Investigating primate tourism in Morocco using a multidisciplinary approach

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Moroccan tourist feeding an adult female Barbary macaque.

By

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Abstract

Wildlife tourism is a growing industry, with potential benefits for the conservation of endangered species. In this thesis, I explore wildlife tourism at a site in Morocco, using a multidisciplinary approach which considers both the attitudes and expectations of tourists, and the responses of, and impacts on, Barbary macaques.

Different types of tourists, mostly Moroccan nationals, visited the site and frequently gave food to the macaques. The desire to feed the monkeys appeared to be driven by different motivations such as the reward from sharing food, the creation of a relationship or taking control over these animals. Such interactions therefore shape a particular tourist experience; this can lead in some cases to a degree of disappointment about the authenticity of the wildlife experience.

Considering how the monkeys responded to tourists, I found evidence that they use a range of behavioural coping mechanisms to cope with the potentially conflicting motivational situations associated with the risks of interacting with tourists and the attraction of potential food. I propose a framework to aid understanding of how the trade-off between threat and attraction can lead to different coping mechanisms being deployed.

Looking at potential effects of tourist provisioning on the health of the macaques, I found evidence for potential negative impacts in terms of increased risk of disease transmission, elevated stress levels and increased body size. The results also highlighted the key issue of not knowing what is optimum health in wild animals, making interpretation of the findings difficult.

The multidisciplinary approach adopted in this thesis provided a useful tool to explore different aspects of primate tourism at the site from both tourist and animal standpoints. This approach led to the development of a new concept, optimal provisioning, which takes into consideration the different costs and benefits of provisioning wildlife to the various parties involved. It is hoped that this approach will prove useful in developing pragmatic solutions to the question of whether and how much provisioning may be acceptable in wildlife tourism contexts.

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FGC: Faecal glucocorticoid

GC: Glucocorticoid

GG: Green Group

GLMM: Generalised linear mixed model

MC: Matched control

PCA: Principal component analysis

TG: Tourist Group

TMI: Tourist-macaque interaction

TP: Tourist presence

UCP: Urine C-peptide

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Chapter 1

Introduction

Wildlife tourism is a growing industry, and one that has the potential to benefit conservation, in particular of endangered species, by increasing public awareness, providing protection for species and their habitats, and contributing to the local and/or national economy (Brightsmith et al. 2008, Ballantyne et al. 2009, Russon and Wallis 2014). However, concerns have been raised recently regarding the potential negative impacts of such tourism on the welfare of the animals involved, and measures proposed to alleviate such impacts (Constantine et al. 2004, Maréchal et al. 2011, Sapolsky 2014, Muehlenbein and Wallis 2014). At the same time, there is an increased expectation and desire among tourists to encounter pristine wildlife in a preserved habitat, unchanged by humans (Russell 1995, Curtin 2009). Despite the ‘green’ movement for reducing human impact on wildlife, the different - and sometimes opposite - interests of the different parties involved in wildlife tourism (i.e. people and animals) often make it difficult to reach a balance that satisfies all. Understanding the perspectives of, and impacts on, these different parties is therefore key to providing advice which will facilitate sustainable wildlife tourism and meet both the needs of the local community and the expectations of tourists, while reducing or eliminating the potential negative impacts on the wildlife involved. Although some studies have investigated wildlife tourism from the point of view of tourists, or have explored its impact on wildlife, only a few studies have attempted to consider simultaneously the standpoints of both tourists and animals (Grossberg et al. 2003, Kauffman 2014); this constitutes an important gap in our knowledge of wildlife tourism.

This thesis investigates primate tourism at a tourist site in the Middle Atlas Mountains of Morocco, using a multidisciplinary approach which considers both the attitudes and expectations of tourists and the responses of, and impacts on, the Barbary macaques they visit there. This work aims not only to contribute to our general understanding of wildlife tourism, but also to the question of animals' responses to anthropogenic disturbance and to the conservation of endangered species more broadly. Specifically, this multidisciplinary study focuses first on the description of the different types of tourists coming to the site, using ethnographic methods to explore their perceptions and motivations for engaging in the feeding of monkeys, and how this behaviour shapes their experience (Chapter 3). Then, I investigate the impacts of tourists on the behaviour (Chapter 4) and health (Chapter 5) of adult Barbary macaques. Finally (Chapter 6), I explore the implications of my findings for wildlife tourism and conservation, discussing more generally the advantages and limitations of adopting a multidisciplinary approach for understanding human-animal relationships. I conclude by giving potential directions for future research.

In this introductory chapter, I first define wildlife tourism and outline a brief history of this phenomenon. Next, I describe the different types of wildlife tourism, consider whether and how wildlife tourism might be used as a tool for conservation, and discuss the value of adopting a multidisciplinary approach to investigate this form of tourism. I then review current knowledge about the two principal components involved in wildlife tourism - tourists and animals - highlighting key gaps in this knowledge, with special attention paid to tourism related to primates. Finally, I introduce the four research aims of this study.

1.1 Wildlife tourism

Definitions

The use of the term 'wildlife' is relatively new, appearing for the first time in William Hornaday's book *Our Vanished Wild life - Its Extermination and Preservation* (1913), but not included in major dictionaries before 1961 (Newsome et al. 2005). Although the term 'wildlife' technically includes both fauna and flora, 'wildlife tourism' is often used to refer just to fauna, as is the case in the present study.

Tourism is defined as "a leisure activity which presupposes its opposite, namely regulated and organised work" (Urry 1990, p.4). This involves the movement of people to various destinations for short periods of time, with the clear intention to return home afterwards (Urry 1990).

There are two kinds of wildlife tourism: consumptive and non-consumptive. Consumptive wildlife tourism is associated with hunting and fishing, where the purpose is to hunt and kill animals. Non-consumptive wildlife tourism focuses on non-lethal experiences with wildlife (Weaver 2001), and is defined as tourism involving encounters with non-domesticated animals located in areas without spatial limitations (i.e. not in enclosures), including activities such as viewing, photographing and sometimes feeding wildlife (Higginbottom 2004). In the present study, the term wildlife tourism is used to refer only to this non-consumptive wildlife tourism.

Wildlife tourism: history

Wildlife tourism is a relatively recent phenomenon, but one that has significantly increased over the last few decades (Higginbottom 2004, Newsome et al. 2005, Ballantyne et al. 2009). Nowadays, wildlife tourism is considered one of the most popular and lucrative areas of the tourism industry (Curtin 2009). This keen interest in wild animals is nevertheless not so recent a phenomenon, and the concept of biophilia introduced by Wilson (1984, p.1) describes this interest as the "innate human emotional affiliation with nature", which includes wildlife. In fact, over many centuries, numerous cultures have had close relationships with wild animals. However, it was not until the 18th and 19th centuries, with the advent of industrial development and the creation of zoological gardens that the idea of visiting and observing wildlife for recreational purposes started. The first zoological garden opened in 1752 in Schönbrunn (Austria), followed by a number of others in different cities (e.g. La Ménagerie du Jardin des Plantes in Paris in 1793, London Zoo in 1828). Although the first animals displayed were of European origin, an interest in exotic wildlife quickly developed, leading to the capture for display of wild animals from all around the world. It was not until the 20th century that improvements in transport (i.e. the development of aeroplanes and ferries) made wildlife expeditions accessible, but then still only to the upper classes due to the costs. More recently, wildlife tourism has become more accessible to a larger number of people with lower incomes. Three important factors are thought to have enabled this development (Shackley 1996).

Firstly, there has been an overall growth and product diversification in world tourism. In addition, there has been development of cheaper and faster access to new destination areas. Finally, mass media has had an important influence on the development of new wildlife tourism destinations by exposing large global audiences to these places. Overall, these factors have led to a dramatic increase in the number of people undertaking wildlife tourism. The impacts of this change are largely unknown, although it is feared the burgeoning of this industry could potentially put catastrophic pressure upon wildlife and habitats (Shackley 1996, Higginbottom 2004, Newsome et al. 2005, Ballantyne et al. 2009).

Different types of wildlife tourism

Defining the different types of wildlife tourism is difficult because each tourist site has its own characteristics; at a basic level, wildlife tourism can be thought to range from mass wildlife tourism to more specialist/niche eco-tourism (Figure 1-1).

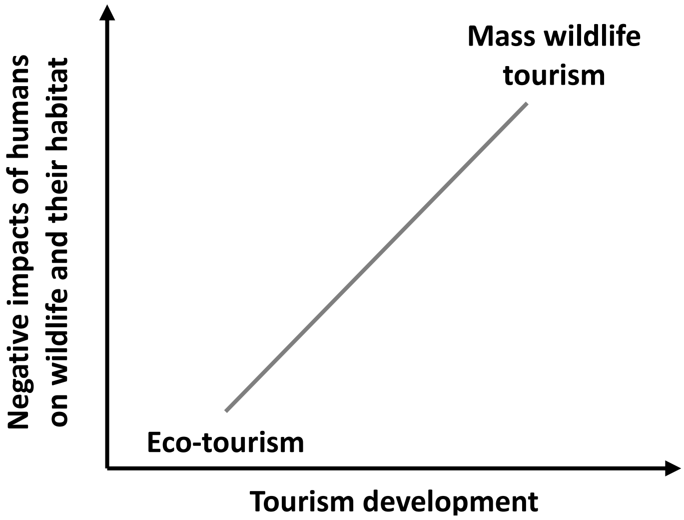


Figure 1-1: The two different types of wildlife tourism according to the negative impacts of humans on wildlife and their habitat, and to tourism development (e.g. tourist number/economic benefits). Adapted from Ivanov and Ivanova (2013).

It is generally considered that wildlife tourism may be viewed from either anthropocentric or ecocentric standpoints (Weaver 2001). Anthropocentric perspectives on wildlife tourism are related to the economic, business, social and cultural side of this activity, whereas the ecocentric standpoints are related to the natural component of the activity, the wildlife. Although anthropocentric and ecocentric standpoints are not necessarily mutually exclusive (Weaver 2001), it is generally thought that anthropocentric perspectives have a utilitarian perception of wildlife, and therefore the potential negative impacts of such tourism on wildlife and their habitat might be disregarded (or less strongly considered), to prioritise the financial benefits. Tourism which focuses primarily on economic benefits is often associated with mass tourism. Mass tourism is defined as a large number of people going to the same location at the same time for leisure purposes (Weaver 2001, González-Tirados 2011, Ivanov and Ivanova 2013). The intensity of mass tourism is believed to lead to detrimental impacts on wildlife and the environment, by negatively affecting the behaviour and health of the animals involved and by altering their natural habitat, therefore making such tourism potentially unsustainable. Mass wildlife tourism is, by definition, very popular, and has been promoted by mass media. Some destinations in remote and fragile environments are brought to public attention by such media, for example by featuring in BBC or National Geographic documentaries. With the interest in nature-based destinations increasing, the tourism industry has driven the building of infrastructure, allowing mass tourists to access more easily these remote places (Shackley 1996).

Another type of wildlife tourism, that is more oriented to ecocentric standpoints and more environmentally responsible, has recently been developed, linked to a general increased interest in preserving nature (Shackley 1996). Such tourism aims to find sustainable alternatives to potentially unsustainable mass wildlife tourism. One of the forms of wildlife tourism that promotes a environmentally responsible tourism, and that aims to contribute to the conservation of wildlife, is ecotourism. The International Union for Conservation of Nature (IUCN) defines ecotourism as: “Environmentally responsible travel and visitation to relatively undisturbed natural areas, in order to enjoy and appreciate nature (and any accompanying cultural features – both past and present) that promotes conservation, has low visitor impact, and provides for beneficially active socio-economic involvement of local populations” (Ceballos-Lascurain 1996, p.20). Ecotourism is a popular concept; however, since the term was first introduced by Ceballos-Lascurain (1996), it has often been used for marketing purposes in the tourism industry to describe wildlife tourism more broadly without taking into consideration the impacts of such tourism on natural habitats (Ross and Wall 1999, Leasor and Macgregor 2014). Ross and Wall (1999) proposed that successful ecotourism should be based on three main factors - biodiversity/conservation, tourism, and local communities - each making positive contributions to the others (Figure 1-2). In order to meet these criteria, wildlife tourism must therefore consider anthropocentric perspectives, as well as the impacts of tourism on wildlife and the natural environment.

