seen in YF, who were found to feed on human food resources significantly more when tourists were present. Once again, the alteration in feeding behaviour can be attributed to tourist pressure and not provisioning, because animals with access to provisioned foods are shown to feed less in comparison to those feeding on wild resources (Warren *et al.*, 2011). The reasoning for this is that provisioned foods are generally greater in energy content and nutrients (Boccia *et al.*, 1995). Nevertheless, this could be due to the fact that human food resources were only available when tourists were present (Pers. Obs.). Interestingly, when tourist density increased, rates of feeding on human food resources decreased. Although this study highlights the positive influence of tourist presence on feeding on human food resources, increasing tourist density had a negative influence. As no significance was found for the influence of tourist presence and density on feeding on natural resources, further research would need to be carried out to confirm these findings.

Rates of grooming behaviours, including allo-groom and self-groom, were significantly greater in YF when tourists were absent. One theory for intra-troop grooming is that it is considered important for cultivating valuable relationships and maintaining social bonds (Kutsukake, 2010). Studies have shown that animals subjected to tourism often demonstrate high levels of inter-group aggression (Reynolds and Braithwaite, 2001; Klailova *et al.*, 2010), which are often mediated through grooming (Aureli, 1997; Aureli and Yates, 2010). Compared to CX, grooming behaviours directed from individuals was significantly greater in YF. It is hypothesised that provisioned animals not only seem to have heightened aggression and therefore a need for more affiliative grooming behaviours, but they also have more time for social interactions due to their increased foraging efficiency rates from access to more nutritious food resources (vervet monkeys, *Chlorocebus aethips pygerthrus*: Saj *et al.*, 1999; Hamadryas baboons, *Papio hamadryas*: Kamal *et al.*, 1997).

Although previous studies have confirmed these findings seen in YF (i.e. that general grooming behaviours are decreased when primates are subjected to tourism) (common chimpanzee, *P. troglodytes*: Wood, 1998), there is no clear explanation as to why YF groomed more when tourists were absent. It can be speculated that as tourist/lemur interactions were significantly greater in the morning, YF had more time for intra-troop social interactions (such as grooming) and resting in the afternoon when tourists were usually absent.

Self-grooming behaviour however, is often considered a SDB when it is performed but not deemed relevant at the time (Maestripieri *et al.*, 1992). Self-grooming is normally classified as relevant when it is performed for hygienic maintenance or social purposes, but deemed irrelevant when it could be a possible indicator of anxiety (Higham *et al.*, 2009; Carder and Semple, 2008; Reamer *et al.*, 2010). Previous studies on primates have shown that SDB have increased due to tourist pressure (Tibetan macaques, *Macaca thibetana*: Matheson *et al.*, 2007; Barbary macaques, *M. sylvanus*: Marechal *et al.*, 2011). Nevertheless, these findings are not supported in this study as rates of self-grooming in YF were found to be significantly greater when tourists were absent.

SDB have only recently been studied in strepsirhines and their function still remains unclear in this taxon (Sclafani *et al.*, 2012; Palagi and Norscia, 2010; Buckley and Semple, 2012). A possible explanation for the findings in this study, is that self-grooming is not a self-directed behaviour in ring-tailed lemurs. The greater rates of self-grooming observed in YF when tourists were absent, could therefore be a possible facilitator for transitions between different behaviours, thus adjusting the motivational state of the actor (ring-tailed lemurs, *Lemur catta*: Buckley and Semple, 2012; sticklebacks, *Gasterosteus aculeatus*: Wilz, 1970; honey bees, *Apis mellifera*: Root-Bernstein, 2010). The lemurs are more engaged in tourist/lemur interactions when the tourists are present, but display greater intra-troop social interactions and resting when they are absent, thus a greater need for motivation to change between the different behaviours.

4.4.2 Summary

Tourist pressure was found to influence activity budget behaviours, most notably resting, allo-groom, self-groom and feeding on human food resources. Tourist presence was found to be negatively related to resting, thus agrees with Hypothesis 1. YF was found to have significantly greater rates of moving compared to CX, thus supporting previous studies that tourist pressure positively increases active-type behaviours.

Feeding on human food resources was found to be significantly greater in YF when tourists were present. Nevertheless, rates of feeding on human food resources decreased with increasing tourist density. Hypothesis 1 states that tourist pressure will negatively affect general feeding (including feeding on natural and human food resources). The findings for Hypothesis 1 are therefore inconclusive, as tourist presence positively influenced feeding on human resources, but tourist density was found to have a negative influence. Additionally, no significance was found for the influence of tourist pressure on feeding on natural food resources, thus Hypothesis 1 is neither accepted nor rejected. Furthermore, closer examination of the data indicates that twenty tourists seen on one day could have in fact influenced the results. The lemurs were often driven away from large groups of tourists by Reserve staff due to persistent pestering and stealing of food (Pers. Obs.).

Rates of overall grooming, including self-groom, were found to be greater when tourists were absent. This does not support Hypothesis 1. Previous studies have hypothesised that self-grooming in ring-tailed lemurs is not a SDB, but for hygienic purposes, and as a means of motivating the actor between behavioural changes (Buckley and Semple, 2012).

This is the first study of its kind to highlight that ring-tailed lemurs, like many other taxa, are affected negatively by tourist pressure. In particular, the effect of tourist pressure on feeding and resting behaviours. Inevitably, any alteration to the activity budget of a species can have adverse effects, possibly affecting their health and survival.

4.5 AIM 2: TO DETERMINE WHETHER TOURISM AS AN EFFECT ON AGGRESSION.

4.5.1 Hypothesis 2: The frequency of inter-troop and intra-troop aggression, aggressive tourist/lemur interactions and aggressive vocalisations are positively related to tourist pressure.

Overall intra-troop aggression and total aggressive tourist/lemur interactions were significantly greater in YF when tourists were present compared to when they were absent. No significance was found for rates of aggressive vocalisations.

Nevertheless, when compared to CX, YF had significantly greater intra-troop aggression and aggressive vocalisations, suggesting that they were the more aggressive troop overall. However, all significant aggressive interactions were directed from Maso and Marika in YF. Rates of inter-troop encounters were also significantly greater during tourist presence, and often involved aggressive interactions (Pers. Obs.). These troop encounters occurred more often on ‘degraded’ and ‘marginal’ land. Tourist proximity and density had no effect on aggressive interactions.

Aggressive behaviours in primates are often witnessed during intra-troop contests for resources (i.e. mates, food), anti-predator behaviour, reproductive periods, and predation (Honess and Marin, 2006). However, high rates of aggression have also been observed in animals subjected to wildlife tourism (Klailova *et al.*, 2010; Reynolds and Braithwaite, 2001), and the results of this study support these findings. Aggression can be regarded as a positive behaviour, as it can intensify social bonds within groups of animals (Honess and Marin, 2006). Nevertheless, the negative consequences may outweigh the positives. Prolonged or reoccurring aggression in individuals can cause a change in habitat activity patterns, decrease immunity, increase physiological stress, and effect communicative behaviours and social development (Berman and Li, 2002; Reynolds and Braithwaite, 2001; Muehlenbein and Ancrenaz, 2009).

It is not surprising that tourist/lemur interactions were greater when tourists were present. However, it is interesting that the relationship was an aggressive one. No aggression was directed towards tourists from lemurs, even though this has been observed in other primate species subjected to tourism (e.g. lion-tailed macaque, *Macaca silenus*: Wheatley and Harya Putra, 1994). All aggression therefore, was directed from the tourists who shouted or threatened to throw objects at lemurs stealing their food or entering their bungalows (Pers. Obs.).

The greater rates of aggressive intra-troop interactions during tourist presence can be explained in terms of resource distribution. In the ‘degraded’ and ‘marginal’ habitat zones, there are many introduced plant species that the lemurs fed on, and it is also the predominant location for tourist/lemur interactions (i.e. including feeding of highly nutritious human food resources); the food resources tend to be clumped. The distribution of food resources in provisioned animal groups can influence behaviours, i.e. dispersed resources result in less aggressive behaviours compared to competition for highly nutritious clumps (Boccia *et al.*, 1995; Isbell, 1991; Koenig, 2002).

YF is one of the larger troops in Berenty Reserve with (12 individuals), and has a greater number of individuals than CX (8 individuals). The 2009 census revealed that the mean number of individuals in the troops was greater for the tourist front troops (14.5) compared to the forest troops (6.3) (Razafindramamana, *2009 Census at Berenty Reserve*; Jolly, Pers. Comms., 2012). Animals may remain in larger groups to enhance their ability to defend resources (Wrangham, 1980). A disadvantage of larger troops however, is that feeding competition is increased between group members, and this is correlated with an increase in intra-troop aggression (Chapman and Chapman, 2000). Larger troops in Berenty Reserve appear to be found in high inter-troop conflict and encounter zones (Pride, 2005), which may explain why YF had greater rates of aggressive vocalisations in comparison to CX. The majority of inter-troop confrontations arise over food resources (Pers. Obs.; Bayart and Simmen, 2005). These findings were also found at Anja Reserve in Madagascar, where heightened aggression was correlated with an increase in lemur population density (Cameron, 2010). Furthermore, YF experienced greater encounters with other troops when tourists were present because the study period coincided with the onset of the mating season (Bayart and Simmen, 2005), and lemurs predominantly mated on 'degraded' and 'marginal' land (Pers. Obs.). Tourist/lemur interactions predominantly took place in these two habitat zones.

Additionally, the 'Local Resource Competition Hypothesis', states that the frequency and intensity of aggression is often increased when the animals are confined to a small space (Clark, 1978; Silk, 1983). The lemur density at the tourist front is approximately 500/km^2, compared to 250/km^2 in the gallery forest (Jolly and Pride, 1999; Jolly *et al.*, 2002; Crawford *et al.*, 2006). There are approximately six lemur troops of varying size at the tourist front in Berenty Reserve; therefore competition for resources, including space, could result in high inter-troop aggression (Jolly *et al.*, 2006). The forest troops, such as CX, have a larger space to roam, and this could explain the reduced aggression seen in this troop.

Maso and Marika accounted for all significant aggressive interactions within YF. Larger troops often have greater female-female competition (Ichino and Koyama, 2006). This heightened competition is once again due to resource distribution; where clumped resources of high nutritional value cause an increase in intra-troop aggression, and ultimately shape the female relationships and dominance hierarchies within the troop (Isbell 1991; Koenig, 2002) (*Section 4.1*).

4.5.2 Hypothesis 3: Intra-troop aggression rates are significantly higher during bouts of tourist-feeding interactions, and specifically when eating human provided foods.

Intra-troop aggression significantly increased in YF when the lemurs fed on human food resources, and when they were fed by tourists. Many studies investigating the impact of provisioning on rates of aggression in primate species, have reported similar findings (Formosan macaques, *Macaca cyclopis*: Hsu *et al.*, 2009; rhesus macaques, *Macaca mulatta*: Hill, 1994; lion-tailed macaques, *Macaca silenus*: Wheatley and Harya Putra, 1994; Japanese macaques, *Macaca fuscata*: Hill, 1999). This intra-troop aggression seen in YF is once again due to competition over provisioned resources, where the intensity of aggression can depend on the type of food resource (Gemmill and Gould, 2008).

4.5.3 Summary

Troop YF displayed greater aggressive interactions when tourists were present, thus Hypothesis 2 can be accepted. YF was significantly more aggressive than CX; however the source of the aggression was predominantly from two related, dominant females. This therefore questions the validity of the findings as the aggression observed could be due to individual differences and not necessarily because of tourist pressure.

Intra-troop aggression rates were found to be significantly higher during tourist-feeding interactions, and when the lemurs fed on human food resources; thus Hypothesis 3 can be also be accepted. The aggression seen in YF was explained in terms of heighted intra-troop and inter-troop competition for clumped food resources of high nutritional value (i.e. human food).

This study is the first of its kind to investigate the impact of tourist pressure on aggressive interactions and feeding of provisioned foods in ring-tailed lemurs. Although further studies need to be conducted to confirm these findings, the does imply that tourism does have an effect on aggression rates in this species.

4.6 AIM 3: TO DETERMINE WHETHER TOURISM HAS AN EFFECT ON DISPLACEMENT ACTIVITIES (SELF-DIRECTED BEHAVIOUR).

4.6.1 Hypothesis 4: Rates of self-directed behaviours (SDB) are positively related to tourist pressure.

Greater rates of scent-marking were found to be significant in YF when tourists were present. None of the other displacement activities (i.e. self-groom < 10 seconds, yawn, self-scratch) were significantly different when tourists were present or absent. Nevertheless, when compared to CX, YF displayed significantly greater rates of 'self-grooming less than 10 seconds'. Interestingly, this SDB was also positively related to an increase in tourist density. Tourist proximity had no effect on SDB behaviours, even though past research has suggested otherwise in different primate species (Barbary macaques, *Macaca sylvanus*: Marechal *et al*, 2011; Tibetan macaques, *Macaca thibetana*: Matheson *et al.*, 2007).

Previous studies have speculated that scent-marking could be a potential SDB in ring-tailed lemurs, as it is in some other primates (Garnett's small-eared bushbabies, *Otolemur garnettii*: Watson *et al*., 1999; Black-tufted marmoset, *Callithrix penicillata*: Barros *et al.*, 2004). SDB are thought to be indicators of anxiety, and are displayed when a situation is stressful (Maestripieri *et al*., 1992; Daniel *et al.*, 2008). Previous studies have shown that tourist pressure caused an increase in the rate of SDB in a variety of different taxa (e.g. Adelie penguins, *Pygoscelis adeliae*: Giese, 1998; Barbary macaques, *Macaca sylvanus*: Marechal *et al*., 2011). The findings in this study agree with this outcome as greater rates of scent-marking were revealed in YF during tourist presence.

Nevertheless, it has also been speculated that scent-marking could be a possible function of resource defence seen in female ring-tailed lemurs attempting to reinforce territory borders (Mertl-Millhollen, 2006). The findings of this study however, showed that males had significantly greater rates of scent-marking compared to females. Therefore, males could be displaying greater rates of scent-marking due to the onset of the mating season (Gould and Overdorff, 2002) (*Section 4.1*). Nevertheless, this should be disregarded as no significant behavioural differences were found between mating and non-mating periods. The third theory for the increased scent-marking during tourist presence is that it is a behaviour based on tradition. It has been observed that ring-tailed lemurs repeatedly over-mark "scent-mark hot-spots" (Kappeler, 1998), which they still return to after a prolonged period of time (i.e. months) (Mertl-Millhollen, 2000). It can be speculated that, the presence of tourists results in heightened aggression (most notably when feeding on provisioned foods), which could lead to an increase in scent-marking behaviours (indicative of stress), which is seen more so in males because of the dominance and feeding priority enforced by the females. This theory is further enforced as a positive relationship was found between aggression and scent-marking (*Section 4.6.2*). From personal observations, it appears that theories of scent-marking being a result of tradition and as a displacement behaviour are operating in conjunction with each other.

It was also revealed that rates of self-grooming behaviours lasting less than ten seconds in YF were greater when tourist density increased. This suggests that 'self-groom less than 10 seconds' could be a SDB in ring-tailed lemurs. This was speculated to be the case in a study carried out on ring-tailed lemurs in Anja Reserve, who were discovered to have increased rates of self-grooming compared to another population subjected to less tourism exposure in Tsaranoro, Madagascar (Cameron, 2010). Nevertheless, Cameron (2010) was not investigating impacts of tourism specifically, and it was concluded that although self-groom could be a SDB in ring-tailed lemurs, rates were greater due to increased lemur population density. This theory could also be applied to YF, as the tourist front has a higher density of lemur numbers, thus is a more stressful environment. However, evidence strongly suggests that the cause of overcrowding at the tourist front is ultimately due to resource distribution, which is largely due to tourism (i.e. introduced tree species in the flowerbeds or provisioned foods), thus short-lived self-grooming behaviours could be an indirect result of this.

4.6.2 Hypothesis 5: Rates of SDB are positively related to inter- and intra-troop aggression and aggressive tourist/lemur interactions.