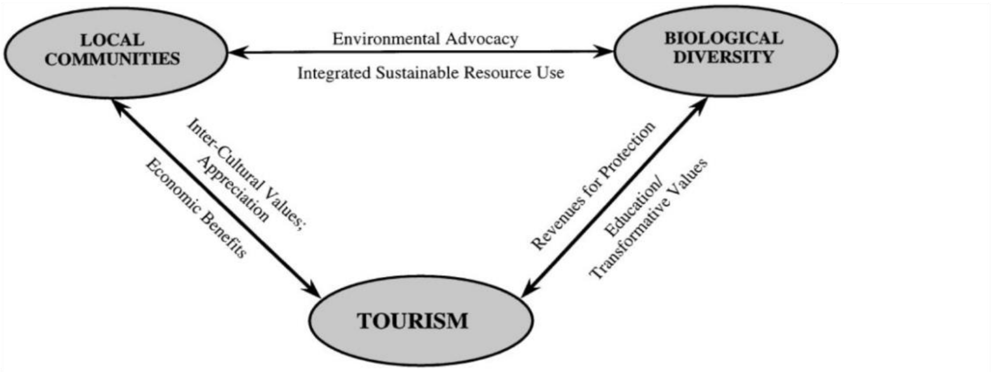


Figure 1-2: The ecotourism paradigm (Ross and Wall 1999)

The singular case of incidental wildlife tourism

Wildlife tourism may be intentional or may also be incidental; the latter occurs when tourists encounter wildlife while engaging in another form of activity or tourism (Roe et al. 1997, Sinha 2001, Newsome and Rodger 2012). For example, many tourists book a tour-guided holiday; here the prime motivation for visiting a country may not to be to see wildlife (Roe et al. 1997). Little research has been conducted on incidental wildlife tourism because it is not considered a 'typical' form of wildlife tourism, and it is difficult to classify (Newsome and Rodger 2012). Incidental wildlife tourism may take place at a tourist site that is already set up for tourism, where other tourists purposely travel to see wildlife or for other activities. It may also occur where there is no such formal setting and no regulations or management purposely organised for wildlife tourism, making the activities of tourists and the economic benefits of such tourism unclear and unpredictable. For example, no fees are charged to tourists who stop at the tourist sites and see monkeys in Morocco (personal observation), or at some sites in Bali (Fuentes et al. 2006), but local shops may benefit from such tourism by selling souvenirs. The motivation of incidental tourists may also strongly influence their perception, experience and behaviour towards the animals they come across, which may lead to negative impacts (Sinha 2001). A study of howler monkeys (*Alouatta pigra*) at Lamanai Archaeological reserve in Belize found that tourists who came primarily to visit the Maya ruins at the site had lower levels of environmental concerns than other tourists who purposely came there to see the wildlife (Grossberg et al. 2003). Furthermore, when incidental tourists encountered howler monkeys, they were more likely than other tourists to have more intensive interactions with them, i.e. to disturb the behaviour of these animals more. Improving environmental education of these tourists was suggested to have potential benefits by reducing the negative impacts of such tourism on the wildlife, and raising general awareness for the conservation of endangered species (Grossberg et al. 2003). Since incidental wildlife tourism is common, and concerns have been raised regarding its potential negative impacts (Grossberg et al. 2003), research on incidental wildlife tourists and their impacts on the animals and their environment is urgently needed.

Wildlife tourism: a tool for conservation?

There is an increased willingness among many people to protect wildlife and its associated habitats, and this has led to the development of a wildlife tourism that aims to preserve the natural environment, including its flora and fauna (Shackley 1996). It has been proposed that wildlife tourism might be beneficial for the conservation of endangered animal species, and in particular primate species, by increasing their population numbers, raising public awareness and producing positive economic outcomes (Brightsmith et al. 2008, Ballantyne et al. 2009, Russon and Wallis 2014). One of the most famous examples of wildlife tourism that is considered to be successful in this respect is mountain gorilla (*Gorilla beringei beringei)* tourism, first developed in 1979; this has been credited with contributing to the mountain gorilla population growing from 252-285 individuals in 1978 to 864 animals in 2010 (Gray et al. 2011). In addition, the local communities around tourism sites appear to have a more positive attitude towards mountain gorillas and their conservation than before such tourism, and have enjoyed some economic benefits from this activity (Blomley et al. 2010). Another study in British Columbia suggested that by their presence, tourists were displacing male brown bears (*Ursus arctos*), enhancing feeding opportunities for subordinate individuals such as females and their offspring, potentially increasing their chances of survival, and ultimately potentially increasing bear population size (Nevin and Gilbert 2005).

However, despite the potential contribution of tourism to the conservation of endangered species, concerns have also been raised regarding the potential negative impacts of wildlife tourism on the welfare of the animals involved (Maréchal et al. 2011, Sapolsky 2014, Muehlenbein and Wallis 2014). For example, a recent study of wild western lowland gorillas (*Gorilla gorilla gorilla*) found that close proximity with tourists was associated with higher physiological stress levels (Shutt et al. 2014), while another study of the same species found that close tourist proximity was related to higher rates of human-directed aggression, an increase in human-directed monitoring, and a decrease in feeding rates, which was suggested potentially to have an impact on health (Klailova et al. 2010). Tourism might also affect wildlife in other ways, including providing unbalanced nutrition via provisioning (e.g. nesting birds: Plummer et al. 2013a), causing stress (e.g. European pine marten, *Martes martes*: Barja et al. 2007; yellow-eyed penguin, *Megadyptes antipodes*: Ellenberg et al. 2007), increasing risks of disease transmission (Mulhenbein and Wallis 2014), and leading to degradation of habitat (Russon and Wallis 2014). In order to limit such negative impacts, regulations have been produced and implemented for watching and swimming with whale-sharks (*Rhincodon typus*) in Australia (CALM 2003, 2004, 2005), for whale/dolphin watching in Canada and around the world (Lien 2001, Carlson 2008), and for great ape tourism (Macfie and Williamson 2010), although these regulations are often transgressed (Scarpaci et al. 2003, Catlin and Jones 2010, Goldsmith 2014). No such guidelines are available for other primate species, even though primate tourism is dramatically increasing in locations where they are found (Russon and Wallis 2014).

Overall, wildlife tourism might produce significant conservation benefits, if the costs in terms of animal welfare are minimised, and any negative impacts are counter-balanced by benefits at the population level (Russon and Wallis 2014). Therefore, understanding and quantifying the impacts of tourism on the welfare of the animals involved is crucial for the establishment of sustainable wildlife tourism, which can in turn realise the potential benefits for the conservation of species.

A multidisciplinary approach: considering standpoints of both tourist and wildlife

Recently, there has been an increased interest in the multiple interactions of human and wildlife; in particular the study of the complex and diverse links between human and non-human primates has led to the emergence of the field of ethnoprimatology (Sponsel 1997, Wheatley 1999, Fuentes and Wolfe 2002). In this research field, humans are viewed as a full part of the environment within which primates live and evolve (Fuentes and Wolfe 2002, Fuentes 2010). Humans and primates co-exist within overlapping ecological niches, and co-influence the behaviour and health of each other by their regular interactions, which in turn may have an impact on each species' evolution (Fuentes and Hocking 2010, Fuentes 2010). Therefore, ethnoprimatological approaches may contribute to understanding of human and primate behaviour, and their co-evolution (Fuentes and Hocking 2010).

Ethnoprimatology may also provide a powerful tool for conservation, as it adopts a multidisciplinary approach to increase understanding of human and primate interconnections within the ecosystem they co-share (Fuentes and Wolfe 2002). Considering elements of human culture and ecology alongside primate behaviour, health and ecology could be an important step in developing effective conservation action (Fuentes and Wolfe 2002).

In the context of wildlife tourism, tourists and wildlife are the main components of this co-shared ecosystem. A conceptual framework of tourist-wildlife relationships has been created which highlights the importance of understanding both the tourist experience and the impacts of such tourism on animal welfare (Reynolds and

Braithwaite 2001). Therefore, consideration of wildlife tourists' perceptions, motivations and experiences, as well as exploration of their impacts on the animals involved, are key to understanding such interconnections.

1.2 Perspectives of tourists involved in wildlife tourism

Amongst the different human stakeholders in wildlife tourism, tourists as customers are key to this activity (Reynolds and Braithwaite 2001). Nevertheless, little research has been conducted on these tourists, for example to understand their motivations, their perceptions and their experiences (Reynolds and Braithwaite 2001). If wildlife tourism is to be beneficial for the other groups of people involved in this activity (e.g. the local community, business agencies, and potential conservation management), the tourist experience must be satisfactory, and for this to be achieved it is important to understand tourists' perceptions and motivations for engaging in their chosen activity (Reynolds and Braithwaite 2001).

Tourist perceptions of wildlife

Franklin (1999) suggested that humans' view of wildlife is mainly determined by their cultural and social environment. As the majority of wildlife tourism involves tourists from western countries, it was proposed by Curtin (2009) that a romantic perception of nature by western people may have led to the development of wildlife tourism, and more recently ecotourism. In fact, a number of people have proposed that urbanisation and lack of contact with the natural environment often build a romantic and pure idea of nature in our imagination (Urry 1990, Curtin 2005). Moreover, developments in technology and control over the environment in western countries are believed to have modified our representation of nature from dangerous and pestilent, to a fragile equilibrium that humans have the responsibility to protect (Urry 1990). Hence, it is thought that typical wildlife tourists (those who travel intentionally to see wildlife) can be viewed as western, educated, and urbanised, with a romantic representation of wildlife (Curtin 2009).

This characteristic socio-cultural background of wildlife tourists may underpin their representation of what a wild animal should be, and their attraction to particular charismatic species. Some animal species are more readily sought after by tourists than others, and this distinction was suggested to be generally based on size, beauty, charisma, accessibility and likeness to humans (Benefield et al. 1986, Curtin 2005). Primates have been shown to be particularly attractive for tourists, presumably because of their morphological and behavioural similarities to humans (Newsome et al. 2005, Russon and Wallis 2014). Furthermore, some studies have reported that humans refer to primates in terms associated with children, suggesting that humans have an emotional attraction regarding these animals (Russell 1995, Knight 2011). For example, Earthwatch tourists visiting rehabilitated orang-utans in Borneo aimed to interact with them by exchanging affective physical contact, and talked about them in terms associated with children (Russell 1995). In Costa Rica, the majority of tourists who encountered monkeys described them as cute, friendly, entertaining and interesting (Kauffman 2014). This attraction leads many tourists to interact physically with primates, which commonly involves feeding them (Kauffman 2014).

The motivations/expectations of wildlife tourists

Tourist motivations for engaging in wildlife tourism have been recognised by a number of researchers as being among the main factors influencing tourist experience (Beaumont 1998, Muloin 1998, Reynolds and Braithwaite 2001). When tourists are asked to describe how they feel about their wildlife encounter experience and the psychological benefits from it, the main themes that emerge are wonderment, awe, authenticity and well-being (Curtin 2005, 2009). Curtin (2009) suggested that these feelings may have positive effects on tourists' psychological and physical health. Experience with wildlife may therefore fulfil these needs. However, when tourists come with a deeply romantic vision of wildlife and these expectations are not met, the shock and disappointment of reality might have negative impacts on their experience (Fredline and Faulkner 2001, Higginbottom et al. 2006). It is thought that such disappointment may come from a lack of authenticity and uniqueness, resulting from the number of tourists who live the same experience at the same time, and the unpredictability or the brevity of the encounter (Schanzel and McIntosh 2000, Curtin 2006, 2010). The expectation of authenticity, privilege, wonderment and a feeling of well-being, which are an integral part of wildlife tourism encounters, would consequently not be achieved. Managing these expectations therefore has an important effect on tourist experience, and this is directly related to the type of interactions tourists may have with wildlife. In the case of incidental tourists, their motivations and expectations toward wildlife are generally unclear and poorly studied (Grossberg et al. 2003), and therefore it is difficult to understand how these shape their experience when encountering wildlife.

The experience: Interacting with wildlife

In non-consumptive tourism, there are different ways to interact with wildlife, ranging from long-distance observation to physical contact. I describe below the four main components of non-consumptive tourists' experience with wildlife; these are not mutually exclusive.

Seeing, looking at, watching and observing: ways of 'seeing' animals

Wildlife tourism is based on the concept of seeing wild animals in their natural environment. However, there are different ways of 'seeing' animals, such as seeing, looking at, watching and observing (Marvin 2005). Visual encounters with animals might be defined by these four visual terms, which each represent a distinctive experience (Marvin 2005). For instance, seeing an animal is "registering the fact that the animal is present and visible" (Marvin 2005, p.4), while looking is defined as purposely directing the eyes toward an animal, which involves the action of looking as opposed to the involuntary event of seeing. Watching is a term employed when the viewing is attentive and a longer time is devoted to this action. Finally observing is associated with "concentrated, attentive, viewing guided by a particular interest." (Marvin 2005, p.5).

Overall, these terms reflect the fact that different tourists' experience in relation to wildlife might be highly variable. An example is provided by the "ready-to-view" wildlife tourism that occurs in monkey parks in Japan (Knight 2010). Tourists involved in such tourism might see or look at Japanese macaques (*Macaca fuscata*), but close interactions with them and the short time devoted to the visits do not actually allow them to watch or observe these animals. Similar examples are found with Komodo dragon (*Varanus komodoensis*) tourism (Walpole 2001), or with tourism related to large carnivores in Africa (Goodwin and Leader-Williams 2000); in both settings, animals are lured with food into particular locations to facilitate their 'quick' viewing. By contrast, tourists spend up to one hour with a group of mountain gorillas (Goldsmith 2014) or during other safari-like observations in Africa (Trapper 2006), which enables them to watch and observe these animals from a distance in their natural setting, shaping a very different tourist experience.

Taking pictures

Photography is an important part of the tourist experience, with photographs representing a souvenir or a trophy to bring back home (Russell and Ankenman 1996). Many tourists appear to be satisfied with their experience only when they have the opportunity to take a picture. Russell and Ankenman (1996, p.73) reported a tourist remarking after taking a series of pictures of orang-utans (*Pongo pygmaeus*), "Now I can go home happy", suggesting that the goal of her trip was to photograph an orang-utan. Lemelin (2006) suggested a similar idea about the importance of photography for polar bear (*Ursus maritimus*) Arctic tourism. Russell and Ankenman (1996) also suggested that the memory of the trip was biased by the intention of the tourists to photograph their own perception of their tourist experience. For instance, the authors described that some tourists viewed orang-utans as like children, and therefore they would take pictures of themselves carrying a young orang-utan in their arms, or feeding them. Other tourists would view these primates as wild animals living in pristine nature, unviolated by human presence. For these tourists, the ultimate photograph would be an orang-utan in the forest, isolated from human presence (Russell and Ankenman 1996). Similar suggestions were proposed by Lemelin and Wiersma (2007, p.37); on polar bear Arctic tourism, "photographs were viewed as trophies, as a way to stimulate memories, and as detraction from the experience". Photographs can therefore be considered by tourists as a souvenir of their own interpretation of their experience with wildlife.