Significantly greater rates of scent-marking were apparent with increasing inter-troop aggression in YF. Previous studies examining the relationship between aggression and SDB found similar results (long-tailed macaques, *Macaca fascicularis*: Aureli *et al.*, 1989; Barbary macaques, *Macaca sylvanus*; long-tailed macaques, *Macaca fascicularis*: Aureli, 1997). Additionally, Marechal *et al.* (2011) demonstrated a link between tourist pressure, aggression and SDB. Nevertheless, no significant relationship was found between rates of SDB and aggressive tourist/lemur interactions in this study. Although scent-marking appears to be a possible SDB in ring-tailed lemurs, it also has other uses involving territory defence, ownership of resources, mate attraction, and self-advertisement (Lewis, 2006; Roberts, 2012; Pochron *et al.*, 2005a).

The link between scent-marking and aggression has been seen in a diverse range of taxa, including amphibians, reptiles, mammals and arthropods (Roberts, 2012). In strepsirhines, this aggression-SDB link has been associated with intra-sexual aggression and territory ownership (Milne-Edward's sifaka, *Propithecus edwardsi*: Pochron *et al.*, 2005b; ring-tailed lemur, *Lemur catta*: Scordato and Drea, 2007; Verreaux's sifaka, *Propithecus verreauxi verreauxi*: Lewis, 2005). Additionally, saddleback tamarins (*Saguinus fuscicollis fuscicollis*) in a region of closely overlapping home ranges, demonstrated greater scent-marking where aggressive encounters occurred (Roberts, 2012). Scent-marking appeared to increase during inter-troop encounters, as demonstrated in this study.

4.6.3 Summary

Scent-marking was found to be significant in YF when tourists were present; no significant differences were seen in the other SDB behaviours. Nevertheless, when compared to CX, YF had greater rates of 'self-groom less than ten seconds', which was also found to increase with tourist density. Tourist proximity had no influence on SDB.

Possible explanations for the increased rates of scent-marking were discussed, including influence of tourist pressure, tradition and the onset of the mating season. However, the latter should be disregarded as no significant behavioural differences were found between mating and non-mating periods. The findings suggest that scent-marking has many functions, but possibly relates to anxiety and tradition in ring-tailed lemurs. Greater rates of self-grooming [less than ten seconds] when tourist density increased, were thought to be ultimately due to tourist pressure. Hypothesis 4 can be accepted as SDB were positively related to some elements of tourist pressure.

As inter-troop aggression increased, so did the rate of scent-marking in YF. This was explained in terms of competition for resources and overlapping home ranges, possibly due to tourist pressure and introduced tree species in the area creating clumped food patches. Nevertheless, Hypothesis 5 can only be partially accepted as rates of scent-marking were positively related to aggression, but no relationships were found between other SDB and intra-troop aggression and aggressive tourist/lemur interactions. Nevertheless, this is one of the first studies of its kind to examine the link between tourism, rates of aggression and SDB in strepsirhines.

4.7 AIM 4: TO DETERMINE WHETHER TOURISM HAS AN EFFECT ON HOME RANGE SIZE AND HABITAT USE.

4.7.1 Hypothesis 6: Home range size and habitat zones are affected by tourist pressure.

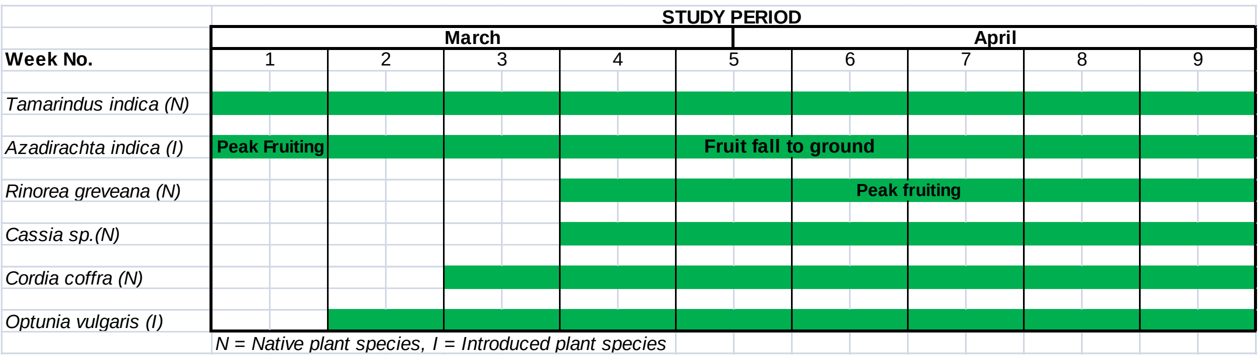
The minimum convex polygons (MCP) revealed that YF had similar size home ranges during March and April, whilst the home range size for CX in March was considerably larger than that of April. CX appeared to venture several hundred metres out of the reserve forest to feed on plant species on 'degraded' and 'marginal' land (Pers. Obs.). These findings were supported by kernel density estimators (KDE). YF appeared to have one main centre of activity at the tourist front, which barely changed over the two month study period. In April however, they had a second centre of activity near the Mandrare River in the reserve forest (where more native plant species are found). CX had three main centres of activity in March; the two largest being found in the reserve forest by the Mandrare River and the smaller centre was found by the 'main gate' (where many introduced plant species were apparent). In April however, CX spent the majority of their time in the reserve forest, adjacent to the Mandrare River.

The ‘home range’ is defined as the area an animal utilises frequently (Koyama *et al.*, 2006). In this study, it also included excursions made by YF or CX into adjacent home ranges, as these were deemed important when investigating short-term changes in home range size (e.g. changes between March to April). The home ranges in Berenty Reserve have remained relatively stable since they were first monitored in 1989 (Jolly and Pride, 1999; Mertl-Millhollen, 2000; Gould, 2006; Koyama *et al.*, 2006). However, when comparing previous home range data for CX, it appears that the troop’s home range has shifted approximately 100 metres south in the past six years (Soma, 2006). Nevertheless, a longitudinal study (i.e. months, or even years) investigating habitat size and usage should be carried out to confirm these findings.

It is thought that the size of these home ranges in the frugivorous-folivorous lemur inhabitants is dependent on forest habitat (i.e. floral composition) and ultimately the distribution of food resources (including the abundance of introduced plant species and provisioned food from tourism) (Bayart and Simmen, 2005). Ultimately, home range and group size are thought to be closely associated, where larger groups are normally apparent when there is increased inter-troop competition, and resources within the home range are of high quality; as observed in YF (Wrangham, 1980; Jolly *et al.*, 2002). Animals select yields that are not only high quality per unit handling time, but also of high nutritional value (Mertl-Millhollen *et al.*, 2003).

Provisioned animals have been observed to have home ranges that do not change size or alter shape, as seen in YF for March and April. Provisioned Japanese macaques (*Macaca fuscata*), not only relocated to tourist regions to take advantage of human food resources, but they ultimately reduced their home range size (Japanese macaques, *Macaca fuscata*: Koganezawa and Imaki, 1999). YF's home range is generally smaller than that of CX because there is a uniform distribution of resources at the tourist front (i.e. they are surrounded by introduced plants species and are provisioned by tourists) (Curtis and Zaramody, 1998). These high quality resources mean they do not have to travel far outside their core home range, and in not doing so, they can ultimately defend their resources more easily.

CX had a larger home range in March compared to April, because they travelled outside of their home range core to exploit rare resources (Sauther *et al.*, 2002; Jolly and Pride, 1999; Sussman, 1991; Gould, 2006). This behaviour, known as 'habitat shifting', is often seen in New World primates subjected to aseasonal environments (Erhart and Overdorff, 2008). However, the contrary is apparent at Berenty, where the strict seasons give rise to staggered flowering and fruiting of numerous, sought after plant species around the reserve (Figure 4.1).



<u>FIGURE 4.1</u> Representation of the Approximate Time of Fruiting and Flowering of Key Feeding Plants Observed in March and April in Berenty Reserve (*Source and adapted from:* Saotra Solonirina Rakotonomenjanahary, research assistant at Berenty Reserve).

During March, CX travelled out of the reserve forest, not only to the main gate, but also beyond the tourist bungalows to feed on the fruit of *Azadirachta indica*, an introduced plant species lining 'degraded' and 'marginal' paths (Pers. Obs.).

Nevertheless, CX was still predominantly found in the reserve forest, near the Mandrare River, as this region is rich with native plants such as the Kily tree (*Tamarindus indica*) (Soma, 2006).

In April, YF had two centres of activity: one still at the tourist front, and one 50 metres into the reserve forest. A possible reason for this is that introduced species, such as *A. indica*, had finished fruiting, and instead native species such as *Rinorea greveana*, began fruiting in the reserve forest (Figure 4.1 and 4.2). This suggests that YF is not solely dependent on introduced plant species and human food resources. CX spent almost the whole of April in the reserve forest, also feeding on native plant species (Pers. Obs.).

Finally, with regards to use of habitat zones, YF was predominantly found in 'marginal' land, followed closely by 'reserve forest'. Only 11% of focals were recorded in 'degraded' zones. CX unsurprisingly, was recorded to be predominantly found in the reserve forest, with equal percentage of focals in 'marginal' and 'degraded' land. Nevertheless, as expected, YF spent a significantly greater amount of time in the 'degraded' zone compared to CX, and CX was found to spend a significantly greater amount of time in 'reserve forest'. Interestingly however, YF was predominantly found in the 'degraded' zone significantly more when tourists were absent and in the 'marginal' zone when tourists were present. From personal observations, it was seen that YF would obtain food from tourists in 'degraded' zones, but would then carry them and travel to adjacent 'marginal' zones to feed on these resources, possibly to avoid intra-troop and inter-troop conflicts over the resource. When tourists were absent however, YF would travel across 'degraded' zones (including travelling across the open-plan restaurant), and often sit in the flower beds (Pers. Obs).

4.7.2 Hypothesis 7: Terrestriality and troop elevation are affected by tourist pressure.

Terrestriality was found to be significantly greater in YF when tourists were present, and conversely, elevation was greater when tourists were absent. Tourist proximity was found to influence these behaviours; as tourists moved closer, terrestriality in YF increased, and thus elevation decreased. Tourist density had no impact. These findings can be explained in terms of tourist interaction. Previous studies have shown that tourist presence has caused primates to move higher into the tree canopies (black howler monkeys, *Alouatta caraya*: Treves and Brandon, 2005; pygmy marmosets, *Cebuella pygmaea*: de la Torre *et al.*, 2000), whilst others were not affected (Borg, 2011). This suggests that some primate species are more adaptable to tourist habituation that others. Like YF, a provisioned group of Japanese macaques were found to be more terrestrial in tourist presence due to the gain of food resources (Koganezawa and Imaki, 1999).

The ring-tailed lemurs at Berenty Reserve have been observed to be more terrestrial than other populations in the Antserananomby Forest in Madagascar, and it was suggested this was because the lemurs are more habituated at Berenty (Cameron, 2010). From personal observations, YF are not fearful of the tourists and freely interact with them for food resources. By nightfall they venture into the ‘reserve forest’ zones to nest in kily trees (*Tamarindus indica*).

4.7.3 Summary

CX was found to have a considerably larger home range in March than April, because the troop ventured out of the home range core to feed on high energy, introduced species on ‘degraded’ and ‘marginal’ land. The home range use and size for YF was similar in March and April, and generally smaller than that of CX. A possible reason for this was due to tourist food provisioning, resulting in YF not needing to venture too far beyond the home range core for additional resources. Although home range size and habitat use were therefore affected by tourist pressure, the effects were not necessarily negative in the short-term. Regardless, Hypothesis 6 can be accepted. It is important to note however, that this region of Madagascar is known to experience variations in climate. The study period coincided with particularly dry months for that time of year (Hajarimanitra Rambeloarivony, PhD student at Berenty Reserve: Pers. Comm.), thus this could have had some impact on home range size and shape.

YF was also found to become more terrestrial as tourist proximity increased. This was to gain access to nutritious, human food resources. Therefore, Hypothesis 7 can be accepted. However the influence of tourist pressure appeared to be a positive one. Nevertheless, any alterations to home range size and shape could ultimately lead to future survival problems affecting foraging abilities and survival (Orams, 2002).

4.8 STUDY SHORT-COMINGS AND FURTHER RESEARCH

In hindsight, this study could have been improved by investigating adults of one sex only. The confounding variable of ‘sex’ highlighted that behavioural differences relating to aggression were apparent between males and females. Ring-tailed lemur females are known to be significantly more aggressive than males (Jolly and Pride, 1999; Palagi *et al.*, 2005), and this was seen when investigating individual differences within the troops. As this study investigated the effects of tourism on aggression, it would be advised to study only adult males or adult females (and thus gain a larger sample size of one sex), to ensure a similar baseline of aggression. Nevertheless, this study highlighted the sex differences between behaviours affected by tourism, and clearly showed that one sex was more aggressive and involved in more tourist/lemur interactions than the other.

Further research should be carried out during the peak tourist season to compare the results to the findings of this study. Approximately 400 tourists visited Berenty during the study period, which coincided with the low tourist season, thus as many as 1000 tourists could be expected over a two month period in the high season (Mampionondrainy Randrianasolo, receptionist at Berenty Reserve: Pers. Comm.). Previous studies have shown that increasing tourist density greatly influences behaviours; hence greater counts of aggression, SDB and changes in activity budgets would be expected to be seen as tourist density increased (Constantine *et al.*, 2004; Lott and McCoy, 1995; Barja *et al.*, 2007; Ellenberg *et al.*, 2007).

Further studies could also investigate behaviours and home range size in: different fruiting seasons, different ring-tailed lemur populations in Madagascar, captive ring-tailed lemur populations, different regions, and other troop comparisons in Berenty. Research investigating behavioural changes in small areas which are only characterised by one forest type, are not representative of those populations in other areas, thus the findings of this study cannot necessarily be applied to other populations in different regions (Axel and Maurer, 2011).

A longitudinal study (i.e. more than one year) would take into account the influence of climate on the staggered fruiting and leafing seasons, and therefore different home range sizes and habitat usage would be expected to be seen throughout the study period. Nevertheless, the home ranges of the lemur troops at

Berenty have remained relatively stable since 1989 (suggesting that they return to the same feeding plants every year), thus longitudinal research is likely to get similar results to those seen for March and April in this present study (Jolly and Pride, 1999; Mertl-Millhollen, 2000; Gould, 2006; Koyama *et al.*, 2006). Investigating the effect of tourism on different lemur populations in different regions (including captive populations and other troops in Berenty) would take into account additional confounding variables including different habitats, troops of various size, and access to different feeding plants. If the findings were similar to the outcome this study (i.e. heightened aggression, greater rates of scent-marking during tourist presence, and alterations in activity budget behaviours), then the theory that tourism influences such behaviours would have greater support.

Furthermore, this study has provided a stepping stone for further research to be conducted in the form of hormonal analyses investigating whether physiological stress levels in the lemurs were also influenced by tourist pressure. Previous studies have linked tourist pressure to increased glucocorticoid levels in primates (Marechal *et al*., 2011), that were not always correlated with SDB (Higham *et al.*, 2009), thus this would have aided in further explanations of the findings in this study.

4.9 BROADER IMPLICATIONS AND CONCLUSIONS

This study was the first of its kind to investigate the effects of tourist pressure on ring-tailed lemur behaviours, home range size, and habitat use. Tourist pressure was shown to negatively influence resting and feeding (on human food resources) activity budget behaviours, and intra-troop aggression. Jolly *et al.* (2006) once asked the question “is the territorial aggression shown in Berenty evolved natural behaviour or is it a pathological response to overcrowding?" The findings of this study suggest that tourism and habituation are the key factors in explaining the overcrowding and consequent aggression seen in lemur populations, thus the heightened aggression has not evolved naturally. It was suggested that the intra-troop and inter-troop competition for highly clumped, nutritious human food resources and introduced plant species, were the underlying causes of the observed heightened aggression, overcrowding at the tourist front, disruption of activity budget behaviours, and causes of home range size alterations.

Furthermore, this study supported the theory that self-grooming (lasting less than ten seconds) in ring-tailed lemurs was perhaps not a SDB, but was hypothesised to be a potential means of motivating the actor between behavioural transitions. Nevertheless, it could also be involved with hygienic maintenance, thus further research would need to be conducted to investigate these theories. Additionally, a strong assumption was made that greater rates of scent-marking was due to the indirect influence of tourist presence. It was speculated that heightened aggression, caused by inter-troop and intra-troop feeding competition for highly nutritious human food resources and introduced plant species, resulted in greater rates of scent-marking. However, it was concluded that scent-marking was an indicator of anxiety and tradition; both operating at the same time. As the theory of scent-marking being a SDB is a new topic of investigation in this species, further research would need to be carried out to confirm these findings.