Aggression/conflict

A few studies have reported aggressive behaviour by tourists towards wildlife (Newsome et al. 2004, 2005), with the majority of cases involving different macaque species (Tibetan macaques, *Macaca Thibetana*: Zhao 2005; Formosan macaques, *Macaca cyclopis*: Hsu et al. 2009; long-tailed macaques, *Macaca fascicularis*: Sha et al. 2009; Barbary macaques, *Macaca sylvanus*: Maréchal et al. 2011). Aggression by tourists may occur for different reasons such as self-defence, or play (Zhao 2005), and the aggression may be intentional or non-intentional. For instance, in Morocco, it is relatively common to observe people throwing objects, branches or snowballs at Barbary macaques, chasing them, threatening them with aggressive gestures, sometimes without realising that the gesture may be perceived as aggressive by the animal (personal observation). In Mt. Emei Monkey Park in China, 26 Tibetan macaques were killed or injured between April 1986 and December 1987 by locals and visitors, for sport or out of self-defence (Zhao and

Deng 1992), and four of these animals died after conflicts with humans related to feeding interactions. In Morocco, aggression between tourists and adult male macaques has been linked to an increase in anxiety and physiological stress levels in these animals (Maréchal et al. 2011), indicating that aggression by tourists is of concern for the welfare of the animals involved. To prevent such aggressive behaviour, regulations have been specified in some parks, for example in Japan (Knight 2011), on how tourists should behave to avoid such interactions occurring; nevertheless aggression towards wildlife still occurs commonly, in particular during feeding interactions (Sha et al. 2009).

Feeding wildlife

Feeding of animals is common practice in wildlife tourism (Orams 2002), and this particular type of interaction potentially has a considerable impact on the whole tourist experience, for example shaping tourists' perception of wildlife and their expectations, as well as strongly affecting the other types of interactions described above. Provisioning might alter tourists' view of being in wilderness, an important component of much wildlife tourism; for example, the display of Japanese macaques, lured to an open feeding station by food supplementation, might be viewed as a mega-zoo, where animals are not wild any more but rather conditioned and controlled by humans (Knight 2006). However, by provisioning these macaques, the management tries to ensure their daily presence in the park; this is important for the tourists, who expect to see and interact closely with monkeys. This proximity may in turn enable tourists to take pictures while directly interacting with these animals, embodying themselves as part of the experience captured by the photograph (Russell and Ankenman 1996). A similar example of feeding interactions with tourists can be found with wild marine mammal tourism, where tourists have the possibility of swimming and interacting with sharks (Clua et al. 2011).

Feeding wildlife can be problematic, and it is often prohibited, because it may have serious consequences for both humans and animals. The risk of being attacked by an animal is one of the most common issues associated with feeding wildlife (e.g. grizzly bear, *Ursus arctos ssp*: Clarke 1990, bottlenose dolphin, *Tursiops truncatus*: Orams et al. 1996, large mammals in South Africa: Durrheim and Leggat 1999). For example, feeding interactions with macaques were reported often to result in threats from animals to tourists, with injuries resulting from animal subsequent attacks (Tibetan macaques: McCarthy et al. 2009; Formosan macaques: Hsu et al. 2009; long-tailed macaques: Sha et al. 2009). Nevertheless, people seem to be highly motivated to interact physically with wildlife and, despite the associated risks and regulations prohibiting it, people often engage in such behaviour, which suggests there are compelling reasons for people to seek such close interactions.

Overall, feeding interactions can significantly shape wildlife tourists' perspectives. Understanding how tourists perceive such interactions, and their motivations for engaging in feeding of wildlife, may help us to understand the tourist experience; this information in turn may be used to facilitate the development of wildlife tourism which fulfils the needs of tourists, while minimising the impacts on the animals involved.

1.3 Wildlife tourism from the animals' standpoint

If wildlife tourism is to be used as a tool for conservation, it is crucial to understand the impacts of such tourism on the animals involved (Russon and Wallis 2014). There are two main elements of animal welfare which could be affected by tourists in the short and long-term: behaviour and health. A number of studies have considered changes in animal behaviour in response to tourist disturbance as an *indicator* of animal welfare, interpreting the occurrence or magnitude of changes in behaviour as being indicative of the intensity of the human disturbance (Burger 1981, Klein et al. 1995, Blumstein 2014). Other studies have suggested that changes in behaviour may *cause* a reduction in welfare; for example decreasing feeding time associated with tourist disturbance may lead to decreased energy intake, which may ultimately affect the health of animals (Lott and McCoy 1995, de la Torre et al. 2000, Constantine et al. 2004). These interpretations of changes in behaviour - as indicators or causes of welfare reduction - are not mutually exclusive.

Overall, impacts on either or both of behaviour and health might have important consequences for animal population dynamics, and therefore have implications for the species' conservation (Figure 1-3). Understanding animals' behavioural responses to tourists, and also tourist impacts on their health, are therefore important for effective conservation management, and for the development of environmentally responsible and ethically acceptable wildlife tourism.

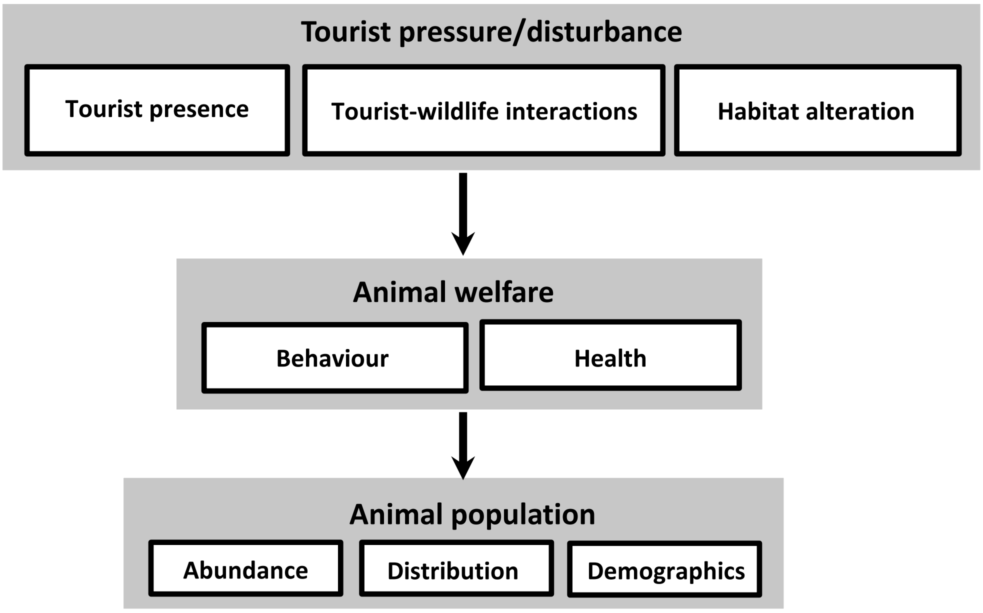


Figure 1-3: Potential effects of tourists on wildlife.

Behavioural responses to tourists

The impacts of tourists on animals are generally assessed in terms of changes in behaviour. Animals exhibit different behavioural responses when exposed to humans, and these can be classified into three general categories: avoidance, habituation and attraction (Whittaker and Knight 1998; Figure 1-4).

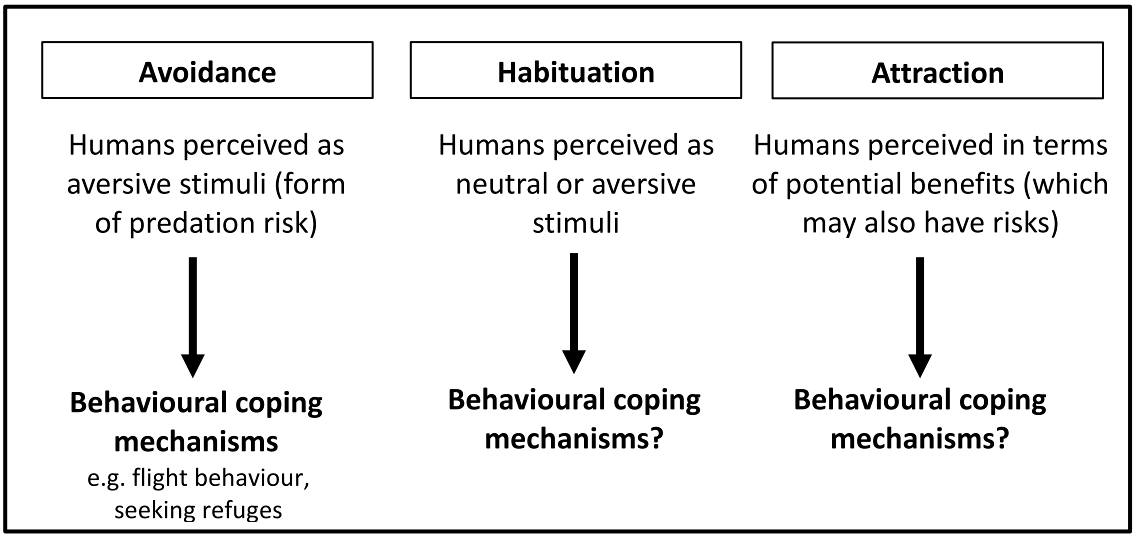


Figure 1-4: Wildlife responses to human disturbance, adapted from Whittaker and Knight (1998), Frid and Dill (2002), and Gill et al. (2001).

Avoidance is defined by Knight and Cole (1991) as an aversion to negative consequences associated with a stimulus, meaning that animals tend to cope with such stimuli by distancing themselves from them. Recently it has been proposed that human disturbance such as tourism might be perceived and responded to by animals in a similar way to predation risk; their behavioural response may reflect a trade-off between the costs associated with the perceived risk, and the benefits or necessity of other activities such as feeding (Frid and Dill 2002). It is generally thought that marked changes in animals' behaviour, such as the occurrence of avoidance behaviour, might reflect the intensity of human disturbance, and therefore might be used to measure whether humans have negative impacts on wildlife (Burger 1981, Klein et al. 1995, Blumstein 2014). However, Gill et al. (2001) suggested that a lack of avoidance behaviour does not necessarily reflect the fact that animals are unaffected by human presence, and animals might still be stressed by such presence. In this case, the animal might be exposed to a prolonged stress by not fleeing in the presence of humans, and a prolonged stress exposure may have high costs in term of reduced fitness (Sapolsky et al. 2000). When animals do not flee from the presence of humans, this might also reflect habituation or even attraction.

Habituation is defined by Bejder et al. (2009) as a waning of response to a repeated stimulation which is not followed by any kind of reinforcement. Another definition by Rankin et al. (2009) suggests that habituation may also be achieved when animals are repeatedly exposed to stressful stimuli. In this case, animals might be less affected by, or learn to cope with, the aversive stimuli (Rankin et al. 2009).

Therefore, habituation to humans does not imply that animals do not respond to human disturbance at all, or even that they do not avoid such disturbance, but rather that animals modulate their behavioural responses by reducing the intensity of such responses, or by using different behavioural responses (Gill et al. 2001, Higham and Shelton 2011). For example, animals might reduce their flight distance when humans approach if they have become habituated to human presence (e.g. Alpine and the Red-billed choughs, *Pyrrhocorax graculus and P. pyrrhocorax*: Jiménez et al. 2011; capuchins, *Cebus libidinosus*: Sabbatini et al. 2006).

Finally, attraction is defined by Knight and Cole (1991) as the strengthening of an animal's behaviour because of positive reinforcement which is generally linked with food, and this implies that the animals move toward the stimulus. In the case of wildlife tourism, this generally corresponds to humans feeding animals to attract them into close proximity, and in order to interact with them. Despite their attraction to humans in relation to food, animals might still perceive humans offering food as posing a potential risk, and therefore tourists might present a conflicting motivational situation. In fact, a number of studies have reported occurrences of aggression by tourists to animals, and such aggression often occurs during feeding interactions, as seen for example in Tibetan macaques (Zhao 2005) and Barbary macaques (Maréchal et al. 2011). Therefore animals might respond to humans using a range of coping mechanisms, which may include avoidance behaviour.

Overall, animals might respond in different ways to human disturbance, ranging from avoiding people to being attracted to them. In situations where animals are attracted to humans because of the food they receive, different behavioural responses, e.g. avoidance, habituation or attraction, may not be mutually exclusive. Understanding how animals cope behaviourally with tourists may help us to understand how tourists are perceived by animals, and how animals cope with such conflicting motivational situations.

Assessing behavioural responses to tourists

Tourists might affect animals' behaviour simply by being present, by interacting with them or by altering their habitat (Figure 1-3). Provisioning, which is often associated with wildlife tourism, may have important impacts on behaviour, with associated behavioural changes reflecting the use of behavioural coping mechanisms (Wilson 1972, Maestripieri et al. 1992, Sachser et al. 1998).

Short-term effects of tourist pressure might influence animals' activity budgets. Most studies in this area have explored how animals allocate time during tourist presence to different activities, including feeding/foraging, resting, moving, vigilance and social behaviour (Lott and McCoy 1995, de la Torre et al. 2000, Constantine et al. 2004). The activity budget of animals is mostly governed by the trade-off between feeding and predator avoidance (Reynolds and Braithwaite 2001, Frid and Dill 2002). Since tourists can be perceived as both a food source (Orams 2002) and a potential predator (Frid and Dill 2002), they may markedly alter the activity budgets of wild animals and induce avoidance behaviour. For example, provisioning wildlife may reduce animals' feeding and foraging efforts, while increasing their periods of resting and/or their vigilance (Fa 1986, Majolo et al. 2013). Avoidance behaviour is a basic coping mechanism to deal with aversive stimuli (Stankowich and Blumstein 2005), and animals do appear to use such behaviours to cope with tourists. For example, black howler monkeys were found to be more likely to move away when more tourists were present (Treves and Brandon 2005), and marmosets were seen to reduce the use of the lower forest strata when tourists were present in the area (de la Torre et al. 2000), suggesting that these animals used active avoidance mechanisms, which might in turn reduce their feeding opportunities. Examples of avoidance behaviour and change in activity budget associated with tourist density were also found in other animal species, such as bottlenose dolphins (Constantine et al. 2004), and Asian rhinoceros (*Rhinoceros unicornis:* Lott and McCoy 1995), and it was suggested that a prolonged decrease in resting or feeding might have negative effects on the energy balance of the animals involved, and ultimately on their health.

Tourists might also have short-term effects on animals' social behaviour, including affiliative, agonistic, play and mating behaviour. A number of studies have reported an increase in the rates of conspecific aggression associated with tourists, especially during provisioning (Reynolds and Braithwaite 2001, Hsu et al. 2009, Majolo et al. 2013). Aggressive interactions can have serious consequences, such as increased stress, disease transmission, injuries or even death (Reynolds and Braithwaite 2001, Zhao 2005). Only a few studies have explored the effects of tourists on positive social behaviour such as play, affiliative behaviour or mating. For example, pygmy marmosets (*Callithrix pygmaea*) showed a reduction in social play when in the presence of tourists (de la Torre et al. 2000), while male Barbary macaques showed a decrease in grooming frequency when tourists were in close proximity (Majolo et al. 2013). In addition, tourist pressure may also affect mating or parenting behaviour; for example disturbing turtle nesting behaviour (Jacobson 1994), or flushing parent birds from the nest, reducing offspring's chance of survival (Klein et al. 1995). Although many studies have reported negative impacts of tourists on animals' social behaviour, to my knowledge, no study has reported positive or no impacts, nor have any tested directly whether social behaviour may be used as a coping mechanism to cope with such disturbance.

Finally, tourists might also affect other types of behaviour, such as displacement activities, which are defined as behaviours with a lack of apparent relevance to the context in which they occur (Tinbergen 1952, Anselme 2008). These activities have been suggested to reflect the emotional state of an animal, such as frustration, uncertainty or anxiety (Tinbergen 1952, McFarland 1966, Maestripieri et al. 1992), and it has also been suggested that these behaviours might be used as coping mechanisms to deal with aversive stimuli (Koolhaas et al. 2007). Since tourists might be perceived as potential stressors, studies have investigated the impacts of tourists on the expression of displacement behaviours by animals, in order to evaluate their welfare (Wiepkema 1983, Maréchal et al. 2011). A number of studies reported that in the presence of tourists, animals showed increased rates of displacement activities. For example, Royal penguins (*Eudyptes schlegeli*) performed more bill-shaking during and following tourist approaches (Holmes et al.

2005), and mountain gorillas were observed to have higher self-scratching rates during tourist visits than when no tourists were present (Muyambi 2005).

Assessing whether such behavioural responses may represent mechanisms to cope with tourists may help us to better understand the interactions and relationships between tourists and wildlife. Since behavioural changes in relation to tourist disturbance might have an impact on the health of animals, it is important to understand if and how tourists affect the behaviour of the animals they see.

Impacts of wildlife tourists on the health and survival of the animals involved

Good health is vital for animals' survival, and to help them cope with the challenges of the environment. Animals' health varies mostly because of environmental factors, such as climatic variation, predation and food availability. Tourists as an environmental factor may present both risks to, and benefits for, the health of animals. The effects of wildlife tourism on the survival and health of animals visited can be considered in terms of surveillance/protection, stress, disease transmission, and nutrition/provisioning.

Surveillance/protection

Tourists may provide some survival benefits to wild animals, by serving as protection against predators. A recent study found that human observers (researchers) were apparently used by samango monkeys (*Cercopithecus mitis erythrarcus*) as a 'shield' against predators such as leopards (Nowak et al. 2014). On the other hand, tourists may increase the concentration of predators within an area because of feeding opportunities. For example, it was found that bird nest-predation increased in tourist destinations in northern Finland, with this being related to the higher density of corvids present in these locations (Lepczyk and Warren 2012).

The presence of tourists might also increase the level of surveillance against poachers, and other forms of human disturbance such as illegal habitat degradation (Macfie and Williamson 2010). For example, the density of snares and the number of poachers' tracks were lower in areas frequented by either researchers or tourists in the Virunga Volcanoes region, reducing the risks of mountain gorillas being injured or killed (McNeilage 1996). However, it has also been argued that wildlife tourism, which is generally associated with habituation to human presence, would reduce gorillas' avoidance behaviour when in the presence of humans, and therefore might facilitate poaching (Macfie and Williamson 2010). Indeed, it was found that many habituated gorillas were killed during periods of instability in Kahuzi-Biega National Park (Yamagiwa 1999), and in Virunga National Park (Kalpers et al. 2003).

Stress

One of the main concerns regarding the well-being of tourist-exposed wild animals is stress. Frequent exposure to tourists and other human disturbances may be perceived as stressful by animals, which might lead to the chronic activation of physiological stress responses (Muehlenbein et al. 2012, Russon and Wallis 2014). When the physiological stress levels of an animal are chronically high, this can produce pathological effects, impairing, for example, reproduction and the immune system, which can consequently reduce chances of survival (Sapolsky et al. 2000, Romero and Wikelski 2001). A number of studies have found that exposure to tourism leads to elevated physiological stress levels. For example, Barja et al. (2007) found that the physiological stress levels of European pine marten were positively related to the daily number of tourists. Similar results have been found in yellow-eyed penguin (Ellenberg et al. 2007) and hoatzin chicks (*Opisthocomus hoazin*: Müllner et al. 2004), suggesting that large tourist numbers may represent a stressor that stimulates cortisol production. Recently, however, a study on wild male Barbary macaques found that none of the different measures of tourist number considered, such as mean number present per day or maximum number of tourists per day, was associated with physiological stress levels (Maréchal et al. 2011). In addition, in other studies, although human presence was associated with an increase in physiological stress levels, it was found that animals habituated to human presence had a smaller increase in physiological stress levels when in the presence of tourists than did non-habituated animals (Magellanic penguins, *Spheniscus magellanicus*: Fowler 1999; orangutans: Muehlenbein et al. 2012; western lowland gorillas: Shutt et al. 2014). These results suggest that the relationships between animals' physiological stress levels and tourism may be influenced and mediated by a number of factors, and to date, little research has been conducted which attempts to understand such effects.

Disease transmission

Introducing diseases from humans is considered one of the most serious risks to the survival of wild animals, and in particular for primates, because their behavioural and physical similarity to humans makes them particularly vulnerable to human-primate disease transmission (Macfie and Williamson 2010, Muehlenbein and Wallis 2014). A number of disease outbreaks reported in wild animals have been suggested to be related to human-animal transmission (Goodall 1986, Nizeyi et al. 2001, Hill et al. 2001, Graczyk et al. 2002), although only a few studies have been able to confirm the occurrence of such transmission (e.g. Salzer et al. 2007, Goldberg et al. 2007, Rwego et al. 2008). Tourists are a particular concern in this respect because of their own exposure to pathogens while travelling from one location to another, the risk they pose in terms of exposing animals to novel pathogens, and their poor knowledge, attitudes and practices in relation to their own health (Muehlenbein and Wallis 2014). For example, a study at Sepilok Orang-utan Rehabilitation Centre in Sabahfound that 15% of tourists who visited the centre presented at least one disease symptom such as a cough, sore throat, congestion, fever or diarrhoea (Muehlenbein et al. 2010), and only half of the tourists reported having been vaccinated for at least one of common diseases such as tuberculosis, hepatitis A and B, polio, and measles (Muehlenbein et al. 2008). Despite serious concerns about the risks of tourist-animal disease transmission, to date there is no confirmed case of such transmission, perhaps because it is nearly impossible to trace the exact source of infection (Muehlenbein and Wallis 2014).

However, monitoring disease symptoms in both tourists and animals might help to better understand the risks and occurrence of tourist-animal disease transmission.

<u>*Nutrition/provisioning*</u>

Feeding of animals is often associated with wildlife tourism, and food may be provided by park staff, or by tourists themselves (Russon and Wallis 2014). Provisioning may be used to lure animals for display to tourists (Knight 2011) or to improve the health of the animals (López-Bao et al. 2010, Hilgartner et al. 2014). Therefore provisioning may present both risks and benefits for the health of wild animals.

A number of studies have found that provisioning can increase population numbers by increasing the number of offspring produced (Persson 2005, Kennedy et al. 2008, Robb et al. 2008), and also their chance of survival (Fa 1984). For example, in Japanese macaques, provisioning has been found to shorten inter-birth intervals and increase infant survival, thus increasing reproductive success (Garcia et al. 2011, Kurita 2014). Attempting to increase animal populations by increasing the chances of survival and reproduction is the reason why a number of conservation projects, outside of the context of tourism, use provisioning. This technique has been adopted, for example, with endangered species such as the kakapo (*Strigops habroptilus:* Clout et al. 2002), the Spanish Imperial eagle (*Aquila adalberti:* Blanco et al. 2011), and the European white stork (*Ciconia ciconia*: Hilgartner et al. 2014). However, provisioning – particularly that related to tourism – may have negative effects on the health of animals. Provisioning can provide too much high-energy food, leading to diet-related disease such as diabetes or cardiovascular diseases (Ginsberg 2000, Sapolsky 2014), or it could provide contaminated food, which can have detrimental effects on gastro-intestinal health (Blanco et al. 2011). An increase in reproduction, and therefore population size, associated with provisioning may also create conflicts with the local human community in relation to crop and/or town raiding (Japanese macaques: Knight 2011, Kurita 2014; Barbary macaques: Perez and Bensusan 2005), and cause damage to the habitat (Knight 2011).

Provisioning may also have indirect impacts on other health-related factors described above, such as stress and disease transmission, making it a key factor to understand when considering the impacts of tourists on the health of animals. For example, aggression between conspecifics has been found to be higher in provisioned populations of a number of primate species (Japanese and rhesus macaques, *Macaca mulatta*: Hill 1999; male Barbary macaques: Majolo et al. 2013), and aggression has been positively related to physiological stress levels (Honess and Marin 2006). In addition disease transmission is thought to be more likely when physical contact between humans and animals occurs, as often happens during feeding interactions, as a result of an increased risk of exchanging contaminated fluids, blood or waste matter (Honess et al. 2006).

Overall, wildlife tourists may positively or negatively affect the wild animals they have come to see; these effects may have important consequences at the population level and therefore for the conservation of a species. Exploring the impacts of provisioning may be particularly important for understanding the impacts of tourists on the health of wild animals.

Assessing the health of wild animals

A number of studies have attempted to assess how exposure to tourists affects animals' health (Maréchal et al. 2011, Muehlenbein et al. 2012, Knapp et al. 2013). Such effects have mainly been evaluated by looking at fitness-related measures such as survival and reproduction (Berman and Li 2002, Kurita 2014), while a few studies have assessed measures of physical health such as body condition (Jolly 2009, Knapp et al. 2013, Borg et al. 2014). Considering both fitness-related and physical health measures simultaneously may help to provide a better understanding of whether and how tourists affect the health of wildlife.

Indicators of fitness

The measures of fitness of an animal may be used as an indirect indicator of general health, and can be assessed through measures such as survival, reproductive success, inter-birth interval and infant survival.

Exposure to tourism could affect the fitness of an animal in a number of different ways. Tourists might have negative effects on fitness by decreasing animals' chances of survival (e.g. as a result of facilitating poaching, or due to vehicle collisions). Tourists might decrease breeding success by increasing animals' stress levels (Fa 1984) or through poor food quality supplementation (Plummer et al

2013a). On the other hand, they might indirectly increase animals' survival by reducing predation (Coleman and Hill 2014) or by increasing their energy intake through provisioning, which can shorten inter-birth intervals and increase infant survival (Kurita 2014). Overall, the results from these different studies indicate that the effects of tourists on the fitness of animals may vary, and since conservation of endangered species depends to a great extent on individual animals' fitness, understanding these effects is important.

Indicators of body condition

Body condition provides a measure of the recent and current health status of an individual (Stevenson and Wood 2006). However optimal body condition is often unknown, and this is particularly true for wild animals. Recently a number of non-invasive methods have been developed and used to assess animals' body condition, mostly in laboratory, farm and captive animals (Honess et al. 2005, Pritchard et al. 2005, Deschner et al. 2008, Khan et al. 2012); these methods might provide useful tools for assessing the health of wild animals (Jolly 2009, Kersey and Dehnhard 2014). For example, body condition may be evaluated via visual assessment of physical features such as body size (Borg et al. 2014), coat condition (Jolly 2009, Borg et al. 2014), injuries (Westin 2007), and via biological sample collection to assess parameters such as parasite load and diversity (Goldberg et al. 2007, Rwego et al. 2008) and hormone levels (Kemnitz et al. 2002, Maréchal et al. 2011, Muehlenbein et al. 2012, Shutt et al. 2014).

A number of studies, using a range of different measures of body condition, have documented negative effects in animals exposed to tourism. For example, higher physiological stress levels in the presence of tourists were found in orang-utans (Muehlenbein et al. 2012) and western lowland gorillas (Shutt et al. 2014), poor coat quality associated with exposure to tourism has been documented in ring-tailed lemurs (*Lemur catta* : Jolly 2009) and Barbary macaques (Borg et al. 2014), and higher glucose, potassium and uric acid levels were seen in provisioned compared to non-provisioned northern Bahamian rock iguanas (*Cyclura cychlura:* Knapp et al. 2013); these studies all suggest that tourists might negatively affect the body condition of these animals. Only a few studies have investigated the impacts of provisioning, linked to tourists directly or indirectly, on body condition (Altmann et al. 1993, Kemnitz et al. 2002, Knapp et al. 2013, Borg et al. 2014). To my knowledge, none have explored the impacts of tourist provisioning on the energy balance of animals; such impacts could be measured using recently developed techniques for assessing energy balance, such as the measurement of urinary C-peptide levels (Kruszynska 1987, Sherry and Ellison 2007).