The ring-tailed lemur, endemic to the island of Madagascar, is considered 'near threatened' by the International Union for Conservation of Nature (Andrainarivo *et al.*, 2008). This study therefore highlights the need for further research to be conducted investigating the influence of tourist pressure on behaviours, and whether this human disturbance will affect the long-term survival and fecundity of this species. Currently, it appears that this artificial provisioning has increased the overall health of those populations studied at Berenty Reserve. Provisioning of animals has been found to decrease infant mortality (Lyles and Dobson, 1988), increase growth and weight (Strum, 1991) and improve overall body condition (Eley *et al.*, 1986). Nevertheless, an improvement in health has also led to a population rise, overcrowding and consequent aggression at Berenty Reserve. Heightened aggression in primates is speculated to alter habitat activity patterns, decrease immunity, increase physiological stress, and negatively affect communicative behaviours (Berman and Li, 2002; Reynold and Braithwaite, 2001; Muehlenbein and Ancrenaz, 2009). Additionally, this greater exposure to tourism increases the risk of disease transmission (Malik and Johnson, 1994; Strum, 1994) and loss of learned foraging behaviours (Samuels and Altmann, 1991); ultimately impacting survival during years of drought in Madagascar (Gould *et al.*, 1999).

This study will hopefully encourage conservation and tourism bodies to improve monitoring of food provisioning, and find ways to control the overcrowding of populations. Ultimately, as the ring-tailed lemur is seen as the "flagship species" of Madagascar, these control measures could then be enforced on those lemur species that are more endangered.

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APPENDICES

APPENDIX 1

Identification of individuals in Troops YF and CX

TROOP	Individual ID	Malagasy-English Translation	Distinguishing Features for Identification
YF *(n = 8)*	*Maso*	"Eye"	Big eyes. No hair on right thigh. Slight ginger colouring on tail.
	Marika	"No mark"	Slender limbs. No obvious characteristics.
	Sofina	"Ear"	Short, cut-off tail. Large cut on right ear.
	(H)Avanana	“Right”	Small cut on left ear. Pink genitalia.
	Rambo	"Tail"	White tail underneath. Large male.
	Kely	“Small/Little”	Big eyes. Brown mark on left forelimb. Second smallest male.
	Mainty	"Black"	Black marks on right hindlimb. Large male.
	Volo	"Hair"	Smallest male. 'Quiff' hairline.
CX *(n = 6)*	*Reny*	"Mother"	Mother to smallest baby, Yoda. Black mark on left forelimb. Bad fur condition.
	Tsipika	"Straight line"	Dark, obvious black lines over eyelids. Small genitalia.
	Tsia	"No"	Mother to larger baby, Fat Baby. Large genitalia.
	Mandidy	"Cut"	Large cut on right ear. Black mark on left hindlimb.
	Pentina	"Spot"	Black spot on central shoulder blades. Nasal bone all white.
	Orona	"Nose"	More dominant male. Short nasal bone colouration.

APPENDIX 2

Example of the Scan Sample Data Collection Sheet

DATE:
TROOP:
TIME:

SCAN SAMPING																
Focal ID	**No. of observers**			**No. of lemurs**									**Prox.**	**E.**	**T.**	**Hab.**
	Tour.*	R	O	Move	Feed	Rest	Grm	S-grm	Tour Int.	SDB	O	X				

Tour. = Number of tourists; R = Number of researchers; O = Number of Other

Grm = Groom; S-grm = Self-groom; SDB = Self-directed behaviour (i.e. yawn, self-scratch); O = Other; X = Out of sight

Prox. = Proximity of nearest observer to centre of the troop (in category metres of 1 – 7)

E. = Elevation (metres); T. = Terrestriality (counts); Hab. = Habitat Zone (R, D, M or O)

APPENDIX 3

Results of the Normality Distribution Analysed Using the Kolmogorov-Smirnov Test on all Data Variables for All Focals for YF (n = 336) and CX (n = 252)

a) Event Behaviours

		YF TROOP (*n* = 336)		**CX TROOP** (*n* = 252)	
		Z	P	Z	P
Event Behaviours	Aggression to Adult Male	9.015	< 0.001	8.159	< 0.001
(Counts/Hour)	Aggression from Adult Male	8.942	< 0.001	8.560	< 0.001
	Aggression to Adult Female	8.812	< 0.001	8.362	< 0.001
	Aggression from Adult Female	7.851	< 0.001	7.875	< 0.001
	Aggression to Other	9.722	< 0.001	8.572	< 0.001
	Aggression from Other	9.509	< 0.001	ND	ND
	Total Intra-troop Aggression	5.453	< 0.001	6.219	< 0.001
	Aggression to Unknown	9.543	< 0.001	8.340	< 0.001
	Aggression from Unknown	9.546	< 0.001	8.447	< 0.001
	Total Inter-troop Aggression	9.177	< 0.001	8.246	< 0.001
	Troop Encounter	9.663	< 0.001	8.341	< 0.001
	Aggression to Tourist	9.509	< 0.001	ND	ND
	Tourist Noise	9.747	< 0.001	ND	ND
	Tourist Mimic	ND	ND	ND	ND
	Tourist Rock	9.727	< 0.001	ND	ND
	Tourist Throw	9.694	< 0.001	ND	ND
	Tourist Other	ND	ND	ND	ND
	Total Aggressive Tourist/Lemur Interactions	9.791	< 0.001	ND	ND
	Yip Vocalisation	9.476	< 0.001	8.447	< 0.001
	Squeal Vocalisation	9.664	< 0.001	8.495	< 0.001
	Territorial Call	9.513	< 0.001	ND	ND
	Chutter Vocalisation	9.710	< 0.001	8.273	< 0.001
	Unknown Vocalisation	9.694	< 0.001	ND	ND
	Total Counts of Aggressive Vocalisations	7.911	< 0.001	8.331	< 0.001
	Tourist Neutral	8.670	< 0.001	8.273	< 0.001
	Tourist Stroke	9.705	< 0.001	ND	ND
	Tourist Play	9.702	< 0.001	ND	ND
	Tourist Feed	9.727	< 0.001	ND	ND
	Tourist Other	9.621	< 0.001	ND	ND
	Total Non-Aggressive Tourist/Lemur Interactions	8.664	< 0.001	8.273	< 0.001
	Self-Scratch	3.373	< 0.001	2.947	< 0.001
	Self-Groom < 10 Seconds	4.464	< 0.001	4.148	< 0.001
	Startle	8.645	< 0.001	7.060	< 0.001
	Yawn	8.325	< 0.001	8.161	< 0.001

ND = No data were recorded for those behaviours during the study.

b) State Behaviours and Scan Samples

		YF TROOP (*n* = 336)		CX TROOP (*n* = 252)	
		Z	P	Z	P
State Behaviours	Feed on Human Food	9.192	< 0.001	8.354	< 0.001
(Mins/Hour)	Feed on Natural Food	2.942	< 0.001	2.247	< 0.001
	Move	1.586	0.013	1.980	0.001
	Rest	1.479	0.025	1.144	0.146
	Groom Adult Male	9.652	< 0.001	8.273	< 0.001
	Groom Adult Female	9.326	< 0.001	8.333	< 0.001
	Groom Other	9.565	< 0.001	8.395	< 0.001
	Groom Unknown	ND	ND	ND	ND
	Groom Tourist	ND	ND	ND	ND
	Receive Grooming from Adult Male	9.457	< 0.001	8.374	< 0.001
	Receive Grooming from Adult Female	9.446	< 0.001	8.356	< 0.001
	Receive Grooming from Other	9.139	< 0.001	8.363	< 0.001
	Receive Grooming from Unknown	ND	ND	ND	ND
	Receive Grooming from Tourist	ND	ND	ND	ND
	Allo-Groom	5.594	< 0.001	5.865	< 0.001
	Self-Groom	2.885	< 0.001	3.018	< 0.001
	Scent Mark	5.547	< 0.001	5.739	< 0.001
	Other	9.394	< 0.001	8.273	< 0.001
	Out of Sight	8.833	< 0.001	7.993	< 0.001
	Aggressive Tourist/Lemur Interaction	9.479	< 0.001	ND	ND
	Non-Aggressive Tourist/Lemur Interaction	8.412	< 0.001	8.273	< 0.001
Scan	Average Tourist Number	7.286	< 0.001	8.376	< 0.001
(Counts/30 Mins)	Average Researcher Number	6.671	< 0.001	8.344	< 0.001
	Average Other Number	8.017	< 0.001	8.237	< 0.001
	Total Number of Observers	5.333	< 0.001	7.917	< 0.001
	Move	2.404	< 0.001	3.325	< 0.001
	Feed	1.805	0.003	1.781	0.004
	Rest	2.128	< 0.001	1.241	0.092
	Groom	6.798	< 0.001	7.803	< 0.001
	Self-Groom	3.300	< 0.001	4.117	< 0.001
	Observer/Lemur Interaction	8.858	< 0.001	8.273	< 0.001
	Self-Directed Behaviours	7.521	< 0.001	7.919	< 0.001
	Other	7.453	< 0.001	6.713	< 0.001
	Out of Sight	8.393	< 0.001	5.564	< 0.001
	Proximity (category metres)	4.791	< 0.001	4.264	< 0.001
	Elevation (m)	1.725	0.005	1.602	0.012
	Terrestriality (%)	3.774	< 0.001	4.017	< 0.001
	Habitat Zone	5.761	< 0.001	8.167	< 0.001

ND = No data were recorded for those behaviours during the study.
Highlighted data = Not significant when P < 0.05, thus normally distributed.

APPENDIX 4

Mean Event Behaviours for Troops YF (n = 8) and CX (n = 6)

		YF TROOP *(n = 8)* Mean ± S.E.			CX TROOP *(n = 6)* Mean ± S.E.		
Event Behaviours	Aggression to Adult Male	0.39	±	0.10	0.30	±	0.15
(Counts/Hour)	Aggression from Adult Male	0.29	±	0.09	0.06	±	0.04
	Aggression to Adult Female	0.44	±	0.30	0.21	±	0.12
	Aggression from Adult Female	0.76	±	0.18	0.40	±	0.17
	Aggression to Other	0.18	±	0.07	0.06	±	0.03
	Aggression from Other	0.01	±	0.01	0.00	±	0.00
	Total Intra-troop Aggression	2.07	±	0.35	1.03	±	0.13
	Aggression to Unknown	0.18	±	0.09	0.14	±	0.04
	Aggression from Unknown	0.18	±	0.05	0.09	±	0.02
	Total Inter-troop Aggression	0.37	±	0.10	0.23	±	0.05
	Troop Encounter	0.22	±	0.03	0.23	±	0.03
	Aggression to Tourist	0.01	±	0.01	0.00	±	0.00
	Tourist Noise	0.02	±	0.02	0.00	±	0.00
	Tourist Mimic	0.00	±	0.00	0.00	±	0.00
	Tourist Rock	0.06	±	0.03	0.00	±	0.00
	Tourist Throw	0.02	±	0.01	0.00	±	0.00
	Tourist Other	0.00	±	0.00	0.00	±	0.00
	Total Aggressive Tourist/Lemur Interactions	0.11	±	0.04	0.00	±	0.00
	Yip Vocalisation	0.26	±	0.06	0.13	±	0.05
	Squeal Vocalisation	0.17	±	0.05	0.06	±	0.03
	Territorial Call	0.23	±	0.10	0.00	±	0.00
	Chutter Vocalisation	0.15	±	0.04	0.01	±	0.01
	Unknown Vocalisation	0.02	±	0.01	0.00	±	0.00
	Total Counts of Aggressive Vocalisations	0.83	±	0.13	0.19	±	0.08
	Tourist Neutral	0.88	±	0.28	0.02	±	0.02
	Tourist Stroke	0.04	±	0.02	0.00	±	0.00
	Tourist Play	0.03	±	0.02	0.00	±	0.00
	Tourist Feed	0.14	±	0.08	0.00	±	0.00
	Tourist Other	0.01	±	0.01	0.00	±	0.00
	Total Non-Aggressive Tourist/Lemur Interactions	1.10	±	0.36	0.02	±	0.02
	Self-Scratch	4.20	±	0.30	3.83	±	0.33
	Self-Groom < 10 Seconds	2.76	±	0.19	1.81	±	0.17
	Startle	0.48	±	0.05	0.68	±	0.05
	Yawn	0.69	±	0.13	0.22	±	0.05

APPENDIX 5

Inter-troop Comparison of Event Behaviours between YF and CX Using a Mann-Whitney U Test

		YF TROOP (n = 8) Mean ± S.E.			CX TROOP (n = 6) Mean ± S.E.			Mann-Whitney U Test		
								U	Z	P
Event	Aggression to Adult Male	0.39	±	0.10	0.30	±	0.15	18.000	-0.777	0.491
Behaviours	Aggression from Adult Male	0.29	±	0.09	0.06	±	0.04	6.000	-2.350	0.020
(Counts/Hour)	Aggression to Adult Female	0.44	±	0.30	0.21	±	0.12	23.000	-0.132	0.950
	Aggression from Adult Female	0.76	±	0.18	0.40	±	0.17	11.000	-1.688	0.108
	Aggression to Other	0.18	±	0.07	0.06	±	0.03	13.000	-1.446	0.181
	Aggression from Other	0.01	±	0.01	0.00	±	0.00	21.000	-0.866	0.755
	Total Intra-troop Aggression	2.07	±	0.35	1.03	±	0.13	3.500	-2.649	0.005
	Aggression to Unknown	0.18	±	0.09	0.14	±	0.04	19.500	-0.593	0.573
	Aggression from Unknown	0.18	±	0.05	0.09	±	0.02	16.000	-1.048	0.345
	Total Inter-troop Aggression	0.37	±	0.10	0.23	±	0.05	18.000	-0.780	0.491
	Troop Encounter	0.22	±	0.03	0.23	±	0.03	19.500	-0.607	0.573
	Aggression to Tourist	0.01	±	0.01	0.00	±	0.00	21.000	-0.866	0.755
	Tourist Noise	0.02	±	0.02	0.00	±	0.00	18.000	-1.271	0.491
	Tourist Mimic	0.00	±	0.00	0.00	±	0.00	24.000	0.000	1.000
	Tourist Rock	0.06	±	0.03	0.00	±	0.00	15.000	-1.620	0.282
	Tourist Throw	0.02	±	0.01	0.00	±	0.00	15.000	-1.631	0.282
	Tourist Other	0.00	±	0.00	0.00	±	0.00	24.000	0.000	1.000
	Total Aggressive Tourist/Lemur Int.	0.11	±	0.04	0.00	±	0.00	9.000	-2.260	0.059
	Yip Vocalisation	0.26	±	0.06	0.13	±	0.05	12.500	-1.498	0.142
	Squeal Vocalisation	0.17	±	0.05	0.06	±	0.03	11.000	-1.734	0.108
	Territorial Call	0.23	±	0.10	0.00	±	0.00	0.000	-3.236	0.001
	Chutter Vocalisation	0.15	±	0.04	0.01	±	0.01	7.000	-2.350	0.029
	Unknown Vocalisation	0.02	±	0.01	0.00	±	0.00	15.000	-1.631	0.282
	Total Counts of Aggressive Voc.	0.83	±	0.13	0.19	±	0.08	1.500	-2.911	0.001
	Tourist Neutral	0.88	±	0.28	0.02	±	0.02	1.000	-3.040	0.001
	Tourist Stroke	0.04	±	0.02	0.00	±	0.00	15.000	-1.620	0.282
	Tourist Play	0.03	±	0.02	0.00	±	0.00	15.000	-1.620	0.282
	Tourist Feed	0.14	±	0.08	0.00	±	0.00	15.000	-1.617	0.282
	Tourist Other	0.01	±	0.01	0.00	±	0.00	21.000	-0.866	0.755
	Total Non-Aggressive Tourist/Lemur Int.	1.10	±	0.36	0.02	±	0.02	1.000	-3.037	0.001
	Self-Scratch	4.20	±	0.30	3.83	±	0.33	17.500	-0.841	0.414
	Self-Groom < 10 Seconds	2.76	±	0.19	1.81	±	0.17	0.500	-3.041	0.001
	Startle	0.48	±	0.05	0.68	±	0.05	7.000	-2.212	0.029
	Yawn	0.69	±	0.13	0.22	±	0.05	2.000	-2.853	0.003

Highlighted data = Significant when P < 0.05. Int. = Interactions. Voc. =Vocalisations

APPENDIX 6

Mean State Behaviours for Troops YF (n = 8) and CX (n = 6)

		YF TROOP *(n = 8)* Mean ± S.E.			CX TROOP *(n = 6)* Mean ± S.E.		
State Behaviours	Feed on Human Food	0.32	±	0.14	0.07	±	0.05
(Mins/Hour)	Feed on Natural Food	12.57	±	0.90	17.63	±	1.96
	Move	11.22	±	0.44	7.98	±	0.36
	Rest	26.33	±	0.89	28.49	±	1.59
	Groom Adult Male	0.05	±	0.02	0.00	±	0.00
	Groom Adult Female	0.13	±	0.05	0.02	±	0.01
	Groom Other	0.04	±	0.02	0.02	±	0.01
	Groom Unknown	0.00	±	0.00	0.00	±	0.00
	Groom Tourist	0.00	±	0.00	0.00	±	0.00
	Receive Grooming from Adult Male	0.08	±	0.08	0.01	±	0.00
	Receive Grooming from Adult Female	0.09	±	0.05	0.01	±	0.01
	Receive Grooming from Other	0.08	±	0.03	0.01	±	0.00
	Receive Grooming from Unknown	0.00	±	0.00	0.00	±	0.00
	Receive Grooming from Tourist	0.00	±	0.00	0.00	±	0.00
	Allo-Groom	2.13	±	0.20	1.35	±	0.36
	Self-Groom	4.78	±	0.41	3.43	±	0.39
	Scent Mark	0.69	±	0.07	0.53	±	0.30
	Other	0.10	±	0.03	0.00	±	0.00
	Out of Sight	0.49	±	0.09	0.45	±	0.12
	Aggressive Tourist/Lemur Interaction	0.03	±	0.02	0.00	±	0.00
	Non-Aggressive Tourist/Lemur Interaction	0.87	±	0.34	0.01	±	0.01

APPENDIX 7

Inter-troop Comparison of State Behaviours between YF and CX Using a Mann-Whitney U Test

		YF TROOP *(n = 8)* Mean ± S.E.			CX TROOP *(n = 6)* Mean ± S.E.			Mann-Whitney U Test U	Z	P
State	Feed on Human Food	0.32	±	0.14	0.07	±	0.05	14.000	-1.344	0.228
Behaviours	Feed on Natural Food	12.57	±	0.90	17.63	±	1.96	9.000	-1.936	0.059
(Mins/Hour)	Move	11.22	±	0.44	7.98	±	0.36	0.000	-3.098	0.001
	Rest	26.33	±	0.89	28.49	±	1.59	16.000	-1.033	0.345
	Groom Adult Male	0.05	±	0.02	0.00	±	0.00	10.500	-1.930	0.081
	Groom Adult Female	0.13	±	0.05	0.02	±	0.01	11.000	-1.716	0.108
	Groom Other	0.04	±	0.02	0.02	±	0.01	18.000	-0.827	0.491
	Groom Unknown	0.00	±	0.00	0.00	±	0.00	24.000	0.000	1.000
	Groom Tourist	0.00	±	0.00	0.00	±	0.00	24.000	0.000	1.000
	Receive Grooming from Adult Male	0.08	±	0.08	0.01	±	0.00	24.000	0.000	1.000
	Receive Grooming from Adult Female	0.09	±	0.05	0.01	±	0.01	5.500	-2.486	0.013
	Receive Grooming from Other	0.08	±	0.03	0.01	±	0.00	7.000	-2.245	0.029
	Receive Grooming from Unknown	0.00	±	0.00	0.00	±	0.00	24.000	0.000	1.000
	Receive Grooming from Tourist	0.00	±	0.00	0.00	±	0.00	24.000	0.000	1.000
	Allo-Groom	2.13	±	0.20	1.35	±	0.36	15.000	-1.162	0.282
	Self-Groom	4.78	±	0.41	3.43	±	0.39	10.000	-1.807	0.081
	Scent Mark	0.69	±	0.07	0.53	±	0.30	12.000	-1.549	0.142
	Other	0.10	±	0.03	0.00	±	0.00	3.500	-2.755	0.005
	Out of Sight	0.49	±	0.09	0.45	±	0.12	20.000	-0.516	0.662
	Aggressive Tourist/Lemur Int.	0.03	±	0.02	0.00	±	0.00	15.000	-1.617	0.282
	Non-Aggressive Tourist/Lemur Int.	0.87	±	0.34	0.01	±	0.01	0.000	-3.169	0.001

Highlighted data = Significant when P < 0.05 .Int. = Interaction.

APPENDIX 8

Mean Scan Sample Results for Troops YF (n = 8) and CX (n = 6)

		YF TROOP (*n = 8*) Mean ± S.E.			CX TROOP (*n = 6*) Mean ± S.E.		
Scan	Average Tourist Number	0.39	±	0.05	0.01	±	0.01
(Counts/30 Mins)	Average Researcher Number	2.43	±	0.02	2.05	±	0.00
	Average Other Number	0.23	±	0.03	0.05	±	0.02
	Total Number of Observers	3.05	±	0.07	2.11	±	0.02
	Move	1.36	±	0.05	0.70	±	0.05
	Feed	1.80	±	0.04	1.58	±	0.07
	Rest	3.36	±	0.04	2.78	±	0.12
	Groom	0.26	±	0.02	0.10	±	0.02
	Self-Groom	0.65	±	0.05	0.32	±	0.02
	Observer/Lemur Interaction	0.16	±	0.03	0.00	±	0.00
	Self-Directed Behaviours	0.13	±	0.02	0.06	±	0.01
	Other	0.16	±	0.02	0.13	±	0.02
	Out of Sight	0.12	±	0.01	0.34	±	0.06
	Proximity (category metres)	3.24	±	0.04	3.38	±	0.04
	Elevation (m)	4.02	±	0.09	4.09	±	0.07
	Terrestriality (%)	17.65	±	1.24	14.13	±	0.63
	Habitat Zone	2.07	±	0.06	1.18	±	0.01

APPENDIX 9

Inter-troop Comparison of Scan Sample Results between YF and CX Using a Mann-Whitney U Test

		YF TROOP (*n = 8*) Mean ± S.E.			CX TROOP (*n = 6*) Mean ± S.E.			Mann-Whitney U Test		
								U	Z	P
Scan	Average Tourist Number	0.39	±	0.05	0.01	±	0.01	0.000	-3.140	0.001
(Counts/30 Mins)	Average Researcher Number	2.43	±	0.02	2.05	±	0.00	0.000	-3.105	0.001
	Average Other Number	0.23	±	0.03	0.05	±	0.02	1.000	-2.973	0.001
	Total Number of Observers	3.05	±	0.07	2.11	±	0.02	0.000	-3.105	0.001
	Move	1.36	±	0.05	0.70	±	0.05	0.000	-3.102	0.001
	Feed	1.80	±	0.04	1.58	±	0.07	6.500	-2.262	0.020
	Rest	3.36	±	0.04	2.78	±	0.12	0.000	-3.098	0.001
	Groom	0.26	±	0.02	0.10	±	0.02	0.000	-3.098	0.001
	Self-Groom	0.65	±	0.05	0.32	±	0.02	0.000	-3.098	0.001
	Observer/Lemur Interaction	0.16	±	0.03	0.00	±	0.00	0.000	-3.172	0.001
	Self-Directed Behaviours	0.13	±	0.02	0.06	±	0.01	4.500	-2.523	0.008
	Other	0.16	±	0.02	0.13	±	0.02	17.500	-0.844	0.414
	Out of Sight	0.12	±	0.01	0.34	±	0.06	8.000	-2.066	0.043
	Proximity (category metres)	3.24	±	0.04	3.38	±	0.04	6.000	-2.339	0.020
	Elevation (m)	4.02	±	0.09	4.09	±	0.07	16.000	-1.033	0.345
	Terrestriality (%)	17.65	±	1.24	14.13	±	0.63	9.000	-1.939	0.059
	Habitat Zone	2.07	±	0.06	1.18	±	0.01	0.000	-3.109	0.001

Highlighted data = Significant when P < 0.05.

APPENDIX 10

Sex Differences in the Combined Males and Females for Both Troops Using a Mann-Whitney U Test

a) Event Behaviours

		Male (*n = 6*) Mean ± S.E.			Female (*n = 8*) Mean ± S.E.			Mann-Whitney U Test U	Z	P
Event	Aggression to Adult Male	0.14	±	0.07	0.51	±	0.11	6.000	-2.331	0.020
Behaviours	Aggression from Adult Male	0.34	±	0.12	0.08	±	0.03	9.500	-1.893	0.059
(Counts/Hour)	Aggression to Adult Female	0.01	±	0.01	0.59	±	0.28	0.000	-3.176	0.001
	Aggression from Adult Female	0.76	±	0.12	0.49	±	0.21	11.500	-1.623	0.108
	Aggression to Other	0.04	±	0.01	0.20	±	0.07	8.000	-2.103	0.043
	Aggression from Other	0.00	±	0.00	0.01	±	0.01	21.000	-0.866	0.755
	Total Intra-troop Aggression	1.29	±	0.19	1.87	±	0.40	18.500	-0.711	0.491
	Aggression to Unknown	0.05	±	0.02	0.26	±	0.07	4.500	-2.569	0.008
	Aggression from Unknown	0.17	±	0.05	0.12	±	0.04	18.500	-0.720	0.491
	Total Inter-troop Aggression	0.22	±	0.05	0.38	±	0.10	17.500	-0.845	0.414
	Troop Encounter	0.21	±	0.03	0.24	±	0.03	19.000	-0.674	0.573
	Aggression to Tourist	0.00	±	0.00	0.01	±	0.01	21.000	-0.866	0.755
	Tourist Noise	0.00	±	0.00	0.02	±	0.02	18.000	-1.271	0.491
	Tourist Mimic	0.00	±	0.00	0.00	±	0.00	24.000	0.000	1.000
	Tourist Rock	0.02	±	0.02	0.04	±	0.03	21.500	-0.450	0.755
	Tourist Throw	0.01	±	0.01	0.01	±	0.01	22.000	-0.362	0.852
	Tourist Other	0.00	±	0.00	0.00	±	0.00	24.000	0.000	1.000
	Total Aggressive Tourist/Lemur Int.	0.03	±	0.02	0.08	±	0.04	20.000	-0.603	0.662
	Yip Vocalisation	0.26	±	0.06	0.15	±	0.06	13.500	-1.368	0.181
	Squeal Vocalisation	0.19	±	0.06	0.07	±	0.03	10.000	-1.868	0.081
	Territorial Call	0.06	±	0.02	0.19	±	0.11	22.000	-0.270	0.852
	Chutter Vocalisation	0.07	±	0.05	0.10	±	0.04	18.500	-0.760	0.491
	Unknown Vocalisation	0.02	±	0.01	0.01	±	0.01	19.000	-0.906	0.573
	Total Counts of Aggressive Voc.	0.60	±	0.08	0.52	±	0.21	18.500	-0.712	0.491
	Tourist Neutral	0.25	±	0.10	0.71	±	0.32	21.000	-0.397	0.755
	Tourist Stroke	0.01	±	0.01	0.03	±	0.02	21.500	-0.450	0.755
	Tourist Play	0.02	±	0.02	0.02	±	0.01	22.500	-0.270	0.852
	Tourist Feed	0.03	±	0.03	0.11	±	0.08	21.000	-0.539	0.755
	Tourist Other	0.00	±	0.00	0.01	±	0.01	21.000	-0.866	0.755
	Total Non-Aggressive Tourist/Lemur Int.	0.30	±	0.13	0.89	±	0.42	21.000	-0.396	0.755
	Self-Scratch	4.18	±	0.38	3.94	±	0.28	19.500	-0.582	0.573
	Self-Groom < 10 Seconds	2.48	±	0.19	2.25	±	0.29	16.500	-0.970	0.345
	Startle	0.63	±	0.08	0.52	±	0.05	14.500	-1.236	0.228
	Yawn	0.60	±	0.20	0.40	±	0.08	22.000	-0.259	0.852

Highlighted data = Significant when P < 0.05. Int. = Interaction. Voc = Vocalisation.

b) State Behaviours and Scan Samples

		Male (n = 6) Mean ± S.E.	female (n = 8) Mean ± S.E.	Mann-Whitney U Test U	Z	P
State Behaviours *(Mins/Hour)*	Feed on Human Food	0.25 ± 0.17	0.19 ± 0.10	20.000	-0.537	0.662
	Feed on Natural Food	12.22 ± 0.98	16.63 ± 1.64	8.000	-2.066	0.043
	Move	9.89 ± 0.75	9.79 ± 0.78	22.000	-0.258	0.852
	Rest	28.61 ± 1.30	26.24 ± 1.09	13.000	-1.420	0.181
	Groom Adult Male	0.03 ± 0.02	0.03 ± 0.02	21.500	-0.357	0.755
	Groom Adult Female	0.16 ± 0.06	0.03 ± 0.02	8.000	-2.113	0.043
	Groom Other	0.01 ± 0.01	0.05 ± 0.02	8.000	-2.206	0.043
	Groom Unknown	0.00 ± 0.00	0.00 ± 0.00	24.000	0.000	1.000
	Groom Tourist	0.00 ± 0.00	0.00 ± 0.00	24.000	0.000	1.000
	Receive Grooming from Adult Male	0.00 ± 0.00	0.09 ± 0.08	9.000	-2.257	0.059
	Receive Grooming from Adult Female	0.11 ± 0.06	0.01 ± 0.01	14.000	-1.344	0.228
	Receive Grooming from Other	0.01 ± 0.01	0.07 ± 0.03	13.000	-1.452	0.181
	Receive Grooming from Unknown	0.00 ± 0.00	0.00 ± 0.00	24.000	0.000	1.000
	Receive Grooming from Tourist	0.00 ± 0.00	0.00 ± 0.00	24.000	0.000	1.000
	Allo-Groom	2.09 ± 0.19	1.57 ± 0.33	17.000	-0.904	0.414
	Self-Groom	4.94 ± 0.45	3.65 ± 0.39	9.000	-1.936	0.059
	Scent Mark	0.96 ± 0.21	0.37 ± 0.10	6.000	-2.324	0.020
	Other	0.02 ± 0.01	0.08 ± 0.03	17.500	-0.873	0.414
	Out of Sight	0.50 ± 0.06	0.45 ± 0.12	18.000	-0.775	0.491
	Aggressive Tourist/Lemur Int.	0.00 ± 0.00	0.03 ± 0.02	15.000	-1.617	0.282
	Non-Aggressive Tourist/Lemur Int.	0.20 ± 0.11	0.73 ± 0.37	21.000	-0.396	0.755
Scan *(Counts/30 Mins)*	Average Tourist Number	0.21 ± 0.07	0.24 ± 0.10	23.000	-0.131	0.950
	Average Researcher Number	2.30 ± 0.08	2.25 ± 0.08	19.000	-0.647	0.573
	Average Other Number	0.14 ± 0.06	0.15 ± 0.04	21.500	-0.323	0.755
	Total Number of Observers	2.65 ± 0.19	2.64 ± 0.20	20.000	-0.518	0.662
	Move	1.18 ± 0.15	1.00 ± 0.13	19.500	-0.582	0.573
	Feed	1.73 ± 0.09	1.68 ± 0.05	16.000	-1.034	0.345
	Rest	3.23 ± 0.10	3.02 ± 0.15	17.000	-0.904	0.414
	Groom	0.20 ± 0.04	0.18 ± 0.04	22.000	-0.258	0.852
	Self-Groom	0.52 ± 0.07	0.50 ± 0.08	21.000	-0.387	0.755
	Observer/Lemur Int.	0.08 ± 0.03	0.10 ± 0.04	24.000	0.000	1.000
	Self-Directed Behaviours	0.12 ± 0.03	0.09 ± 0.01	16.000	-1.035	0.345
	Other	0.15 ± 0.01	0.14 ± 0.02	21.000	-0.389	0.755
	Out of Sight	0.14 ± 0.04	0.27 ± 0.05	9.000	-1.936	0.059
	Proximity (category metres)	3.34 ± 0.04	3.28 ± 0.05	18.000	-0.780	0.491
	Elevation (m)	4.10 ± 0.10	4.02 ± 0.06	18.000	-0.775	0.491
	Terrestriality (%)	16.48 ± 1.63	15.88 ± 1.02	22.000	-0.258	0.852
	Habitat Zone	1.76 ± 0.20	1.63 ± 0.17	22.000	-0.259	0.852

Highlighted data = Significant when $P < 0.05$.