In general, it is difficult to determine the causal relationships between tourists and these measures of health, not least because effects might only be seen in the long-term (Knapp et al. 2013). This might explain why little research has been conducted to determine the effects of tourists on wild animals’ body condition.

1.4 Research aims of the thesis

Despite a growing interest in the use of wildlife tourism as a tool for conservation (Brightsmith et al. 2008, Ballantyne et al. 2009), particularly for primates (Russon and Wallis 2014), tourists' expectations and motivations for engaging in such an activity, and the nature of their actual experience, as well as the impacts of tourism on the animals involved, are still poorly understood. An understanding of wildlife tourism from the standpoints of both the tourists and animals is important for facilitating the development of a tourism 'product' which adequately meets the diverse needs of tourists, while reducing or eliminating negative impacts on the animals and ultimately contributing to their conservation. In particular, provisioning may be one of the principal activities, which might strongly influence both tourist experience and animal welfare. Understanding both tourist and animal standpoints regarding provisioning may inform decisions about what level of provisioning may be acceptable, or indeed optimal (in terms of balancing the desires of tourists and costs and/or benefits to animals), in turn facilitating development of an improved wildlife tourism product and addressing key conservation goals.

To date, only a very few studies have investigated wildlife tourism using a multidisciplinary approach to understand the complex relationships between tourism activity and the animals (Sandbrook 2007, Fuentes 2010, Kauffman 2014). Our knowledge is limited to the study of just a few tourist sites, and the tourists' perspectives in each of these studies were not studied in depth using the ethnographic methods that are needed to gain real insights into their motivations and experience. In the present study, I aim to explore key issues related to primate tourism in Morocco, by looking at the standpoints of both tourists and animals.

Seeing and interacting with wild Barbary macaques in Morocco

The present study was conducted at a tourist site located in Ifrane National Park, where the one of the largest remaining populations of wild Barbary macaques lives (van Lavieren and Wich 2010). Primate tourism in Morocco is a relatively recent, rapidly growing and unregulated activity (Maréchal et al. 2011, Majolo et al. 2013), and little is known about the tourists or their impacts on the Barbary macaques involved. Recently, concerns have been raised regarding the negative effects of such tourism on the welfare of these animals (Maréchal et al. 2011, Majolo et al. 2013, Borg et al. 2014). As interest grows in developing the tourism potential of Barbary macaques as a tool for the conservation of this endangered species and its habitat, studies investigating the impacts of such tourism are urgently needed (Barbary macaques Action Plan 2011). The majority of tourists at this site stop there opportunistically, for only a few minutes to a few hours, on the way to other destinations. They generally feed the macaques and take some pictures, and then leave. Little research has been conducted on such incidental wildlife tourism (Grossberg et al. 2003, Maréchal et al. 2011, Majolo et al. 2013). However, as wild primates have become increasingly habituated to people, and as humans have encroached further into primates' habitats, these incidental encounters are becoming more common (Fuentes 2010). The site for the current study therefore provides an opportunity to investigate tourists' experience and motivations in this setting.

Research aims

The general goal of my study is to investigate the nature of primate tourism at the field site in Morocco, using a multidisciplinary approach. In order to meet this goal, I address four explicit and complementary research aims:

Research aim 1: To explore tourists' motivations for, and perceptions of, feeding monkeys, and to investigate how this behaviour shapes their experience (Chapter 3).

Research aim 2: To investigate if and how wild Barbary macaques use behavioural coping mechanisms to cope with tourists (Chapter 4).

Research aim 3: To explore the impacts of tourist provisioning on the health of wild Barbary macaques, using a range of non-invasive health measures (Chapter 5).

Research aim 4: To explore the implications of the findings of this study for wildlife tourism and conservation, including assessing the value and limitations of the multidisciplinary approach adopted in this work (Chapter 6).

Chapter 2

General field and laboratory methods

2.1 Study species

The genus *Macaca* includes a large number of species, between 20 and 23 (Thierry et al. 2004), all but one of which are found in Asia. The Barbary macaque is the exception and the only species of non-human primate living naturally in North Africa (Fooden 2007). Macaques' high ecological and dietary plasticity, their sociality, morphology and frequent coexistence with humans make these species ideal candidates to investigate tourist effects on non-human primates (Barbary macaques: O'Leary and Fa 1993, long-tailed macaques: Fuentes 2006b, Tibetan macaques: Matheson et al. 2007).

2.1.1 Morphology and life history

Barbary macaques are commonly known as the tail-less macaque, although a small tail is still present (Fooden 2007). The species is sexually dimorphic with males weighing 15.3-17.0 kg and standing 55-60 cm tall, whereas females weigh approximately 10.2-11.0 kg and stand 45 cm tall (Fa 1989). Barbary macaques are among the few primate species which experience extreme climatic variation (in Middle Atlas Mountains, temperatures vary from -10°C to +45°C). Winter and summer are considered the harshest seasons because of low food availability, leading to weight loss during these seasons (Young et al. 2012, Ménard 2002). Their fur thickness also varies considerably, being thicker in the winter months and moulted during the spring months (Fooden 2007).

The Barbary macaque is a seasonal breeder (Fooden 2007). In Morocco, the mating season occurs between late September and late December (Young et al 2013). Females show an increase in perineal swelling size during the mating season, which is considered to be a signal of ovulation and is attractive to males (Mohle et al. 2005, Brauch et al. 2007, Young et al. 2013). However, smaller perineal swellings remain throughout the year in some groups, such as tourist provisioned groups that rely on high energy food, as has also been observed in Japanese macaques (Mori et al. 1997). The birth season occurs in spring, between late March and June. Females generally give birth to one infant per year, that they suckle for approximately one year until the next infant is born (Fooden 2007). In this species, males are known for their high levels of male-infant interactions, and newborn infants are used as a social facilitator between males (Paul et al. 1996). Juvenile stage is reached at 1 year old and lasts until 4 years old; females and males reach sexual maturity between 4-5 years of age (Ménard et al. 1985, Deag 1980).

2.1.2 Social structure

Barbary macaques live in multi-male, multi-female groups of 10 to 90 individuals in the wild, but group size can reach up to 200 under provisioned conditions (Ménard 2002, Paul 2006). Females stay in their maternal group, and males generally emigrate to another group when they reach maturity (Fooden 2007). Barbary macaques are considered a tolerant species, grade 3 on a classification ranging from 1 to 4 (Thierry 2000), where species scored 1 are the most despotic (e.g.

Japanese macaques), and 4 are the most tolerant (e.g. Tonkean macaques, Macaca tonkeana). Although a hierarchy among males exists, their interactions seem to be relatively tolerant (Thierry and Aureli 2006). Aggressive escalations are generally prevented by high tolerance between individuals (Thierry 2000). The hierarchy of females is more linear, with more despotic relationships, and follows a matrilineal basis with mothers dominant over daughters and older sisters over younger ones (Paul and Kuester 1996).

2.1.3 High ecological plasticity: Habitat, Climate and Diet

Wild Barbary macaques are found in highly fragmented forest areas through mountainous regions in Morocco and Algeria (Ménard and Vallet 1997, Mouna and Ciani 2006). One of the largest populations remains in the Middle Atlas Mountains, Morocco, where the ecosystem is principally composed of Atlas cedar (*Cedrus atlantica*) paired with a lower storey including arborescent and herbaceous vegetation (e.g. *Quercus rotundifolia, Quercus faginea, Juniperus thurifera Ilex aquifolium, Cytisus battandieri, Cistus laurifolius* and *Bupleurum spinosum*) (SENS 2006, Tarnier and Delacre 2007). This ecosystem is considered to have the highest biodiversity of Morocco with over 1,015 plant species, 200 bird species, 28 amphibians/reptiles and 34 mammal species including Barbary macaques (SENS 2006, Tarnier and Delacre 2007). Many of these species are endemic, rare or threatened, making this ecosystem of high importance for biodiversity and conservation. Middle Atlas temperate forest is characterised by marked seasonal variations in climate and day length (Hanya et al. 2011). The seasonal climate varies between cold/wet winter with minimal temperatures of -8°C and hot/dry summer with maximal temperatures of +45°C in 2012 (Meoweather 2012). Spring and autumn are characterised by high levels of precipitation, and annual rainfall averages between 500 mm to 1200 mm. Altitude ranges from 1400 to 2200 m (ASRMT 2006). To survive in this extremely variable climate, the Barbary macaque must have high physical, physiological and behavioural plasticity (Ménard 2002).

The Barbary macaque has a varied diet, consisting mainly of leaves, seeds, fruit, fungi and invertebrates, which varies according to the food resources available in each season (Fa 1984, Deag 1983, Ménard 2002, Hanya et al. 2011). The habitat is considered to have poor food quality throughout the year; however, winter and summer are generally the poorest seasons (Ménard 2002, Hanya et al. 2011). Recently, bird chicks and rabbits have been discovered to be consumed by Barbary macaques during the summer months (Young et al 2012). Young et al. (2012) hypothesised that the low quality and availability of food during summer might favour this extremely rare meat consumption behaviour. The poor quality food available in their habitat might favour macaques' attraction to human food items and, therefore, facilitate their encounters with tourists.

2.1.4 Current conservation status

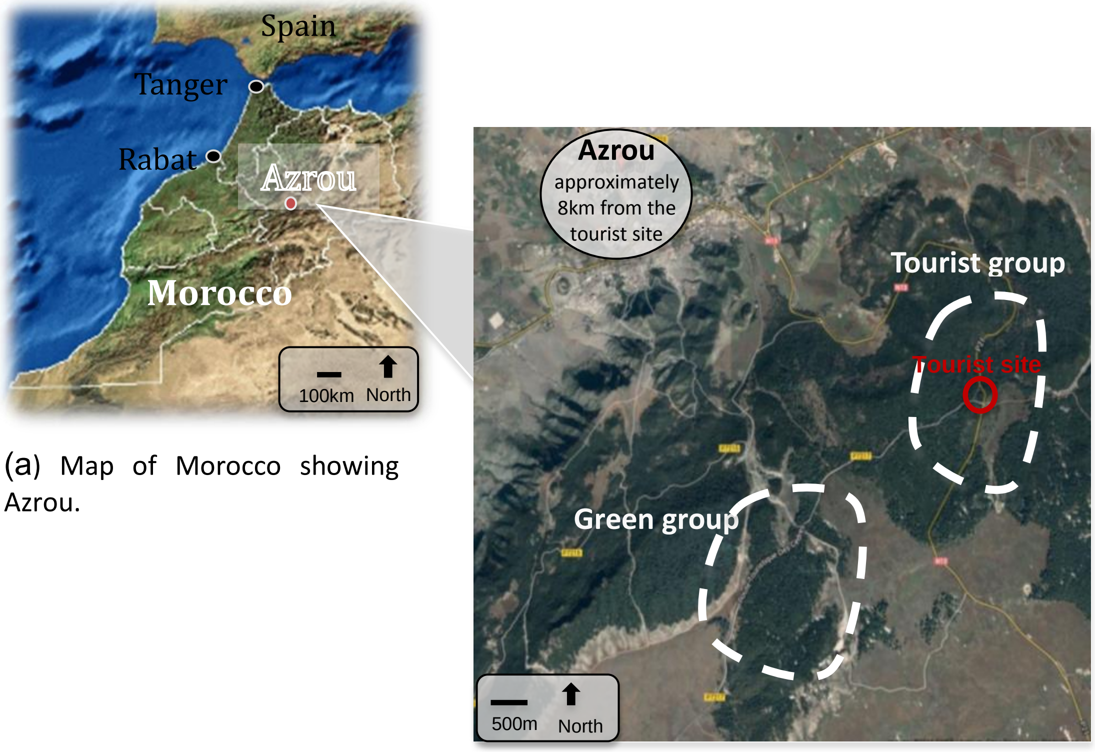
The wild population of Barbary macaques in Morocco has dramatically declined from an estimated 17,000 in 1975 (Taub 1975) to fewer than 6,000 individuals in 2010 (van Lavieren and Wich 2010). Barbary macaques receive some protection under national and international legislation; the species is listed on Appendix II of the Convention on International Trade in Endangered Species (CITES, EC 338/97, Annex B) and was classified for the first time as Endangered by the International Union for Conservation of Nature (IUCN) in 2008 (Butynski et al. 2008). In order to estimate the population decline, there have been repeated surveys of the species (Mouna and Ciani 2006, van Lavieren and Wich 2010). A decline in numbers from 17,000 to fewer than 6,000 within 20 years is thought to be due to two principal reasons: the degradation of the habitat by deforestation, and the illegal trade of monkeys as pets (van Lavieren 2008). The Middle Atlas Mountains are home to the largest remaining populations of this species, but even there numbers are in decline (van Lavieren and Wich 2010).

Recently, a conservation project in North of Morocco was established by Sian Waters: Barbary Macaque Conservation in the Rif (BMCRif: www.barbarymacaque.org). The project works with local people to evaluate and prevent the decline of the Barbary macaque in Northern Morocco. In addition, the Moroccan Primate Conservation Foundation (MPC: mpcfoundation.nl), established by Els van Lavieren, has undertaken a number of activities to increase public awareness and reduce illegal trade in animals. Tourists are one of the main targets of the illegal trade (van Lavieren 2008). Primate tourism has the potential to make a significant contribution to the conservation of endangered primate species by increasing financial benefits to the local community and increasing public awareness. As interest grows in developing the tourism potential of Barbary macaques as a tool for their conservation (Mouna and Ciani 2006), studies investigating the effects of tourism on the macaques are urgently needed.

2.2 Study sites and study subjects

The research was conducted in Ifrane National Park located in the Middle Atlas Mountains, Morocco. The study was carried out close to the city of Azrou on two groups of Barbary macaques, the Tourist Group, and the Green Group (Figure 2-1). Ifrane National Park, which was created in October 2004, is 1400-2200 m above sea level and covers an area of 51,800 ha (Annuaire Statistique Regional Mekanes Tafilalet 2006).

The males from the Tourist Group were studied for the first time in 2010 for my MRes project on the impacts of tourism on behaviours and physiological stress levels among male Barbary macaques. This study led to two publications - Maréchal et al. (2011) and Majolo et al. (2013). In 2011, another MRes project was conducted on both the Tourist Group and the Green Group, investigating the difference in body size, coat quality and parasite load between these groups (Borg et al. 2014).



(a) Map of Morocco showing Azrou.

(b) Map of Ifrane National park and the study sites.

Figure 2-1: (a) Map of Morocco, North-West Africa, showing the town of Azrou located in the Middle Atlas Mountains. (b) Map of Ifrane National Park and the study sites. The two study sites are approximately 2km apart. Tourist Group (GPS: N33° 25'; W005° 10'), and Green Group (GPS: N33° 23; W005° 15'). Map Source: Google-Maps (2014). The white lines represent the homr range of each group.

2.2.1 Subject identity

Two groups of well-habituated Barbary macaques were studied: The Tourist Group (TG) which experiences high tourism pressure every day and the Green Group (GG) which experiences only sporadic tourism encounters, approximately 2-3 brief tourist encounters every 2 weeks mainly in autumn and winter (personal observation). TG was first studied in 2010 (Maréchal et al. 2011) and GG was first habituated and studied in 2008. For group compositions, see Table 2-1.

Table 2-1: Composition for each group by sex and age classes during the study period from January to December 2012. The numbers in bracket are the numbers of individuals who died or disappeared during the study period.

Group	Adult Male	Adult Female	Sub-adult Male	Sub-adult Female	Juveniles (2/3 years old)	Infants (1 year old)	Newborn infants	Total
TG	12 (2)	12 (1)	2	1	6	7	5 (2)	41
GG	6	6	1	0	6	5	6	30

Data collection was carried out on all adults in both groups (17 TG and 11 GG); sub-adults and young adults in TG (2 males and 2 females) and in GG (1 male) were excluded as they had not reached their full body size. In TG, one female disappeared at the start of the study period, and one adult male died on 5th of April 2012; therefore they were both excluded from data analysis. Another adult male from TG disappeared on the 25th of October 2012 but is included in the study data. Hence, data on 8 adult males and 9 adult females were collected through the study period in TG and data on 5 adult males and 6 adult females for GG.

2.2.2 Dominance hierarchy

All dyadic agonistic interactions, displacements and submissive behaviours were recorded *ad libitum* throughout the study period (January 2012 to December 2012). The outcomes of these conflicts (i.e. clear winner/loser) were used to construct a hierarchy matrix. In total 675 (TG) and 417 (GG) dyadic aggressive intra-sexual interactions were observed. Dominance rank was assessed separately for males and female using corrected normalized David’s Scores (de Vries et al. 2006). The Steepness package (Leiva and de Vries 2011) in R 2.14.0 (R Development Core Team 2011) was used to give a continuous measure of dominance which is based on proportions of wins calculated for each dyad.

Dominance rank among males in the tourist group changed considerably when two males disappeared, one on the 5th of April and one on the 25th of October 2012. Hence, the David's Scores results (Table 2-2) are presented separetely for the periods 18/01/12 to 04/04/12, 05/04/12 to 25/10/12, and 26/10/12 to 31/12/12.

Table 2-2: Male dominance hierarchy with David's scores in the TG divided by episodes when males disappeared.

Rank	18/01 to 04/04/12		05/04 to 25/10/12		26/10 to 31/12/12	
	ID	**score**	**ID**	**score**	**ID**	**score**
1	Nu	6.48	Ga	6.11	Tw	4.75
2	Ga	6.00	Nu	5.83	Ga	4.46
3	Ki	5.25	Ki	5.35	Ki	3.53
4	Tw	4.33	Tw	3.89	Do	2.75
5	Mi	4.11	Do	2.95	Fi	2.42
6	Do	3.57	Fi	2.58	Ch	2.00
7	Ch	2.57	Ch	1.00	Pe	1.07
8	Fi	2.44	Pe	0.25		
9	Pe	1.22				
	N	79	N	216	N	36
	Steepness	0.63	Steepness	0.88	Steepness	0.61
	p value	<0.001	p value	<0.001	p value	0.001

Female dominance rank in TG was stable through the year (Table 2-3).

Table 2-3: Female dominance hierarchy with David's scores in TG in 2012.

Rank	ID	score
1	Sa	8.00
2	Ly	7.00
3	Ol	6.00
4	Le	5.00
5	Ba	4.00
6	Ma	3.00
7	Pa	2.00
8	Ci	1.00
9	Te	0.00
	N	420
	Steepness	1.00
	p value	<0.001

The dominance hierarchies for both males and females in GG in 2012 were stable through the year (Table 2-4).

Table 2-4: Dominance hierarchies with David's scores in GG in 2012. (a) males and (b) females.

a)

Rank	ID	score
1	Ar	3.55
2	Oz	2.85
3	Lw	1.55
4	Ge	1.40
5	No	0.65
	N	93
	Steepness	0.72
	p value	0.002

b)

Rank	ID	score
1	An	5.00
2	Da	4.00
3	Jo	2.96
4	Ke	2.03
5	He	1.00
6	Re	0.00
	N	320
	Steepness	0.99
	p value	<0.001

2.3 Data collection

The project received ethics approval from the Ethics Committee of the University of Roehampton (December 2011, Appendix A1) and research permission for the work in Morocco from the Haut Commissariat aux Eaux et Forêts et à la Lutte contre la Désertification, Royaume du Maroc (approval Nº 235; Appendix A2).

Data on macaques were collected by Laëtitia Maréchal (Principal investigator) and four field assistants at any one time, with a total of 7 research assistants through the study period. All research assistants were trained prior to data collection and the data collection only started when inter-observer reliability was above 95%. Inter-observer reliability was assessed between the main researcher and each assistant on the same observations. This was done for each type of data collected (i.e. behavioural, health and ecological data). If inter-observer reliability was not above 95%, data were discarded and training persisted until reaching 95% inter-observer reliability.

Field data were collected from January 2012 to January 2013. Data on the macaques were collected by the whole research team, five days per week for TG (3 days during weekdays and 2 days during weekends), and 2-3 days per week for GG, for approximately 10 h per day, from 7:30 am to 5:30 pm. Each researcher had a specific task per day, either collecting behavioural data or faecal and urine samples. These data were recorded using a Psion loaded with Pendragon Forms Version 5.1 (© Pendragon Software Cooperation, U.S.A.). Ethnographic material was collected only by Laëtitia Maréchal, either opportunistically while collecting data on macaques, or during the weekends when I spent time with local people and tourists at the tourist site, throughout the whole study period (sample consent form in English and French, Appendix A3).

2.3.1 Ethnography (Chapter 3)

I used a range of ethnographic methods and followed a social anthropological approach. There are several steps to consider.

Observer background

I am a white French woman, 29 years old at the time of the study. I conducted my conversations and interviews in French or English, depending on my interlocutor, which enabled me to interact relatively easily with local people and tourists. Prior to the present project, I had extensive experience in Morocco and in particular in Azrou, where I spent over a year collecting data on Barbary macaques, first as a research assistant for a PhD project in 2008-2009, then for my MRes project in 2010. As research assistant, I spent a nine month placement collecting behavioural and ecological data for a PhD project on the socio-ecology of wild Barbary macaques. Following this experience, and as part-fulfilment of an MRes in Primatology, I investigated the effect of tourism on the behaviour, anxiety and stress levels of wild male Barbary macaques from the Tourist Group studied in the present thesis.

Observer's role

My role in relation to the participants was crucial to ensure facilitation of the study and acceptance by the participants. Qualitative observational research must have a thoughtful and well-understood relationship between the researcher and research participants (Connelly and Clandinin 1990). In the present study, there were different participants who required a different approach for the collection of ethnographic material, and therefore my role was defined differently.

First, I regularly interacted at the tourist site with the local community which was categorised into two groups: fossil sellers and horse riders. With them, I clearly defined my research, telling them that my goal was to understand tourism at this site. In order to build a relationship with them I used the method of participant observation-. To do so, I spent time with them selling fossils, assisting tourists riding on their horses, waiting, drinking tea, preparing and eating tagine as well as playing games of chess with them. While sharing these activities I collected information through informal conversations.

Tourists were present at the site for only for a short period of time each, from a few minutes to a few hours, which only allowed me to create a superficial relationship with them. I therefore use a different approach with tourists, called neutral observer. I recorded tourists' behaviours, comments or discussions when they were at the tourist site. I also conducted a number of short 'informal' interviews and conversations.

Defining the research question

Although I had previously worked at the site and I had some ideas of the different issues there, I decided not to define my research questions related to the ethnographic part of the study precisely before going to the field in order to have an open mind when considering primate tourism at the site. Several aspects of tourism were explored such as the local economy, types of tourists, tourist activities and perceptions of tourism. When I came back from the field, I wrote a summary of a ‘typical day at the tourist site’, enabling me to synthesise my observations and conversations collected through the study period. The main research topic for this part of my thesis was defined based on this synthesis. The core connection between all observations and conversations with tourists and locals was interacting with the macaques, and particularly feeding these animals. I therefore based my research questions in the thesis on understanding this specific tourist activity: feeding monkeys.

Selecting qualitative research tools

In order to investigate feeding monkeys as a tourist experience in Morocco, I used two different research tools, including primary (i.e. fieldwork) and secondary research (i.e. existing material). I used two main research approaches during my fieldwork, observations and informal conversations. I spent 12 months at the tourist site, 5 days a week, collecting observations *ad libitum* on local community and tourist behaviours, comments and discussions. During the week days, I was also collecting data on macaques (faecal, urine and scans) while recording observations on tourists. When I had the opportunity, I conducted informal conversations with local community and tourists, and in particular during weekends. I recorded all my observations and summaries of conversations in a notebook. The secondary research is based on sources such as books and publications, which were used in order to put my findings into context. When my research topic was defined, I read a number of sources on feeding wildlife. Integrating information about this topic was made harder as the resources are limited. I explored resources in a range of disciplines in addition to social anthropology such as biological anthropology, conservation biology and psychology, where relevant information was often limited to short observations described in one or two sentences.

By integrating both primary and secondary research, I was able to explore the motivations of tourists to feed monkeys, and more broadly in relation to feeding wildlife, and how this activity shaped the tourist experience.

2.3.2 Behavioural data (Chapter 4)

Quantitative behavioural data on tourism

Quantitative data were collected in order to characterise the behaviour of tourists at different times at the tourist site. During scans every 30 min, the following data were recorded:

- **Number of tourists in the area**, defined as within a 100 m radius (maximum visible distance) of a point judged to be the centre of the macaque study group.
- **Number of tourists in the nearest tourist group**, defined as the number of tourists in the group closest to the focal macaque. A tourist group is defined as one, two or more tourists being in close proximity (< 3m) to each other.
- **Distance between the focal macaque and tourists in the nearest tourist group**, defined as the distance between the focal macaque and the closest tourist within the nearest tourist group.
- **Noise levels** around the monkey group. Due to time constraint, the acoustic disturbance from human activities was evaluated using a scoring system from 1 to 6 (Table 2-5), a method developed in a previous study at the site (Maréchal 2010).

Table 2-5: A six-point scoring scale for assessment of acoustic disturbance. For points 3-6, noise from vehicles is not included. Noise of vehicles passing was only considered when no human was present at the tourist site.

Category	Noise levels
1.	No acoustic disturbance from human activities.
2.	Noise from vehicles passing on the road only.
3.	Low noise levels from a small group of humans in conversation.
4.	Medium noise levels from several humans speaking loudly and/or laughing.
5.	High noise levels due to several humans speaking loudly, screaming and/or laughing.
6.	Extremely high noise levels due to several humans speaking loudly, screaming, singing, playing music and/or laughing.

Behavioural data on the macaques.

A mix of behavioural observation techniques was used: continuous focal and scan sampling and *ad libitum* data collection (Altmann 1974). Each study day followed the same pattern of behavioural observations. We generally located the group at approximately 7:30 am for the Tourist Group; however this was more variable for the Green Group. Each hour, a group scan (type 1) was recorded for 10 minutes, and each half hour, a group scan (type 2) was recorded for 5 minutes (see below for details of scan types). These group scans were followed by continuous focal sampling for 10 to 20 minutes (see explanation below) of a selected individual. In addition, *ad libitum* group scans (type 3) were collected including different data detailed below when an interaction between tourists and macaques occured. Data were collected, alternating group scans (type 1) and continuous focal sampling until the end of the study day (approximately 5:30 pm). *Ad libitum* data were recorded at any time.

Continuous focal sampling

Each individual was followed for 10 minutes, once a day, each study day, using continuous focal sampling (Altmann 1974). In order to investigate coping behaviour linked with human-macaque interactions, an additional 10 min of continuous focal sampling data were collected after the first tourist-macaque interaction within a continuous focal sampling (TMI) ended. The focal individual was randomly selected using randomly generated numbers. If the next focal subject on the random list was not found within 5 min, the following individual on the list was selected. When the focal animal was lost 9e.g. due to disturbances such as by tourists or dogs), observation of the same focal animal was re-started as soon as possible.

During continuous focal samples, data were collected following an ethogram divided into four behavioural categories: general activity, agonistic behaviour, self-directed behaviour and human/macaque interaction (Table 2-6).

Table 2-6: Ethogram of behavioural data collected, after McFarland (2011) and Maréchal et al. (2011).