APPENDIX 11

Comparison of the Average Behaviours for Morning and Afternoon for the 14 Study Subjects Using the Wilcoxon Matched-Pairs Signed-Rank Test. n = 14.

a) Event Behaviours

		Morning (*n = 14*) Mean ± S.E.			Afternoon (*n = 14*) Mean ± S.E.			Wilcoxon M-P Test	
								Z	P
Event Behaviours *(Counts/Hour)*	Aggression to Adult Male	0.44	±	0.03	0.27	±	0.03	-1.000	0.317
	Aggression from Adult Male	0.23	±	0.03	0.15	±	0.01	-1.732	0.083
	Aggression to Adult Female	0.41	±	0.06	0.27	±	0.03	-1.732	0.083
	Aggression from Adult Female	0.72	±	0.05	0.49	±	0.03	-2.121	0.034
	Aggression to Other	0.14	±	0.01	0.12	±	0.01	-1.000	0.317
	Aggression from Other	0.01	±	0.00	0.00	±	0.00	0.000	1.000
	Total Intra-troop Aggression	1.96	±	0.09	1.29	±	0.05	-1.903	0.057
	Aggression to Unknown	0.21	±	0.02	0.12	±	0.02	-0.577	0.564
	Aggression from Unknown	0.12	±	0.01	0.17	±	0.02	-1.414	0.157
	Total Inter-troop Aggression	0.33	±	0.02	0.29	±	0.03	0.000	1.000
	Troop Encounter	0.29	±	0.01	0.16	±	0.01	0.000	1.000
	Aggression to Tourist	0.00	±	0.00	0.01	±	0.00	0.000	1.000
	Tourist Noise	0.03	±	0.01	0.00	±	0.00	0.000	1.000
	Tourist Mimic	0.00	±	0.00	0.00	±	0.00	0.000	1.000
	Tourist Rock	0.07	±	0.01	0.00	±	0.00	0.000	1.000
	Tourist Throw	0.02	±	0.00	0.00	±	0.00	0.000	1.000
	Tourist Other	0.00	±	0.00	0.00	±	0.00	0.000	1.000
	Total Aggressive T/L Int.	0.12	±	0.01	0.01	±	0.00	-1.000	0.317
	Yip Vocalisation	0.24	±	0.02	0.16	±	0.01	-0.577	0.564
	Squeal Vocalisation	0.13	±	0.01	0.12	±	0.01	0.000	1.000
	Territorial Call	0.01	±	0.00	0.25	±	0.03	-1.342	0.180
	Chutter Vocalisation	0.08	±	0.01	0.10	±	0.01	-1.000	0.317
	Unknown Vocalisation	0.01	±	0.00	0.01	±	0.00	0.000	1.000
	Total Counts of Aggressive Voc.	0.47	±	0.03	0.64	±	0.05	-1.100	0.271
	Tourist Neutral	0.81	±	0.09	0.22	±	0.02	-2.264	0.024
	Tourist Stroke	0.03	±	0.01	0.01	±	0.00	0.000	1.000
	Tourist Play	0.01	±	0.00	0.02	±	0.00	0.000	1.000
	Tourist Feed	0.13	±	0.02	0.03	±	0.01	-1.414	0.157
	Tourist Other	0.01	±	0.00	0.00	±	0.00	0.000	1.000
	Total Non-Aggressive T/L Int.	1.00	±	0.12	0.27	±	0.02	-2.032	0.042
	Self-Scratch	4.06	±	0.07	4.03	±	0.08	-0.122	0.903
	Self-Groom < 10 Seconds	2.52	±	0.06	2.18	±	0.05	-1.897	0.058
	Startle	0.65	±	0.02	0.49	±	0.02	-0.816	0.414
	Yawn	0.47	±	0.04	0.51	±	0.02	-0.447	0.655

Highlighted data = Significant when P < 0.05. T/L Int. = Tourist/Lemur Interaction. Voc. = Vocalisation.

b) State Behaviours and Scan Samples

		Morning (n = 14)			Afternoon (n = 14)			Wilcoxon M-P Test	
		Mean ± S.E.			Mean ± S.E.			Z	P
State Behaviours *(Mins/Hour)*	Feed on Human Food	0.38	±	0.04	0.05	±	0.01	-1.890	0.059
	Feed on Natural Food	15.49	±	0.35	13.99	±	0.33	-1.453	0.146
	Move	10.98	±	0.15	8.68	±	0.22	-2.049	0.040
	Rest	25.11	±	0.27	29.40	±	0.33	-2.390	0.017
	Groom Adult Male	0.03	±	0.00	0.04	±	0.00	0.000	1.000
	Groom Adult Female	0.08	±	0.01	0.09	±	0.01	-1.000	0.317
	Groom Other	0.03	±	0.00	0.04	±	0.00	0.000	1.000
	Groom Unknown	0.00	±	0.00	0.00	±	0.00	0.000	1.000
	Groom Tourist	0.00	±	0.00	0.00	±	0.00	0.000	1.000
	Receive Grooming from Adult Male	0.02	±	0.00	0.07	±	0.02	-1.000	0.317
	Receive Grooming from Adult Female	0.04	±	0.00	0.06	±	0.01	-1.000	0.317
	Receive Grooming from Other	0.03	±	0.00	0.07	±	0.01	-1.000	0.317
	Receive Grooming from Unknown	0.00	±	0.00	0.00	±	0.00	0.000	1.000
	Receive Grooming from Tourist	0.00	±	0.00	0.00	±	0.00	0.000	1.000
	Allo-Groom	1.56	±	0.07	2.02	±	0.06	-1.897	0.058
	Self-Groom	4.09	±	0.11	4.31	±	0.10	-1.121	0.262
	Scent Mark	0.72	±	0.05	0.52	±	0.03	-1.000	0.317
	Other	0.07	±	0.01	0.04	±	0.01	0.000	1.000
	Out of Sight	0.59	±	0.04	0.36	±	0.02	-1.508	0.132
	Aggressive Tourist/Lemur Interaction	0.04	±	0.01	0.00	±	0.00	0.000	1.000
	Non-Aggressive Tourist/Lemur Interaction	0.74	±	0.10	0.27	±	0.02	-1.069	0.285
Scan *(Counts/30 Mins)*	Average Tourist Number	0.30	±	0.02	0.15	±	0.02	-1.633	0.102
	Average Researcher Number	2.29	±	0.01	2.25	±	0.01	0.000	1.000
	Average Other Number	0.25	±	0.02	0.05	±	0.00	-1.414	0.157
	Total Number of Observers	2.84	±	0.05	2.45	±	0.03	-1.730	0.084
	Move	1.22	±	0.02	0.94	±	0.03	-1.633	0.102
	Feed	1.75	±	0.03	1.65	±	0.02	-1.134	0.257
	Rest	2.89	±	0.04	3.33	±	0.03	-1.897	0.058
	Groom	0.17	±	0.01	0.21	±	0.01	0.000	1.000
	Self-Groom	0.49	±	0.01	0.53	±	0.02	0.000	1.000
	Observer/Lemur Interaction	0.15	±	0.01	0.04	±	0.00	0.000	1.000
	Self-Directed Behaviours	0.10	±	0.00	0.11	±	0.00	0.000	1.000
	Other	0.16	±	0.00	0.13	±	0.01	0.000	1.000
	Out of Sight	0.23	±	0.01	0.20	±	0.01	-1.000	0.317
	Proximity (category metres)	3.32	±	0.01	3.29	±	0.01	0.000	1.000
	Elevation (m)	4.10	±	0.03	4.01	±	0.02	-1.414	0.157
	Terrestriality (%)	20.56	±	0.32	11.72	±	0.34	-3.109	0.002
	Habitat Zone	1.82	±	0.03	1.55	±	0.04	0.000	1.000

Highlighted data = Significant when P < 0.05.

APPENDIX 12

Comparison of the Average Behaviours for Mating and Non-Mating Periods for the 14 Study Subjects Using the Wilcoxon Matched-Pairs Signed-Rank Test. n = 14.

a) Event Behaviours

		Mating (n = 14)			Non-Mating (n = 14)			Wilcoxon M-P Test	
		Mean ± S.E.			Mean ± S.E.			Z	P
Event Behaviours *(Counts/Hour)*	Aggression to Adult Male	0.49	±	0.04	0.27	±	0.02	-1.134	0.257
	Aggression from Adult Male	0.36	±	0.05	0.09	±	0.01	-1.633	0.102
	Aggression to Adult Female	0.19	±	0.03	0.42	±	0.05	-1.414	0.157
	Aggression from Adult Female	0.74	±	0.06	0.53	±	0.03	-1.134	0.257
	Aggression to Other	0.06	±	0.01	0.18	±	0.01	-1.414	0.157
	Aggression from Other	0.00	±	0.00	0.01	±	0.00	0.000	1.000
	Total Intra-troop Aggression	1.84	±	0.08	1.50	±	0.09	-1.343	0.179
	Aggression to Unknown	0.03	±	0.00	0.25	±	0.02	-1.732	0.083
	Aggression from Unknown	0.22	±	0.03	0.10	±	0.01	-1.414	0.157
	Total Inter-troop Aggression	0.25	±	0.03	0.34	±	0.02	0.000	1.000
	Troop Encounter	0.27	±	0.02	0.20	±	0.01	-1.000	0.317
	Aggression to Tourist	0.00	±	0.00	0.01	±	0.00	0.000	1.000
	Tourist Noise	0.01	±	0.00	0.02	±	0.00	0.000	1.000
	Tourist Mimic	0.00	±	0.00	0.00	±	0.00	0.000	1.000
	Tourist Rock	0.04	±	0.01	0.03	±	0.01	0.000	1.000
	Tourist Throw	0.00	±	0.00	0.02	±	0.00	0.000	1.000
	Tourist Other	0.00	±	0.00	0.00	±	0.00	0.000	1.000
	Total Aggressive Tourist/Lemur Int.	0.05	±	0.01	0.07	±	0.01	0.000	1.000
	Yip Vocalisation	0.30	±	0.03	0.15	±	0.01	-1.732	0.083
	Squeal Vocalisation	0.17	±	0.03	0.10	±	0.01	-1.414	0.157
	Territorial Call	0.10	±	0.02	0.15	±	0.02	-1.000	0.317
	Chutter Vocalisation	0.09	±	0.01	0.09	±	0.01	0.000	1.000
	Unknown Vocalisation	0.00	±	0.00	0.02	±	0.00	0.000	1.000
	Total Counts of Aggressive Voc.	0.66	±	0.04	0.49	±	0.04	-1.732	0.083
	Tourist Neutral	0.44	±	0.06	0.55	±	0.05	-0.447	0.655
	Tourist Stroke	0.01	±	0.00	0.03	±	0.01	0.000	1.000
	Tourist Play	0.03	±	0.01	0.01	±	0.00	0.000	1.000
	Tourist Feed	0.06	±	0.01	0.09	±	0.01	0.000	1.000
	Tourist Other	0.00	±	0.00	0.01	±	0.00	0.000	1.000
	Total Non-Aggressive Tourist/Lemur Int.	0.55	±	0.08	0.69	±	0.06	-0.577	0.564
	Self-Scratch	3.26	±	0.08	4.50	±	0.06	-2.961	0.003
	Self-Groom < 10 Seconds	1.93	±	0.07	2.60	±	0.05	-1.443	0.149
	Startle	0.29	±	0.02	0.73	±	0.02	-2.828	0.005
	Yawn	0.36	±	0.03	0.56	±	0.03	-1.414	0.157

Highlighted data = Significant when P < 0.05. Int. = Interaction. Voc. = Vocalisation.

b) State Behaviours and Scan Samples

		Mating (n = 14) Mean ± S.E.			Non-Mating (n = 14) Mean ± S.E.			Wilcoxon M-P Test Z	P
State Behaviours *(Mins/Hour)*	Feed on Human Food	0.27	±	0.03	0.18	±	0.03	-1.000	0.317
	Feed on Natural Food	16.87	±	0.58	13.50	±	0.27	-0.700	0.484
	Move	7.51	±	0.12	11.18	±	0.16	-3.321	0.001
	Rest	28.13	±	0.37	26.75	±	0.36	-0.566	0.572
	Groom Adult Male	0.01	±	0.00	0.05	±	0.00	0.000	1.000
	Groom Adult Female	0.01	±	0.00	0.13	±	0.01	-1.000	0.317
	Groom Other	0.01	±	0.00	0.04	±	0.00	0.000	1.000
	Groom Unknown	0.00	±	0.00	0.00	±	0.00	0.000	1.000
	Groom Tourist	0.00	±	0.00	0.00	±	0.00	0.000	1.000
	Receive Grooming from Adult Male	0.01	±	0.00	0.07	±	0.02	-1.000	0.317
	Receive Grooming from Adult Female	0.00	±	0.00	0.08	±	0.01	-1.000	0.317
	Receive Grooming from Other	0.01	±	0.00	0.07	±	0.01	0.000	1.000
	Receive Grooming from Unknown	0.00	±	0.00	0.00	±	0.00	0.000	1.000
	Receive Grooming from Tourist	0.00	±	0.00	0.00	±	0.00	0.000	1.000
	Allo-Groom	1.72	±	0.10	1.83	±	0.06	-0.045	0.964
	Self-Groom	4.00	±	0.12	4.32	±	0.09	-0.054	0.957
	Scent Mark	0.85	±	0.07	0.49	±	0.02	-1.098	0.272
	Other	0.04	±	0.01	0.06	±	0.01	-1.000	0.317
	Out of Sight	0.07	±	0.01	0.71	±	0.03	-2.887	0.004
	Aggressive Tourist/Lemur Interaction	0.03	±	0.01	0.01	±	0.00	0.000	1.000
	Non-Aggressive Tourist/Lemur Interaction	0.46	±	0.07	0.53	±	0.06	-1.414	0.157
Scan *(Counts/30 Mins)*	Average Tourist Number	0.25	±	0.02	0.21	±	0.02	-1.342	0.180
	Average Researcher Number	2.06	±	0.01	2.39	±	0.02	-2.449	0.014
	Average Other Number	0.22	±	0.02	0.11	±	0.01	-2.000	0.046
	Total Number of Observers	2.54	±	0.05	2.71	±	0.03	-0.577	0.564
	Move	0.85	±	0.03	1.21	±	0.03	-1.633	0.102
	Feed	1.81	±	0.02	1.64	±	0.02	-0.447	0.655
	Rest	3.02	±	0.04	3.17	±	0.02	-0.707	0.480
	Groom	0.15	±	0.01	0.21	±	0.01	0.000	1.000
	Self-Groom	0.48	±	0.02	0.53	±	0.01	-1.000	0.317
	Observer/Lemur Interaction	0.08	±	0.01	0.10	±	0.01	0.000	1.000
	Self-Directed Behaviours	0.06	±	0.00	0.13	±	0.00	0.000	1.000
	Other	0.15	±	0.01	0.14	±	0.00	0.000	1.000
	Out of Sight	0.31	±	0.02	0.16	±	0.01	-2.236	0.025
	Proximity (category metres)	3.43	±	0.01	3.23	±	0.01	-1.633	0.102
	Elevation (m)	4.62	±	0.03	3.72	±	0.03	-2.739	0.006
	Terrestriality (%)	12.36	±	0.46	18.33	±	0.30	-1.644	0.100
	Habitat Zone	1.69	±	0.05	1.68	±	0.02	-1.732	0.083

Highlighted data = Significant when P < 0.05.