Type	Behaviour	Definition
General activities	Feeding	Foraging, handling and consuming food.
	Grooming (given or received)	One monkey goes through the fur of another monkey with its fingers.
	Resting	Monkey stay in the same position without feeding or social activity.
	Travelling	Monkey is moving; it may also be observed briefly (1-2s) picking up and searching for food items.
	Other	Other activities such as vigilance, self-grooming.
Agonistic behaviours (given or received)	Approach displace	A monkey moves closer to another monkey who moves away from the monkey approaching.
	Aggression grade 1	Facial threat directed to another monkey
	Aggression grade 2	The monkey makes a sudden intense movement towards another monkey.
	Aggression grade 3	A monkey chases another monkey for less than 5 metres, or slap the ground.
	Aggression grade 4	The monkey chases for more than 5m and/or have harmful physical contacts towards another monkey

Type	Behaviour	Definition
Submissive behaviours (given or received)	Make room	The monkey makes (the beginning) of a movement, away from another monkey.
	Give ground	The monkey creates a distance between itself and another monkey, by moving away from it, but not at speed
	Flee	The monkey moves at speed, away from another monkey
	Crouch	The monkey presses itself to the ground, by tucking its arms, legs and head under its body
	Present submission	The monkey presents its hindquarters to another individual
Short affiliative behaviours (given or received)	Teeth-chatterring	The monkey pulls up its eyebrows and scalp, and flattens its ears against the head.
	Sandwich	The infant is handle between two monkeys generally associated with teeth chattering
	Embrace	Two monkeys are facing each other and grab each other by the arms.
	Garb hindquarter	The monkey grabs the hindquarters of another, generally associated with teeth chattering
	Genital inspection	Two females inspect each other’s genitals, generally associated with teeth chattering
Self-directed behaviours	Self-scratching	The monkey uses its nails to scrape its own body.
Tourist macaque interactions (given or received)	Feeding interactions	Tourists give food to macaques by hand, or by throwing it towards them.
	Agonistic interactions	Tourists threaten macaques by throwing an object toward them, or making aggressive gestures towards them.
	Other interactions	Tourists interact with macaques without food or agonistic behaviour. This generally includes taking pictures or being within 2 m of the macaques and looking at them.

Activities defined as general continuous activities are mutually exclusive from each other (i.e. travel, feed, rest, groom, and other). These activities were recorded as durations. Behaviours in other categories were considered to be events and recorded as frequencies. Two events were distinguished when they were separated by at least 10 seconds. Restlessness is defined as the rate of change in activity behaviours. The Composite Index of Sociality (CSI) is calculated using measures of the frequency of grooming (G) and proximity (P) for each dyad over the whole study period, following the equation by Silk (2006):

$$CSI = (G_{ij} / G_{xy} + P_{ij} / P_{xy})/2.$$

The values for G and P in this equation represent the adjusted frequency of grooming or proximity for a dyad ij divided by the mean adjusted frequency of grooming or proximity for all dyads in the group x in the year y. Each frequency is adjusted according to the number of dyads possible within a group.

Group scans (3 types)

Hourly group scans (type 1): Every hour, a group scan lasting 10 minutes was conducted on all visible individuals to assess their general activity. Over the day, from 8:00 am to 5:00 pm, ten scans were completed. Data collected included data on macaques behaviour such as their general activity (i.e. resting, feeding, travelling, allo-grooming or other), and the distance and identity of their nearest male and female conspecifics. The type of food eaten by each macaque was recorded. Human food was defined as food brought to the site and/or given to an animal by tourists (e.g. orange, bread, banana, peanuts, crisp, chocolate, and cookies). Natural food was defined as food found naturally in the ecosystem (e.g. acorn, grass, leaves and fungi). In addition, to scan data climatic data were collected (i.e. temperature and humidity), the number of tourists present in the area and in the nearest tourist group, and the noise levels (as described above).

Thirty minute group scans (type 2): In addition to the hourly scan, every thirty minutes, a group scan lasting 5 minutes was conducted on all visible individuals to assess tourist-macaque interactions, for a total of nineteen scans recorded per day. Data were collected on type of human/macaque interactions (none, other, feeding, agonistic) for each macaque, their height from the ground, as well as the distance from the nearest tourist group and their number.

Ad libitum group scans (type 3): Ad libitum group scans were conducted when a tourist-macaque interaction occurred only in the Tourist Group, using the same data collection categories as during the 30 min scans (i.e. activity, type of human/macaque interactions, the subject's height above the ground, the distance to the nearest tourist group, type of food being eaten). In addition, the ID of each monkey involved in an interaction and the distances between conspecifics involved were collected. An average of 59 (ranging from 44-79) group scans was collected per individual through the study period.

Tourist-macaque interactions (TMI) and matched control data (MC)

In order to investigate how the study animals responded during tourist-macaque interactions (TMI), matched control methods were used (similar to post-conflict/matched control (PC-MC): de Waal and Yoshihara 1983), called TMI-MC in this study. PC-MC is a well-established method (de Waal and Yoshihara 1983) and has been widely used in studies of conflict management (Koshi et al. 2007, Fraser et al. 2010, McFarland and Majolo 2012).

Data on TMI were collected opportunistically during continuous focal sampling. A TMI was defined as 1) any behavioural exchange (i.e. feeding, aggressive or other) between one or several tourists and a monkey, and 2) when tourists were in close proximity, within 2 metres of the focal macaque. A TMI were considered to be over when no subsequent interaction between tourists and the focal monkey occurred for ≥ 30 seconds and the tourists were all over 2 metres from the focal animal. After the first TMI during a continuous sampling observation, an additional 10 min observation was collected. During post-interaction, two distinct scenarios could happen, either 1) the monkey had another or several additional TMIs with the same or other tourists, or 2) the macaque did not have another TMI.

Matched control (MC) data were collected when a monkey had no TMI within 10 min prior to and during the observation. This was assessed using the 30 min scan carried out prior to the observation and/or the confirmation across researchers present at the site. MC data were collected within one week before or after a TMI, at similar time of day (within two hours) in order to match as closely as possible environmental, social and/or touristic condition across the TMI-MC pair (de Waal and Yoshihara 1983, McFarland and Majolo 2012).

2.3.3 Non-invasive collection of primate health data (Chapter 5)

Several non-invasive methods were used to assess primate health.

Body size: via photogrammetry

Photogrammetry was used to determine the body size of each macaque. Despite some disadvantages, such as potential measurement errors that must be controlled for, this technique has proven to be repeatable, reliable and easily conducted (Breuer et al. 2007, Kurita et al. 2012). Digital photos were taken using a digital Fujifilm camera (Finepix T200); Fujinon lens f= 5-50 mm 1: 3.4-5.6. For the camera calibration, the resolution of the image size was Large 1,056 frames, 14 megapixels (4288x3216), picture-taking mode was ‘natural light’ and optical zoom was full (x 10) meaning the focal lens length was constant (50mm). Distances between camera and the subject were measured with a Bosch DLE 40 Laser Measurer, class 2. The size of the monkey, in pixels, was extracted using tpsDIG2 software (Rohlf 2010).

Three factors are important to control to ensure reliability of the measurement: camera calibration (it was essential to keep the same camera settings through the study period), image selection and measurement errors (Breuer et al. 2007). The choice of the image is crucial to reduce measurement errors. Particular attention was taken in selecting the pictures, using criteria including total visibility of the primate body, a sharp image of the subject, the subject being perpendicular to the camera frame and the photograph being taken at monkey height. In addition, all photographs were taken at a distance between 5 to 15 m away (Borg et al. 2014).

Prior data collection, and for the photographic measurement calibration, the conversion factor needs to be determined in order to convert the size of an image of an object (pixels) to the real object size (cm). I determined the conversion factor for each image by measuring the same object of known size at different distances, using the same methods and camera settings as described above. The conversion factor was determined following the equation:

c = object (cm) / [Distance from camera (m) x Size of object in image (pixels)]

An average conversion factor of 0.00297 was obtained. I then compaired the known size of an object with the calculated size of this same object using the equation below, and we obtained an average measurement error of 0.33 cm for the object of known size. Using the average conversion factor, the following equation was also used to assess the size of body parts.

Object size (cm) = Distance from camera (m) x Size of object in image (pixels) x 0.00297

The reliability of the technique was determined by calculating the coefficient of variation (CV) of repeated estimations of animal's body size from the same photography, and of different photographies of the same animal assessed by the same observer. Coefficients of variation of 0.73% within photos, and 4.32 % for the same observer were obtained.

In order to assess macaque body size, a number of measurements were taken. Shoulder measurements were taken when the monkey was sitting facing directly away from the camera, and represented the largest distance of the higher back linked with the arms (see picture 1 and 2 below). I measured the lower back of the monkey sitting at the level where the knees were not visible anymore when looking at the monkey from the back (see picture 1). In addition, when the monkey was standing side on, measurements of the neck (junction between the head and the shoulders), belly (where the belly button is present) and breast (where the nipples are present) were taken, excluding hanging hair (see picture 3). All measurements were made as straight lines. To ensure that each measurement was taken from the same start and end point, we compared the picture being measured with several pictures of the same individual, on which these lines had already been added. For this, images were opened and viewed simultaneously in separate tpsDIG2 windows.

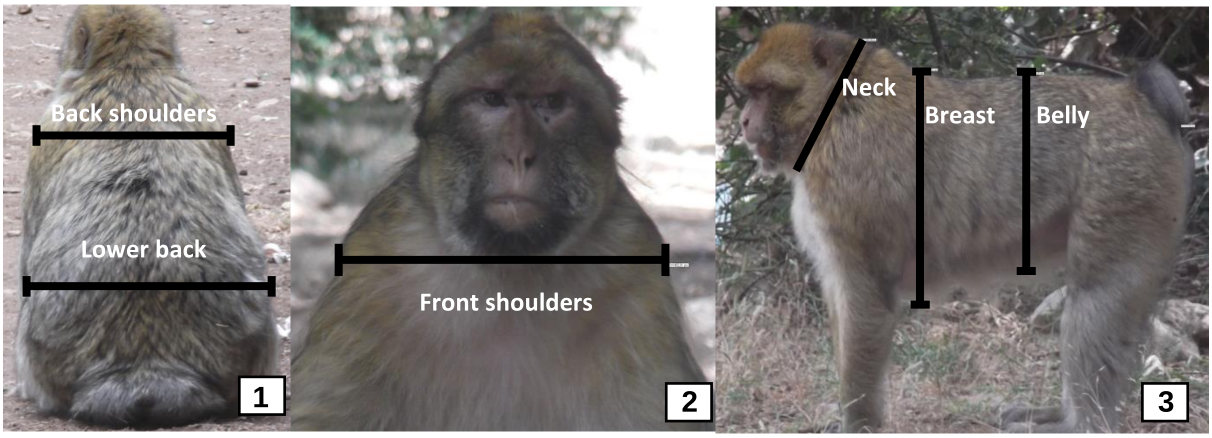


Figure 2-2: Examples of photogrammetry measurements for each body part measured.

Coat condition

Coat condition was estimated using two direct visual scoring systems, collected once a month. On the same day, two researchers assessed the coat condition of an individual macaque using the scoring scale. The identity of the individual and date were recorded. Observation focused on the head, back, sides and legs. The fur around the stomach area was not taken into consideration as different fur quality here may be unrelated to coat condition on the rest of the body (Borg et al. 2014). Data were not collected during days when it rained nor when the humidity was above 80% because humidity and rainfall may affect the appearance of the fur and consequently influence the observation. Coat condition was recorded when individuals had not received any grooming in the 10 min prior to the observation. Different parameters are used to assess coat condition in domestic and captive animals (e.g. fur brightness, softness, and alopecia levels); however softness and optimum feel of coat are somewhat invasive methods that necessitate touching the animal (Marsh 1999). Therefore, only two criteria were evaluated independently: coat quality and levels of alopecia.

❖ Coat quality

Coat quality is defined as the brightness and general appearance of hair. A classification was established using a visual scoring system from 1 to 4 (Table 2-7).

Table 2-7: A four-point visual scoring scale for fur quality assessment in primates.

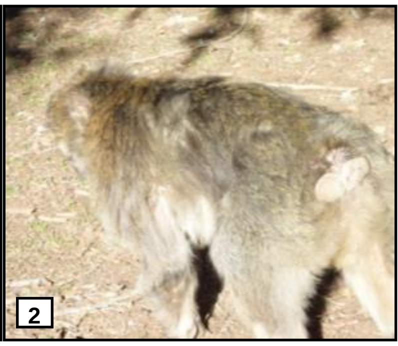
Category	Coat quality	Example picture
1.	Very good quality fur. The quality of fur is very good on the whole body (i.e. head, back, sides, legs). Bright and smooth coat with straight, thick and strong hair.	See example (1) below
2.	Good quality fur. The quality of fur is mainly very good but it is not homogenous on the whole body.	See example (2) below
3.	Poor quality fur. The quality of fur is mainly poor with some parts with good quality fur.	See example (3) below
4.	Extremely poor quality fur. Dull and rough coat with hair broken, fine and weak.	Not seen in either group

❖ Alopecia levels

Alopecia is defined as aggregated hair loss revealing the skin underneath (Honess et al. 2005). In addition, the location of alopecia patches on the individual body was recorded. To assess alopecia levels, a visual scoring system from 1 to 5 was used (Table 2-8), adapted from Honess et al. (2005).

Table 2-8: A five point visual scoring scale for alopecia levels in primates, adapted from Honess et al. (2005).