APPENDIX 13

Kruskal-Wallis Test Results Indicating Individual Differences in Troops YF (n = 8) and CX (n = 6).

a) Event Behaviours

		YF TROOP (n = 8, df = 7)		CX TROOP (n = 6, df = 5)	
		X^2	P	X^2	P
Event	Aggression to Adult Male	27.173	< 0.001	24.010	< 0.001
Behaviours	Aggression from Adult Male	10.930	0.142	16.538	0.005
(Counts/Hour)	Aggression to Adult Female	88.643	< 0.001	19.220	0.002
	Aggression from Adult Female	22.538	0.002	30.581	< 0.001
	Aggression to Other	30.743	< 0.001	11.830	0.037
	Aggression from Other	7.000	0.429	0.000	1.000
	Total Intra-troop Aggression	19.260	0.007	5.025	0.413
	Aggression to Unknown	12.787	0.077	4.122	0.532
	Aggression from Unknown	8.146	0.320	4.018	0.547
	Total Inter-troop Aggression	5.683	0.577	2.335	0.801
	Troop Encounter	6.268	0.509	3.454	0.630
	Aggression to Tourist	7.000	0.429	0.000	1.000
	Tourist Noise	16.145	0.024	0.000	1.000
	Tourist Mimic	0.000	1.000	0.000	1.000
	Tourist Rock	17.157	0.016	0.000	1.000
	Tourist Throw	5.030	0.656	0.000	1.000
	Tourist Other	0.000	1.000	0.000	1.000
	Total Aggressive Tourist/Lemur Interactions	12.363	0.089	0.000	1.000
	Yip Vocalisation	10.018	0.188	8.497	0.131
	Squeal Vocalisation	12.226	0.093	8.146	0.148
	Territorial Call	2.835	0.900	0.000	1.000
	Chutter Vocalisation	7.391	0.389	5.000	0.416
	Unknown Vocalisation	5.030	0.656	0.000	1.000
	Total Counts of Aggressive Vocalisations	3.969	0.783	11.093	0.050
	Tourist Neutral	20.492	0.005	5.000	0.416
	Tourist Stroke	8.120	0.322	0.000	1.000
	Tourist Play	8.048	0.328	0.000	1.000
	Tourist Feed	24.229	0.001	0.000	1.000
	Tourist Other	14.042	0.050	0.000	1.000
	Total Non-Aggressive Tourist/Lemur Interactions	22.796	0.002	5.000	0.416
	Self-Scratch	8.557	0.286	4.187	0.523
	Self-Groom < 10 Seconds	4.345	0.739	9.612	0.087
	Startle	5.407	0.610	0.938	0.967
	Yawn	9.505	0.218	3.562	0.614

Highlighted data = Significant when P < 0.05
Df = Degrees of Freedom.

a) State Behaviour and Scan Samples

		YF TROOP (n = 8, df = 7)		CX TROOP (n = 6, df = 5)	
		X^2	P	X^2	P
State Behaviours *(Mins/Hour)*	Feed on Human Food	16.142	0.024	4.016	0.547
	Feed on Natural Food	8.350	0.303	15.836	0.007
	Move	4.790	0.686	4.714	0.452
	Rest	12.107	0.097	13.515	0.019
	Groom Adult Male	9.600	0.212	5.000	0.416
	Groom Adult Female	8.366	0.301	5.061	0.409
	Groom Other	11.584	0.115	8.096	0.151
	Groom Unknown	0.000	1.000	0.000	1.000
	Groom Tourist	0.000	1.000	0.000	1.000
	Receive Grooming from Adult Male	30.878	< 0.001	4.016	0.547
	Receive Grooming from Adult Female	2.967	0.888	10.040	0.074
	Receive Grooming from Other	10.261	0.174	7.024	0.219
	Receive Grooming from Unknown	0.000	1.000	0.000	1.000
	Receive Grooming from Tourist	0.000	1.000	0.000	1.000
	Allo-Groom	6.902	0.439	14.272	0.014
	Self-Groom	17.626	0.014	14.195	0.014
	Scent Mark	6.914	0.438	64.645	< 0.001
	Other	6.743	0.456	5.000	0.416
	Out of Sight	3.896	0.792	10.074	0.073
	Aggressive Tourist/Lemur Interaction	12.696	0.080	0.000	1.000
	Non-Aggressive Tourist/Lemur Interaction	24.333	0.001	5.000	0.416
Scan *(Counts/30 Mins)*	Average Tourist Number	3.474	0.838	4.016	0.547
	Average Researcher Number	1.992	0.960	2.586	0.763
	Average Other Number	5.737	0.571	4.271	0.511
	Total Number of Observers	2.094	0.954	2.240	0.815
	Move	3.528	0.832	7.768	0.169
	Feed	2.830	0.900	5.240	0.387
	Rest	0.486	0.999	10.265	0.068
	Groom	4.887	0.674	5.860	0.320
	Self-Groom	13.107	0.070	3.651	0.601
	Observer/Lemur Interaction	8.334	0.304	5.000	0.416
	Self-Directed Behaviours	11.521	0.117	8.906	0.113
	Other	5.611	0.586	8.458	0.133
	Out of Sight	4.148	0.763	17.632	0.003
	Proximity (category metres)	6.663	0.465	2.129	0.831
	Elevation (m)	9.218	0.237	1.166	0.948
	Terrestriality (%)	6.056	0.533	1.334	0.931
	Habitat Zone	9.035	0.250	0.541	0.991

Highlighted data = Significant when P < 0.05.
Df = Degrees of Freedom.

APPENDIX 14

*Post-Hoc Mann-Whitney U Test Results Showing Significant Individual Differences in **Troop YF** and the Direction of Significance (n = 8). Continued overleaf.*

	Mainty				Marika				Maso				Rambo				Sofina				Volo			
	Mann-Whitney U Test				Mann-Whitney U Test				Mann-Whitney U Test				Mann-Whitney U Test				Mann-Whitney U Test				Mann-Whitney U Test			
	B	*U*	*Z*	*P*	*B*	*U*	*Z*	*P*	*B*	*U*	*Z*	*P*	*B*	*U*	*Z*	*P*	*B*	*U*	*Z*	*P*	*B*	*U*	*Z*	*P*
Avanana	13	629.000	-2.264	0.024	2	511.500	-4.236	< 0.001	7	733.500	-2.037	0.042	1	735.000	-2.744	0.006	3	645.500	-2.700	0.007	**NS**			
					4	733.500	-2.118	0.034	9	777.000	-2.291	0.022	3	695.500	-2.202	0.028								
					8	709.000	-2.261	0.024	8	722.000	-2.145	0.032	13	598.500	-2.537	0.011								
					11	777.000	-2.291	0.022	10	698.000	-2.707	0.016												
					10	698.000	-2.403	0.016	11	776.000	-1.978	0.048												
					14	684.000	-2.653	0.008	14	680.000	-2.707	0.007	1	777.000	-2.291	0.022								
Kely	**NS**				3	713.000	-2.486	0.013	2	714.000	-2.952	0.003	9	819.000	-1.753	0.080	**NS**				11	798.000	-2.036	0.042
					1	722.500	-1.997	0.046	4	738.000	-2.401	0.016	13	660.000	-1.986	0.047					12	798.000	-2.036	0.042
					2	462.000	-5.042	< 0.001	7	798.000	-2.037	0.022												
					4	697.500	-2.820	0.048	10	703.000	-2.337	0.019												
					8	713.000	-2.208	0.027	8	726.500	-2.084	0.037												
					9	777.000	-2.291	0.022	11	756.000	-2.525	0.012												
					10	705.000	-2.311	0.021	14	702.000	-2.350	0.019												
					11	777.000	-2.291	0.022																
					14	710.000	-2.246	0.025																
Mainty					1	649.000	-3.135	0.002	1	670.000	-2.932	0.003	**NS**				**NS**				12	798.000	-2.036	0.042
					2	478.500	-4.760	< 0.001	2	733.500	-2.476	0.013												
					4	692.500	-2.899	0.004	4	734.000	-2.469	0.014												
					8	717.000	-2.156	0.031	8	730.000	-2.037	0.042												
					9	777.000	-2.291	0.022	7	798.000	-2.037	0.042												
					10	708.000	-2.272	0.023	9	777.000	-2.291	0.022												
					14	697.000	-2.415	0.016	10	707.000	-2.285	0.022												
					3	717.000	-2.430	0.015	14	693.000	-2.468	0.014												
					13	541.000	-3.052	0.002																

All results were significant when P < 0.05, however, after the Dunn-Šidák Correction only results highlighted in yellow are significant when P < 0.00183. ***NS*** *= No Significance. There was no significance between Kely and Avanana. Colours are paired with an individual. Higher values for that individual are highlighted in that their designated colour, thus indicate the direction of significance.*

B = Behavioural Category: 1 = Aggression to Adult Male; 2 = Aggression to Adult Female; 3 = Aggression from Adult Female; 4 = Aggression to Other; 5 = Total Intra-Troop Aggression; 6 = Tourist Noise; 7 = Tourist Rock; 8 = Tourist Neutral; 9 = Tourist Feed; 10 = Total Non-Aggressive Tourist/Lemur Interaction (State); 11 = Feed on Human Food; 12 = Receive Grooming from Adult Male; 13 = Self-Groom; 14 = Non-Aggressive Tourist/Lemur Interaction (Scan)

APPENDIX 14 continued.

	Kely	Mainty	Marika	Maso				Rambo				Sofina				Volo			
				Mann-Whitney U Test				Mann-Whitney U Test				Mann-Whitney U Test				Mann-Whitney U Test			
				B	*U*	*Z*	*P*	*B*	*U*	*Z*	*P*	*B*	*U*	*Z*	*P*	*B*	*U*	*Z*	*P*
Marika				2	625.000	-2.755	0.006	1	609.000	-3.891	< 0.001	1	701.000	-2.316	0.021	1	709.000	-2.171	0.030
				3	738.000	-2.201	0.028	2	462.000	-5.042	< 0.001	2	495.000	-4.492	< 0.001	2	462.000	-5.042	< 0.001
				13	653.000	-2.050	0.040	4	692.500	-2.899	0.001	4	697.500	-3.883	0.005	4	692.000	-2.899	0.004
								3	610.000	-3.474	0.004	9	777.000	-2.291	0.022	8	651.500	-3.278	0.001
								13	532.500	-3.128	0.002	11	777.000	-2.291	0.022	9	777.000	-2.291	0.022
												13	634.000	-2.291	0.026	10	648.000	-3.326	0.001
												3	564.500	-2.820	0.005	14	650.000	-3.297	0.001
																3	758.000	-1.974	0.048
																12	798.000	-2.036	0.042
																13	656.000	-2.023	0.043
Maso								1	630.000	-3.713	< 0.001	1	722.000	-2.096	0.036	2	714.000	-2.952	0.003
								2	714.000	-2.952	0.003	2	753.000	-2.054	0.040	4	734.000	-2.469	0.014
								4	734.000	-2.469	0.014	4	738.000	-2.401	0.016	7	798.000	-2.037	0.042
								11	776.000	-1.978	0.048	7	798.000	-2.037	0.042	8	670.000	-3.117	0.002
												9	777.000	-2.291	0.022	9	777.000	-2.291	0.022
												11	756.000	-2.525	0.012	10	648.000	-3.326	0.001
												3	683.000	-2.185	0.029	14	648.000	-3.326	0.001
Rambo												1	798.000	-2.037	0.042	1	777.000	-2.292	0.022
Sofina																3	670.000	-2.355	0.019
																8	711.000	-2.720	0.007
																10	710.500	-2.728	0.006
																14	715.500	-2.648	0.008
																11	798.000	-2.036	0.042

All results were significant when P < 0.05, however, after the Dunn-Šidák Correction only results highlighted in yellow are significant when P < 0.00183. ***NS*** *= No Significance. Colours are paired with an individual. Higher values for that individual are highlighted in that their designated colour, thus indicate the direction of significance.*

B = Behavioural Category: 1 = Aggression to Adult Male; 2 = Aggression to Adult Female; 3 = Aggression from Adult Female; 4 = Aggression to Other; 5 = Total Intra-Troop Aggression; 6 = Tourist Noise; 7 = Tourist Rock; 8 = Tourist Neutral; 9 = Tourist Feed; 10 = Total Non-Aggressive Tourist/Lemur Interaction (State); 11 = Feed on Human Food; 12 = Receive Grooming from Adult Male; 13 = Self-Groom; 14 = Non-Aggressive Tourist/Lemur Interaction (Scan)

APPENDIX 15

An Example of the Macro Computer Programming Used for the Post-Hoc Mann-Whitney U Test Looking at Individual Differences in Troop YF

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DATASET ACTIVATE DataSet1.
NPAR TESTS
 /M-W= A.toadultmale A.toadultfemale A.fromadultfemale A.toother Totalintratroopaggr Noise Rock
   Feed Totalnonaggr.TL Human AMGive Selfgroom NonAggr BY FocalID1(1 2)
 /M-W= A.toadultmale A.toadultfemale A.fromadultfemale A.toother Totalintratroopaggr Noise Rock
   Feed Totalnonaggr.TL Human AMGive Selfgroom NonAggr BY FocalID1(1 3)
 /M-W= A.toadultmale A.toadultfemale A.fromadultfemale A.toother Totalintratroopaggr Noise Rock
   Feed Totalnonaggr.TL Human AMGive Selfgroom NonAggr BY FocalID1(1 5)
 /M-W= A.toadultmale A.toadultfemale A.fromadultfemale A.toother Totalintratroopaggr Noise Rock
   Feed Totalnonaggr.TL Human AMGive Selfgroom NonAggr BY FocalID1(1 6)
 /M-W= A.toadultmale A.toadultfemale A.fromadultfemale A.toother Totalintratroopaggr Noise Rock
   Feed Totalnonaggr.TL Human AMGive Selfgroom NonAggr BY FocalID1(1 9)
 /M-W= A.toadultmale A.toadultfemale A.fromadultfemale A.toother Totalintratroopaggr Noise Rock
   Feed Totalnonaggr.TL Human AMGive Selfgroom NonAggr BY FocalID1(1 11)
 /M-W= A.toadultmale A.toadultfemale A.fromadultfemale A.toother Totalintratroopaggr Noise Rock
   Feed Totalnonaggr.TL Human AMGive Selfgroom NonAggr BY FocalID1(1 14)
 /M-W= A.toadultmale A.toadultfemale A.fromadultfemale A.toother Totalintratroopaggr Noise Rock
   Feed Totalnonaggr.TL Human AMGive Selfgroom NonAggr BY FocalID1(2 3)
 /M-W= A.toadultmale A.toadultfemale A.fromadultfemale A.toother Totalintratroopaggr Noise Rock
   Feed Totalnonaggr.TL Human AMGive Selfgroom NonAggr BY FocalID1(2 5)
 /M-W= A.toadultmale A.toadultfemale A.fromadultfemale A.toother Totalintratroopaggr Noise Rock
   Feed Totalnonaggr.TL Human AMGive Selfgroom NonAggr BY FocalID1(2 6)
 /M-W= A.toadultmale A.toadultfemale A.fromadultfemale A.toother Totalintratroopaggr Noise Rock
   Feed Totalnonaggr.TL Human AMGive Selfgroom NonAggr BY FocalID1(2 9)
 /M-W= A.toadultmale A.toadultfemale A.fromadultfemale A.toother Totalintratroopaggr Noise Rock
   Feed Totalnonaggr.TL Human AMGive Selfgroom NonAggr BY FocalID1(2 11)
 /M-W= A.toadultmale A.toadultfemale A.fromadultfemale A.toother Totalintratroopaggr Noise Rock
   Feed Totalnonaggr.TL Human AMGive Selfgroom NonAggr BY FocalID1(2 14)
 /MISSING ANALYSIS.
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APPENDIX 16

Post-Hoc Mann-Whitney U Test Results Showing Significant Individual Differences in ***Troop CX*** *and the Direction of Significance (n = 6)*

	Orona				Pentina				Reny				Tsia				Tsipika			
	Mann-Whitney U Test				Mann-Whitney U Test				Mann-Whitney U Test				Mann-Whitney U Test				Mann-Whitney U Test			
	B	*U*	*Z*	*P*	*B*	*U*	*Z*	*P*	*B*	*U*	*Z*	*P*	*B*	*U*	*Z*	*P*	*B*	*U*	*Z*	*P*
Mandidy	4	691.000	-2.184	0.029	2	777.000	-2.292	0.022	1	691.500	-2.710	0.007					3	735.500	-2.442	0.015
Mandidy	8	636.000	-2.201	0.028	6	775.500	-1.988	0.047	7	610.500	-2.434	0.015					4	735.000	-2.744	0.006
Mandidy	11	357.500	-5.071	< 0.001	12	605.500	-3.207	0.001	8	638.500	-2.178	0.029	**NS**				5	798.000	-2.037	0.042
Mandidy									9	726.000	-1.988	0.047								
Mandidy									11	720.000	-2.382	0.017								
Orona					2	777.000	-2.292	0.022	1	651.000	-3.527	< 0.001	3	798.000	-2.037	0.042	1	735.000	-2.746	0.006
Orona					4	680.000	-2.312	0.021	4	581.000	-3.762	< 0.001	4	633.500	-2.936	0.003	3	714.000	-2.951	0.003
Orona					7	647.500	-2.112	0.035	7	662.500	-1.967	0.049	9	683.500	-2.094	0.036	4	546.000	-4.394	< 0.001
Orona					8	593.500	-2.581	0.010	9	584.000	-3.344	0.001	10	601.500	-2.514	0.012	5	798.000	-2.037	0.042
Orona					11	452.500	-4.129	< 0.001	10	595.000	-2.571	0.012	11	393.000	-4.632	< 0.001	6	798.000	-2.036	0.042
Orona					12	582.500	-3.421	0.001	11	284.000	-6.125	< 0.001					9	663.500	-2.305	0.021
Orona																	11	319.500	-5.579	< 0.001
Pentina									1	688.000	-2.760	0.006	3	798.000	-2.037	0.042	2	777.000	-2.292	0.022
Pentina									6	755.500	-1.988	0.047	7	604.500	-2.505	0.012	3	714.000	-2.951	0.003
Pentina									7	488.000	-3.542	< 0.001	8	596.500	-2.554	0.011	4	725.000	-2.746	0.006
Pentina									8	630.500	-2.250	0.024	10	575.000	-2.750	0.006	5	798.000	-2.037	0.042
Pentina									9	66.500	-2.653	0.008	12	544.000	-3.753	< 0.001	6	756.000	-2.525	0.012
Pentina									10	553.500	-2.941	0.003					12	519.500	-3.975	< 0.001
Pentina									11	694.000	-2.672	0.008								
Pentina									12	623.500	-3.047	0.002								
Reny													1	693.500	-2.681	0.007	**NS**			
Reny													11	640.500	-3.153	0.002				
Tsia																	4	777.000	-2.292	0.022
Tsia																	6	798.000	-2.037	0.042

All results were significant when P < 0.05, however, after the Dunn-Šidák Correction only results highlighted in yellow are significant when P < 0.0036571. ***NS*** *= No Significance. Colours are paired with an individual. Higher values for that individual are highlighted in that their designated colour, thus indicate the direction of significance.*

B = Behavioural Category: 1 = Aggression to Adult Male; 2 = Aggression from Adult Male; 3 = Aggression to Adult Female; 4 = Aggression from Adult Female; 5 = Aggression to Other; 6 =Total Counts of Aggressive Vocalisations; 7 = Feed on Natural Food; 8 = Rest; 9 = Allo-Groom; 10 = Self-Groom; 11 = Scent Mark; 12 = Out of Sight (Scan).

APPENDIX 17

The Macro Computer Programming Used for the Post-Hoc Mann-Whitney U Test Looking at Individual Differences in Troop CX

```
DATASET ACTIVATE DataSet1.
NPAR TESTS
  /M-W= A.toadultmale A.fromadultmale A.toadultfemale A.fromadultfemale A.toother
    Totalcountsofvoc.aggression Natural Rest Allogroom Selfgroom ScentMark X_A BY FocalID1(4 8)
  /M-W= A.toadultmale A.fromadultmale A.toadultfemale A.fromadultfemale A.toother
    Totalcountsofvoc.aggression Natural Rest Allogroom Selfgroom ScentMark X_A BY FocalID1(4 10)
  /M-W= A.toadultmale A.fromadultmale A.toadultfemale A.fromadultfemale A.toother
    Totalcountsofvoc.aggression Natural Rest Allogroom Selfgroom ScentMark X_A BY FocalID1(4 12)
  /M-W= A.toadultmale A.fromadultmale A.toadultfemale A.fromadultfemale A.toother
    Totalcountsofvoc.aggression Natural Rest Allogroom Selfgroom ScentMark X_A BY FocalID1(4 13)
  /M-W= A.toadultmale A.fromadultmale A.toadultfemale A.fromadultfemale A.toother
    Totalcountsofvoc.aggression Natural Rest Allogroom Selfgroom ScentMark X_A BY FocalID1(7 8)
 /M-W= A.toadultmale A.fromadultmale A.toadultfemale A.fromadultfemale A.toother
    Totalcountsofvoc.aggression Natural Rest Allogroom Selfgroom ScentMark X_A BY FocalID1(7 10)
 /M-W= A.toadultmale A.fromadultmale A.toadultfemale A.fromadultfemale A.toother
    Totalcountsofvoc.aggression Natural Rest Allogroom Selfgroom ScentMark X_A BY FocalID1(7 12)
 /M-W= A.toadultmale A.fromadultmale A.toadultfemale A.fromadultfemale A.toother
    Totalcountsofvoc.aggression Natural Rest Allogroom Selfgroom ScentMark X_A BY FocalID1(7 13)
 /M-W= A.toadultmale A.fromadultmale A.toadultfemale A.fromadultfemale A.toother
    Totalcountsofvoc.aggression Natural Rest Allogroom Selfgroom ScentMark X_A BY FocalID1(8 10)
 /M-W= A.toadultmale A.fromadultmale A.toadultfemale A.fromadultfemale A.toother
    Totalcountsofvoc.aggression Natural Rest Allogroom Selfgroom ScentMark X_A BY FocalID1(8 12)
 /M-W= A.toadultmale A.fromadultmale A.toadultfemale A.fromadultfemale A.toother
    Totalcountsofvoc.aggression Natural Rest Allogroom Selfgroom ScentMark X_A BY FocalID1(8 13)
 /M-W= A.toadultmale A.fromadultmale A.toadultfemale A.fromadultfemale A.toother
    Totalcountsofvoc.aggression Natural Rest Allogroom Selfgroom ScentMark X_A BY FocalID1(10 12)
 /M-W= A.toadultmale A.fromadultmale A.toadultfemale A.fromadultfemale A.toother
    Totalcountsofvoc.aggression Natural Rest Allogroom Selfgroom ScentMark X_A BY FocalID1(10 13)
 /M-W= A.toadultmale A.fromadultmale A.toadultfemale A.fromadultfemale A.toother
    Totalcountsofvoc.aggression Natural Rest Allogroom Selfgroom ScentMark X_A BY FocalID1(12 13)
  /MISSING ANALYSIS.
```

APPENDIX 18

Comparison of Study Subjects with Significant Behavioural Differences between Morning and Afternoon Using the Wilcoxon Matched-Pairs Signed-Rank Test. Only Displaying Behaviours where two or More Study Subjects were Significant (Omitting 'Habitat Zone'). $n_1 = 294$, $n_2 = 294$.Continued Overleaf.

		Event Behaviours			State Behaviours		Scan Sample						
Study Subject	**Wilcoxon Test**	Paired Tourist Neutral	Paired Total Non-Aggressive Tourist/Lemur Interaction	Paired Yawn	Paired Move	Paired Rest	Paired Average Number of Other	Paired Total Number of Observers	Paired Move	Paired Feed	Paired Rest	Paired Observer Interaction	Paired Terrestriality (%)
Reny	Z	0.000	0.000	-1.732	-0.206	-0.435	-1.000	-0.816	-0.458	-2.011	-2.581	0.000	-0.622
	P	1.000	1.000	0.083	0.837	0.664	0.317	0.414	0.647	0.044	0.010	1.000	0.534
Significant Time of Day										AM	PM		
Sofina	Z	-2.442	-2.203	-2.157	-0.121	-1.965	-2.308	-2.732	-0.073	-0.032	-0.926	-1.890	-1.242
	P	0.015	0.028	0.031	0.904	0.049	0.021	0.006	0.941	0.975	0.354	0.059	0.214
Significant Time of Day		AM	AM	PM		PM	AM	AM					
Tsia	Z	0.000	0.000	-1.000	-2.398	-1.235	0.000	0.000	-1.452	-0.692	-1.377	0.000	-2.264
	P	1.000	1.000	0.317	0.016	0.217	1.000	1.000	0.146	0.489	0.169	1.000	0.024
Significant Time of Day					AM								AM
Tsipika	Z	0.000	0.000	-0.816	-2.156	-1.425	-0.447	-1.089	-2.547	-0.998	-2.057	0.000	-1.963
	P	1.000	1.000	0.414	0.031	0.154	0.655	0.276	0.011	0.318	0.040	1.000	0.050
Significant Time of Day					AM				AM		PM		AM
Volo	Z	-1.000	-1.000	-2.000	-1.582	-2.627	-1.134	-0.687	-2.441	-1.635	-2.524	-1.000	-0.796
	P	0.317	0.317	0.046	0.114	0.009	0.257	0.492	0.015	0.102	0.012	0.317	0.426
Significant Time of Day				PM		PM			AM		PM		
Mainty	Z	-0.365	-0.365	-0.354	-0.093	-1.588	-2.203	-1.548	-0.287	-0.409	-0.433	-0.632	-2.214
	P	0.715	0.715	0.723	0.926	0.112	0.028	0.122	0.774	0.682	0.665	0.527	0.027
Significant Time of Day							AM						AM

Data highlighted in yellow = significant when $p < 0.05$. A.M. (n = 294), P.M. (n = 294). Data highlighted in pink = Morning; Blue = Afternoon (indicating the higher mean values, thus the direction of significance). (Only significant data were presented, hence two focals had no significance and are not shown).

APPENDIX 18 (continued).

		Event Behaviours			State Behaviours		Scan Sample						
Study Subject	**Wilcoxon Test**	Paired Tourist Neutral	Paired Total Non-Aggressive Tourist/Lemur Interaction	Paired Yawn	Paired Move	Paired Rest	Paired Average Number of Other	Paired Total Number of Observers	Paired Move	Paired Feed	Paired Rest	Paired Observer Interaction	Paired Terrestriality (%)
Mandidy	Z	-1.000	-1.000	-1.414	-1.756	-1.495	-1.000	-1.069	-0.655	-1.042	-0.865	0.000	-0.622
	P	0.317	0.317	0.157	0.079	0.135	0.317	0.285	0.512	0.297	0.387	1.000	0.534
Significant Time of Day													AM
Marika	Z	-0.915	-1.732	-0.106	-0.262	-0.052	-1.897	-2.167	-0.677	-1.339	-0.629	-2.428	-1.242
	P	0.360	0.083	0.915	0.794	0.958	0.058	0.030	0.499	0.180	0.530	0.015	0.214
Significant Time of Day								AM				AM	
Maso	Z	-2.254	-2.371	-0.707	-1.410	-1.982	-2.264	-2.328	-2.653	-0.481	-1.554	-2.271	-2.264
	P	0.024	0.018	0.480	0.158	0.048	0.024	0.020	0.008	0.630	0.120	0.023	0.024
Significant Time of Day		AM	AM			PM	AM	AM	AM			AM	
Orona	Z	0.000	0.000	-0.378	-3.423	-2.573	0.000	-1.000	-2.082	-0.036	-2.129	0.000	-1.963
	P	1.000	1.000	0.705	0.001	0.010	1.000	0.317	0.037	0.971	0.033	1.000	0.050
Significant Time of Day					AM	PM			AM		PM		AM
Pentina	Z	0.000	0.000	-1.342	-2.278	-1.699	0.000	-1.414	-2.500	-1.307	-0.314	0.000	-0.796
	P	1.000	1.000	0.180	0.023	0.089	1.000	0.157	0.012	0.191	0.753	1.000	0.426
Significant Time of Day					AM				AM				AM
Rambo	Z	-0.425	-0.316	0.000	-0.278	-0.149	-0.816	-0.426	-1.410	-2.073	-2.285	-0.447	-2.214
	P	0.671	0.752	1.000	0.781	0.881	0.414	0.670	0.159	0.038	0.022	0.655	0.027
Significant Time of Day										AM	PM		

Data highlighted in yellow = significant when $p < 0.05$. A.M. (n = 294), P.M. (n = 294). Data highlighted in pink = Morning; Blue = Afternoon (indicating the higher mean values, thus the direction of significance). (Only significant data were presented, hence two focals had no significance and are not shown).

APPENDIX 19

Comparison of the Average Behaviours for Tourist Presence and Absence for the 8 Study Subjects in Troop YF Using the Wilcoxon Matched-Pairs Signed-Rank Test.
$n_1 = 268$, $n_2 = 68$.

a) Event Behaviours

		Absent (n = 268) Mean ± S.E.			Present (n = 68) Mean ± S.E.			Wilcoxon M-P Z	P
Event	Aggression to Adult Male	0.31	±	0.05	0.74	±	0.22	-1.859	0.063
Behaviours	Aggression from Adult Male	0.17	±	0.04	0.76	±	0.34	-1.120	0.263
(Counts/Hour)	Aggression to Adult Female	0.31	±	0.09	0.94	±	0.44	-1.214	0.225
	Aggression from Adult Female	0.69	±	0.11	1.00	±	0.23	-1.260	0.208
	Aggression to Other	0.14	±	0.04	0.35	±	0.11	-1.262	0.207
	Aggression from Other	0.01	±	0.01	0.00	±	0.00	-1.000	0.317
	Total Intra-troop Aggression	1.63	±	0.19	3.79	±	0.70	-2.366	0.018
	Aggression to Unknown	0.16	±	0.07	0.26	±	0.18	-0.405	0.686
	Aggression from Unknown	0.11	±	0.05	0.47	±	0.21	-1.352	0.176
	Total Inter-troop Aggression	0.28	±	0.11	0.74	±	0.28	-1.260	0.208
	Troop Encounter	0.17	±	0.03	0.41	±	0.10	-2.380	0.017
	Aggression to Tourist	0.00	±	0.00	0.03	±	0.03	-1.000	0.317
	Tourist Noise	0.00	±	0.00	0.12	±	0.06	-1.342	0.180
	Tourist Mimic	0.00	±	0.00	0.00	±	0.00	0.000	1.000
	Tourist Rock	0.00	±	0.00	0.29	±	0.12	-1.604	0.109
	Tourist Throw	0.00	±	0.00	0.09	±	0.05	-1.633	0.102
	Tourist Other	0.00	±	0.00	0.00	±	0.00	0.000	1.000
	Total Aggressive Tourist/Lemur Int.	0.00	±	0.00	0.53	±	0.15	-2.023	0.043
	Yip Vocalisation	0.23	±	0.05	0.35	±	0.12	-1.400	0.161
	Squeal Vocalisation	0.19	±	0.05	0.12	±	0.06	-1.684	0.092
	Territorial Call	0.28	±	0.12	0.03	±	0.03	-1.680	0.093
	Chutter Vocalisation	0.13	±	0.04	0.21	±	0.10	-0.105	0.917
	Unknown Vocalisation	0.02	±	0.01	0.00	±	0.00	-1.604	0.109
	Total Counts of Aggressive Voc.	0.86	±	0.17	0.71	±	0.21	-0.840	0.401
	Tourist Neutral	0.03	±	0.02	4.24	±	0.59	-2.524	0.012
	Tourist Stroke	0.01	±	0.01	0.15	±	0.09	-1.069	0.285
	Tourist Play	0.00	±	0.00	0.15	±	0.08	-1.604	0.109
	Tourist Feed	0.03	±	0.02	0.56	±	0.19	-1.604	0.109
	Tourist Other	0.00	±	0.00	0.06	±	0.04	-1.000	0.317
	Total Non-Aggressive Tourist/Lemur Int.	0.07	±	0.04	5.15	±	0.71	-2.521	0.012
	Self-Scratch	4.24	±	0.28	4.06	±	0.49	-0.140	0.889
	Self-Groom < 10 Seconds	2.70	±	0.21	2.97	±	0.48	-0.700	0.484
	Startle	0.43	±	0.07	0.68	±	0.29	-0.560	0.575
	Yawn	0.75	±	0.11	0.44	±	0.14	-1.680	0.093

Highlighted data = Significant when $P < 0.05$. Int. = Interaction. Voc. = Vocalisations.

b) State Behaviours and Scan Sample

		Absent (n = 268) Mean ± S.E.			Present (n = 68) Mean ± S.E.			Wilcoxon M-P Z	P
State Behaviours *(Mins/Hour)*	Feed on Human Food	0.27	±	0.14	0.54	±	0.20	-0.943	0.345
	Feed on Natural Food	12.21	±	0.77	13.93	±	1.53	-0.420	0.674
	Move	10.76	±	0.52	13.09	±	0.83	-1.400	0.161
	Rest	27.50	±	0.97	21.59	±	1.43	-2.100	0.036
	Groom Adult Male	0.06	±	0.02	0.03	±	0.03	-1.214	0.225
	Groom Adult Female	0.15	±	0.06	0.07	±	0.05	-0.943	0.345
	Groom Other	0.04	±	0.02	0.00	±	0.00	-2.023	0.043
	Groom Unknown	0.00	±	0.00	0.00	±	0.00	0.000	1.000
	Groom Tourist	0.00	±	0.00	0.00	±	0.00	0.000	1.000
	Receive Grooming from Adult Male	0.07	±	0.05	0.07	±	0.07	-1.604	0.109
	Receive Grooming from Adult Female	0.09	±	0.05	0.09	±	0.07	-0.507	0.612
	Receive Grooming from Other	0.08	±	0.04	0.01	±	0.01	-1.521	0.128
	Receive Grooming from Unknown	0.00	±	0.00	0.00	±	0.00	0.000	1.000
	Receive Grooming from Tourist	0.00	±	0.00	0.00	±	0.00	0.000	1.000
	Allo-Groom	2.48	±	0.27	0.66	±	0.22	-2.521	0.012
	Self-Groom	4.96	±	0.29	4.00	±	0.58	-1.540	0.123
	Scent Mark	0.55	±	0.07	1.01	±	0.23	-1.820	0.069
	Other	0.05	±	0.02	0.26	±	0.17	-0.676	0.499
	Out of Sight	0.53	±	0.13	0.37	±	0.20	-0.840	0.401
	Aggressive Tourist/Lemur Int.	0.00	±	0.00	0.18	±	0.10	-1.604	0.109
	Non-Aggressive Tourist/Lemur Int.	0.08	±	0.04	3.97	±	0.70	-2.521	0.012
Scan *(Counts/30 Mins)*	Average Tourist Number	0.00	±	0.00	1.90	±	0.35	-2.521	0.012
	Average Researcher Number	2.44	±	0.03	2.43	±	0.07	-0.560	0.575
	Average Other Number	0.11	±	0.03	0.59	±	0.10	-2.521	0.012
	Total Number of Observers	2.56	±	0.04	4.96	±	0.41	-2.521	0.012
	Move	1.28	±	0.06	1.56	±	0.11	-1.540	0.123
	Feed	1.78	±	0.09	1.88	±	0.17	0.000	1.000
	Rest	3.48	±	0.11	2.94	±	0.18	-1.960	0.050
	Groom	0.27	±	0.03	0.24	±	0.06	-1.540	0.123
	Self-Groom	0.66	±	0.04	0.43	±	0.07	-2.103	0.035
	Observer/Lemur Int.	0.04	±	0.01	0.62	±	0.09	-2.521	0.012
	Self-Directed Behaviours	0.07	±	0.02	0.07	±	0.03	-1.260	0.208
	Other	0.12	±	0.02	0.07	±	0.03	-0.491	0.624
	Out of Sight	0.11	±	0.02	0.09	±	0.04	-0.700	0.484
	Proximity (category metres)	3.28	±	0.04	3.12	±	0.07	-1.960	0.050
	Elevation (m)	4.13	±	0.08	3.56	±	0.15	-2.100	0.036
	Terrestriality (%)	14.04	±	1.19	31.69	±	2.83	-2.521	0.012
	Habitat Zone	1.85	±	0.06	2.91	±	0.04	-2.521	0.012

Highlighted data = Significant when P < 0.05. Int. = Interaction.

APPENDIX 20

Comparison of Study Subjects in Troop YF with Significant Behavioural Differences When Tourists were Present and Absent Using the Wilcoxon Matched-Pairs Signed-Rank Test. Only Displaying Behaviours where two or More Focals were Significant (Omitting 'Habitat Zone and obvious tourist counts and interaction'). $n_1 = 268$, $n_2 = 68$.

		Event Behaviours			**State Behaviours**							**Scan Sample**						
Study Subject	**W Test**	Paired Self-Scratch	Paired Self-Groom < 10 Seconds	Paired Yawn	Paired Feed on Natural Food	Paired Move	Paired Rest	Paired Allo-Groom	Paired Self-Groom	Paired Scent Mark	Paired Out of Sight	Paired Average Researcher Number	Paired Move	Paired Feed	Paired Rest	Paired Self-Groom	Paired Proximity	Paired Elev.
Avanana	Z	-2.493	-1.118	-2.207	-1.792	-1.999	-3.528	-2.667	-2.937	-0.664	-2.023	-3.407	-1.186	-1.506	-3.611	-3.218	-3.488	-3.573
	P	0.013	0.264	0.027	0.073	0.046	< 0.001	0.008	0.003	0.507	0.043	0.001	0.236	0.132	< 0.001	0.001	< 0.001	< 0.001
T Ab/Pr.		Absent		Absent		Absent	Absent	Absent	Absent		Absent	Absent			Absent	Absent	Absent	Absent
Kely	Z	-3.190	-2.282	-1.035	-3.027	-1.792	-2.937	-1.988	-1.616	-1.988	-0.674	-3.163	-2.770	-2.370	-3.347	-1.155	-3.032	-3.427
	P	0.001	0.023	0.300	0.002	0.073	0.003	0.047	0.106	0.047	0.500	0.002	0.006	0.018	0.001	0.248	0.002	0.001
T Ab/Pr.		Absent	Absent		Absent		Absent	Absent		Absent		Absent	Absent	Absent	Absent		Absent	Absent
Mainty	Z	-2.314	-2.262	-1.409	-1.932	-1.755	-3.493	-2.417	-3.250	-0.594	-0.365	-3.391	-1.741	-3.319	-3.632	-2.357	-3.661	-3.770
	P	0.021	0.024	0.159	0.053	0.079	< 0.001	0.016	0.001	0.552	0.715	0.001	0.082	0.001	< 0.001	0.018	< 0.001	< 0.001
T Ab/Pr.		Absent	Absent				Absent	Absent	Absent			Absent		Absent	Absent	Absent	Absent	Absent
Marika	Z	-0.895	-1.075	-1.445	-1.269	-1.699	-3.319	-2.473	-2.091	-1.851	-0.730	-2.973	-0.708	-0.762	-3.497	-2.179	-3.052	-3.298
	P	0.371	0.282	0.149	0.204	0.089	0.001	0.013	0.037	0.064	0.465	0.003	0.479	0.446	< 0.001	0.029	0.002	0.001
T Ab/Pr.							Absent	Absent	Absent			Absent			Absent	Absent	Absent	Absent
Maso	Z	-1.988	-1.888	-0.719	-2.133	-2.555	-2.589	-3.408	-3.215	-1.979	-1.352	-3.029	-2.427	-2.235	-2.451	-2.517	-2.960	-3.414
	P	0.047	0.059	0.472	0.033	0.011	0.010	0.001	0.001	0.048	0.176	0.002	0.015	0.025	0.014	0.012	0.003	0.001
T Ab/Pr.		Absent			Absent	Absent	Absent	Absent	Absent	Absent		Absent	Absent	Absent	Absent	Absent	Absent	Absent
Rambo	Z	-2.665	-2.235	-1.841	-3.472	-3.180	-3.111	-2.040	-2.416	-0.827	-1.604	-3.362	-3.201	-3.386	-2.289	-1.386	-3.266	-3.373
	P	0.008	0.025	0.066	0.001	0.001	0.002	0.041	0.016	0.408	0.109	0.001	0.001	0.001	0.022	0.166	0.001	0.001
T Ab/Pr.		Absent	Absent		Absent	Absent	Absent	Absent	Absent			Absent	Absent	Absent	Absent		Absent	Absent
Sofina	Z	-1.830	-1.530	-2.546	-1.929	-1.303	-3.563	-3.351	-2.729	-1.438	-0.447	-3.140	-1.311	-2.673	-3.477	-2.000	-2.992	-3.404
	P	0.067	0.126	0.011	0.054	0.192	< 0.001	0.001	0.006	0.151	0.655	0.002	0.190	0.008	0.001	0.046	0.003	0.001
T Ab/Pr.				Absent			Absent	Absent	Absent			Absent		Absent	Absent	Absent	Absent	Absent
Volo	Z	-2.303	-2.804	-2.070	-1.095	-2.589	-3.806	-3.309	-3.302	-2.040	-2.023	-3.486	-2.584	-1.513	-3.894	-3.606	-3.412	-3.049
	P	0.021	0.005	0.038	0.274	0.010	< 0.001	0.001	0.001	0.041	0.043	< 0.001	0.010	0.130	< 0.001	< 0.001	0.001	0.002
T Ab/Pr.		Absent	Absent	Absent		Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent		Absent	Absent	Absent	Absent

Data highlighted in yellow = significant when $p < 0.05$. W. = Wilcoxon Matched-Pairs Signed-Rank Test.

T Ab/Pr. = Tourists absent (n = 268)/ present (n = 68). Data highlighted in purple = Absent (indicating the higher mean values, thus the direction of significance). (Only significant data were presented). Elev. = Elevation.

APPENDIX 21

Comparison of the Average State Behaviours for Tourist Presence and Absence for the 8 Study Subjects in Troop YF Using the Mann-Whitney U Test. $n_1 = 268$, $n_2 = 68$.

		Absent (*n*=268) Mean ± S.E.			Present (*n*=68) Mean ± S.E.			Mann-Whitney U Test		
								U	Z	P
State behaviours	Feed on Human Food	0.27	±	0.14	0.54	±	0.20	7956.000	-3.941	< 0.001
(min/hour)	Feed on Natural Food	12.21	±	0.77	13.93	±	1.53	8346.500	-1.079	0.281
	Move	10.76	±	0.52	13.09	±	0.83	7154.500	-2.739	0.006
	Rest	27.50	±	0.97	21.59	±	1.43	7362.500	-2.446	0.014
	Groom Adult Male	0.06	±	0.02	0.03	±	0.03	8942.000	-0.807	0.420
	Groom Adult Female	0.15	±	0.06	0.07	±	0.05	9089.000	-0.093	0.926
	Groom Other	0.04	±	0.02	0.00	±	0.00	8840.000	-1.440	0.150
	Groom Unknown	0.00	±	0.00	0.00	±	0.00	9112.000	0.000	1.000
	Groom Tourist	0.00	±	0.00	0.00	±	0.00	9112.000	0.000	1.000
	Receive Grooming from Adult Male	0.07	±	0.05	0.07	±	0.07	9080.500	-0.234	0.815
	Receive Grooming from Adult Female	0.09	±	0.05	0.09	±	0.07	9047.000	-0.344	0.731
	Receive Grooming from Other	0.08	±	0.04	0.01	±	0.01	9006.000	-0.561	0.575
	Receive Grooming from Unknown	0.00	±	0.00	0.00	±	0.00	9112.000	0.000	1.000
	Receive Grooming from Tourist	0.00	±	0.00	0.00	±	0.00	9112.000	0.000	1.000
	Allo-Groom	2.48	±	0.27	0.66	±	0.22	6840.500	-3.630	< 0.001
	Self-Groom	4.96	±	0.29	4.00	±	0.58	7332.500	-2.501	0.012
	Scent Mark	0.55	±	0.07	1.01	±	0.23	7855.500	-2.165	0.030
	Other	0.05	±	0.02	0.26	±	0.17	8972.500	-0.633	0.527
	Out of Sight	0.53	±	0.13	0.37	±	0.20	8771.000	-0.899	0.369
	Aggressive Tourist/Lemur Int.	0.00	±	0.00	0.18	±	0.10	8308.000	-4.899	< 0.001
	Non-Aggressive Tourist/Lemur Int.	0.08	±	0.04	3.97	±	0.70	2970.500	-13.753	< 0.001

Highlighted data = Significant when P < 0.05. Int. = Interaction.

APPENDIX 22

Comparison of the Average Event Behaviours for Tourist Presence and Absence for the 8 Study Subjects in Troop YF Using the Mann-Whitney U Test. $n_1 = 268$, $n_2 = 68$.

		Absent (*n*=268)			**Present** (*n*=68)			Mann-Whitney U Test		
		Mean ± S.E.			Mean ± S.E.			U	Z	P
Event Behaviours *(Counts/hour)*	Aggression to Adult Male	0.31	±	0.05	0.74	±	0.22	8206.000	-2.085	0.037
	Aggression from Adult Male	0.17	±	0.04	0.76	±	0.34	8164.500	-2.603	0.009
	Aggression to Adult Female	0.31	±	0.09	0.94	±	0.44	8226.500	-2.366	0.018
	Aggression from Adult Female	0.69	±	0.11	1.00	±	0.23	8207.500	-1.723	0.085
	Aggression to Other	0.14	±	0.04	0.35	±	0.11	8315.000	-2.406	0.016
	Aggression from Other	0.01	±	0.01	0.00	±	0.00	9078.000	-0.504	0.614
	Total Intra-troop Aggression	1.63	±	0.19	3.79	±	0.70	6524.500	-4.020	< 0.001
	Aggression to Unknown	0.16	±	0.07	0.26	±	0.18	8887.500	-0.939	0.348
	Aggression from Unknown	0.11	±	0.05	0.47	±	0.21	8314.000	-3.023	0.003
	Total Inter-troop Aggression	0.28	±	0.11	0.74	±	0.28	8119.500	-3.050	0.002
	Troop Encounter	0.17	±	0.03	0.41	±	0.10	8018.000	-2.820	0.005
	Aggression to Tourist	0.00	±	0.00	0.03	±	0.03	8978.000	-1.985	0.047
	Tourist Noise	0.00	±	0.00	0.12	±	0.06	8576.000	-3.988	< 0.001
	Tourist Mimic	0.00	±	0.00	0.00	±	0.00	9112.000	0.000	1.000
	Tourist Rock	0.00	±	0.00	0.29	±	0.12	8174.000	-5.300	< 0.001
	Tourist Throw	0.00	±	0.00	0.09	±	0.05	8710.000	-3.449	0.001
	Tourist Other	0.00	±	0.00	0.00	±	0.00	9112.000	0.000	1.000
	Total Aggressive Tourist/Lemur Int.	0.00	±	0.00	0.53	±	0.15	7504.000	-6.992	< 0.001
	Yip Vocalisation	0.23	±	0.05	0.35	±	0.12	8679.000	-1.189	0.234
	Squeal Vocalisation	0.19	±	0.05	0.12	±	0.06	9058.000	-0.180	0.857
	Territorial Call	0.28	±	0.12	0.03	±	0.03	8868.500	-1.059	0.290
	Chutter Vocalisation	0.13	±	0.04	0.21	±	0.10	8853.000	-0.953	0.340
	Unknown Vocalisation	0.02	±	0.01	0.00	±	0.00	9010.000	-0.875	0.382
	Total Counts of Aggressive Voc.	0.86	±	0.17	0.71	±	0.21	9025.000	-0.176	0.861
	Tourist Neutral	0.03	±	0.02	4.24	±	0.59	2744.500	-14.261	< 0.001
	Tourist Stroke	0.01	±	0.01	0.15	±	0.09	8743.000	-2.746	0.006
	Tourist Play	0.00	±	0.00	0.15	±	0.08	8576.000	-3.988	< 0.001
	Tourist Feed	0.03	±	0.02	0.56	±	0.19	7870.000	-5.196	< 0.001
	Tourist Other	0.00	±	0.00	0.06	±	0.04	8844.000	-2.812	0.005
	Total Non-Aggressive Tourist/Lemur Int.	0.07	±	0.04	5.15	±	0.71	2788.500	-14.046	< 0.001
	Self-Scratch	4.24	±	0.28	4.06	±	0.49	8987.500	-0.177	0.859
	Self-Groom < 10 Seconds	2.70	±	0.21	2.97	±	0.48	9048.500	-0.093	0.926
	Startle	0.43	±	0.07	0.68	±	0.29	8890.000	-0.494	0.621
	Yawn	0.75	±	0.11	0.44	±	0.14	8500.000	-1.228	0.219

Highlighted data = Significant when P < 0.05. Int. = Interactions. Voc. = Vocalisations.

APPENDIX 23

Ethics Form, Approved by the Ethics Committee of the University of Roehampton

The following are attached to the CD-ROM disc accompanying this thesis:

i. Ethics Application Form

ii. Ethics Risk Assessment Form

iii. Overseas Risk Assessment Form (Venture Risk Assessment)