Category	Alopecia levels	Example picture
1.	Very good coat condition; the whole body is complete cover.	See example (1) below
2.	Few small patches of alopecia (2-5 cm^2)	See example (2) below
3.	Large patches of alopecia (≥ 5 cm^2), or numerous small ones totalling 25-50% of the body surface	See example (3) below
4.	Generalised alopecia (not patchy), involving more than 50% of the body	Not seen in either group
5.	Body completely bald (i.e. more skin visible than hair)	Not seen in either group



Physical condition: Injury, scars and lameness

Lameness, injuries and scars were evaluated using direct visual scoring systems. The number of scars and lameness for each individual were assessed once a month by two observers. Lameness was evaluated using a visual scoring scale (0: no lameness, 1: light lameness, 2: lameness affecting animal's movement, 3: lameness seriously compromising animal's movement). In addition, injuries were opportunistically assessed throughout the month using a visual scoring scale (Table 2-9). The location of the injury was also recorded, as well as the identity of the individual and date. When an injury was reported, daily evaluation of the progress of the injury was made until complete visual recovery.

Table 2-9: A six-point visual scoring scale for injury assessment, adapted from Mejdell et al. (2010).

Category	Injury
0.	No visible damage.
1.	Lesion involving hair loss only, e.g. superficial bite.
2.	Lesion involving a moderately sized contusion (bruise) with or without hair loss and/or abrasion in the skin, e.g. photo 2 lesion over the left eye.
3.	Lesion involving a minor laceration (cut) and/or a larger contusion (bruise) with obviously swollen parts with or without hair loss, e.g. photo 3.
4.	Laceration involving injury to deeper tissues or leading to temporal loss of function, e.g. muscle, limping, photo 4.
5.	Extensive and severe injury that may lead to long lasting loss of function (e.g. laceration with extensive soft tissue damage, serious joint damage, fracture) or even death, e.g. photo 5.

Physiological stress levels assessed via faecal samples

Faecal samples were collected according to protocols in Hodges and Heistermann (2003). Whether or not there is diurnal fluctuation of glucocorticoid levels in faecal samples depends largely on the time course of glucocorticoid (GC) metabolism and the excretion of inactivated steroids into the gut, and evidence to date from a range of different primates species shows no circadian cycle in excreted glucocorticoid metabolites in faeces (Ostner et al. 2008, Setchell et al. 2008, Huck et al. 2005). Consequently, in order to maximise the faecal sample collection, faecal samples were collected throughout the day opportunistically. The aim was to collect two faecal samples per week for each individual and no more than one sample per individual per day.

When a monkey was seen defecating and there was no contamination with urine, the faecal sample was collected. The sample was then homogenised by mixing it with a stick and removing all undigested material such as leaves or small stones. About a half thumbnail size (2-3 g portion) of faeces was then transferred to the storage container (Azlon tubes 30ML HDPE). The individual's name, date, sample number and time were written on the storage container using a pencil. The container was placed inside an insulated cool box with ice packs for storage during the day and, subsequently, stored in a freezer at -20°C at the end of the day.

The faecal samples remained frozen during the field period. They were then packed with ice packs and transferred for analysis to the Roehampton University Laboratory (UK). The samples were exported from Morocco to the United Kingdom, under DEFRA licence (N°: TARP/2012/234, Appendix A4). The samples were stored at -20°C in the Roehampton University Hormone Laboratory until analysis.

Hormone analysis for glucocorticoid metabolite concentrations

A total of 1106 faecal samples was analysed (means = 43 (ranging from 47-32) samples per individual for Tourist group; 33 (ranfing from 35-26) samples per individual for Green group). Each sample was freeze-dried and ground to a fine powder before 0.05–0.1 g of sample was extracted in 3 ml of 80% methanol. After vortexing for 10 min, and centrifugation for 20 min at 4500 rpm, the supernatant was separated for analysis. Extraction efficiency, determined by the recovery of tritiated oestradiol added to the samples before extraction (Möhle et al. 2005), previously estimated in Maréchal et al. (2011), was 85.1 ± 5.2%. We analysed faecal extracts for concentrations of glucocorticoid metabolites using a group-specific enzyme immunoassay (EIA) for the measurement of 11β-hydroxyetiocholanolone (Ganswindt et al. 2003) previously validated for monitoring glucocorticoid output in various primate species including Barbary macaques (Heistermann et al. 2006). Assay procedures followed those described in detail by Heistermann et al. (2004); for more details see Appendix A5.

A dilution factor was determined by assaying sets of serial dilutions (1:40- 1:640) of six samples which were presumed low and high GC concentrations based on social seasonal variation (i.e. birth, mating). These dilutions were also used to determine the parallelism with the standard curve (Figure 2-3). Based on this analysis, other samples were analysed with a dilution factor of 1:80 and a few at 1:160 when the initial dilution was too high for estimation of GC concentrations within the linear range for the assay.

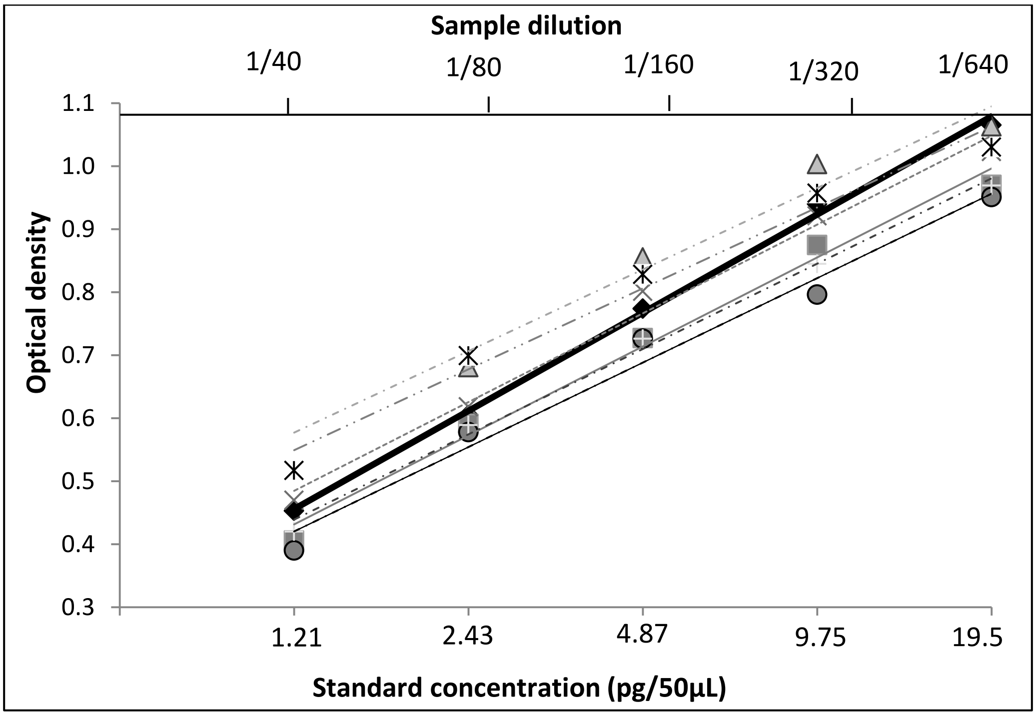


Figure 2-3: Parallelism test between the optical density values of a series of dilutions from selected faecal samples relative to the optical density of the standard curve. The thick black line represents the standard curve; the other lines represent each faecal sample at different dilutions.

The sensitivity of the assay at 90% binding was 2.34 pg. Intra-assay coefficients of variation, calculated from repeated measures of high and low concentration quality controls, were High (N=17)=5.5% and Low (N=16)=8.5%. Inter-assay coefficients of variation were High (N=79)=9.5% and Low (N=75)=13.0%. GC metabolite concentrations in the faecal samples (fGC) were calculated using the following equation:

$$\text{fGC metabolite (ng/g dry faecal weight)} = \frac{\text{Metabolite concentration (pg/50 µl)} \times \text{extract volume (3000 µl)} \times \text{dilution factor} \times \text{(100/recovery factor 85.1)}}{\text{Dry faecal weight (g)} \times \text{sample volume (50 µl)} \times \text{conversion factor from pg to ng (1000)}}$$

Given an excretion lag for cortisol metabolites into faeces of Barbary macaque of between 24h and 48h (Heistermann et al. 2006), FGC concentrations were matched with the behavioural and tourism data from 2 days preceding the faecal sample collection. When behavioural data were not available from 2 days prior to faecal sample collection, behavioural data collected the day before faecal sample collection were used.

C-peptide assessed via urine samples

We collected 1-2 urine samples per week for each individual, opportunistically throughout the day. Deschner et al. (2008) and Emery Thompson et al. (2009) found no significant circadian effects on C-peptide levels in bonobo and chimpanzee urine. We collected urine samples from identified individuals sitting in trees or on rocks, either on a plastic sheet placed beneath urinating individuals in trees (Knott 1998), or by pipetting the urine from leaves or rocks (Krief et al. 2005, Leendertz et al. 2010). Only urine samples uncontaminated by faeces were used; however, as soil matter does not seem to affect C-peptide measurement (Higham et al. 2011b), urine samples contaminated by soil matter were collected. The identity of the urinating animal, data and time of collection were recorded. The samples were transferred into 1.5 ml micro-centrifuge tubes with cap (Fisherbrand, FB74031) and placed inside an insulated cool box with ice packs for storage during the rest of the day. In order to avoid any degradation of the urine samples, the samples were immediately frozen in the field and, subsequently, stored in a freezer at -20°C at the end of the day. Using the same protocol as for faecal sample transfers, urine samples were then analysed at Roehampton University. This procedure followed the recommendations by Higham et al. (2011b).

Hormone analysis for urinary C-peptide levels

A total of 755 urine samples was analysed (means = 32 (ranging from 39-22) samples per individual for Tourist group; 19 (ranging from 24-15) samples per individual for Green group). However, urine samples with a volume less than 0.2µl (N=118) were removed from the data analysis because there was not enough volume to repeat the analysis if needed, for example at different dillution. We used the IBL international GMBH, C-peptide ELISA kit (Art. No. RE53011) to analyse C-peptide concentrations in urine samples. This kit has previously been used in macaques (long-tailed macaques and rhesus macaques: Girard-Buttoz et al. 2011) and in olive baboons (Lodge 2012). Each sample was defrosted an hour prior to assay, well-mixed and centrifuged for 1 min until clear, using a micro centrifuge

(Sigma 1-14). Prior to assay, urine samples were diluted in distilled water following Girard-Buttoz et al. (2014). Urine samples were then kept in a fridge (+4°C) to be used up to 48h after being defrosted. Other assay procedures followed those described in detail in the IBL international instruction book (2009), found in Appendix A6.

The appropriate dilution factor for the samples determined by assaying sets of serial dilutions (1:2- 1:16) for four samples which were presumed low and high C-peptide concentrations based on social seasonal variations (i.e. pregnancy, birth and mating seasons), and these dilutions were also used to determine parallelism with the standard curve (Figure 2-4).

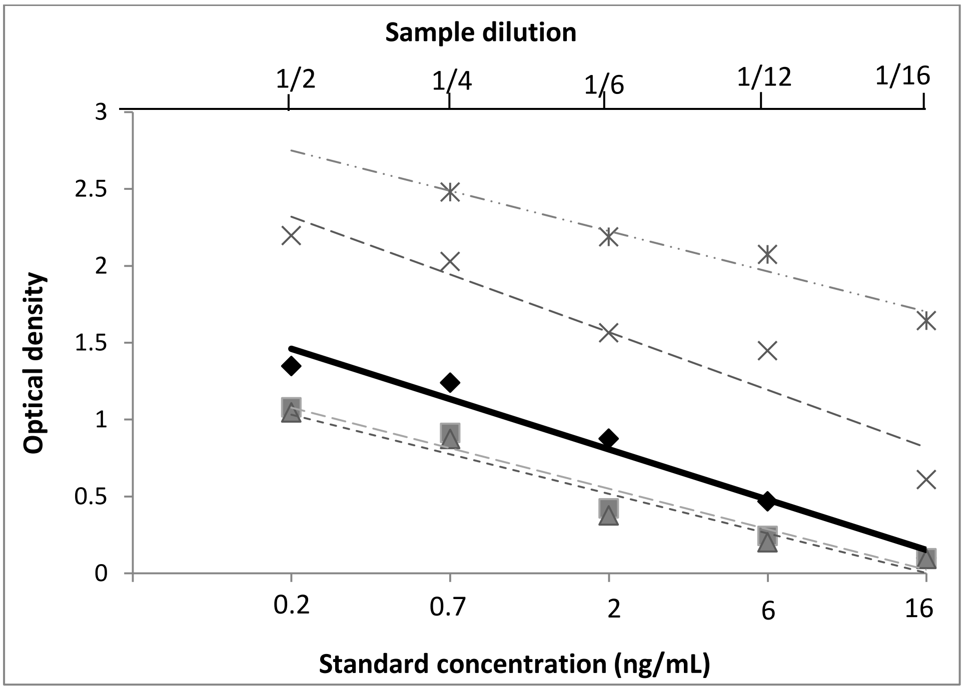


Figure 2-4: Parallelism test between the optical density values of a series of dilutions from selected urine samples relative to the optical density of the standard curve. Thick black line represent the standard curve; the other lines represent each urine sample at different dilutions.

Based on this analysis, on the first day the sample was defrosted at room temperature for 1 hour, and then diluted (dilution 1:2) and analysed. The urine sample was then kept in the fridge at +4°C for a maximum of 48h. If the initial dilution was outside of the linear range for the assay, the dilution factor was increased or decreased as appropriate, and the sample analysed again the second day. The concentrations of C-peptide in different samples were highly variable, and the samples were analysed with a dilution factor ranging from 1:1 to 1:100. 95.6% of the samples were analysed within 24h, as recommended by Higham et al. (2011b). However, some samples were analysed 48h after defrosting due to the high variability of C-peptide concentration. To ensure that the time variation for running the assay (within 48h after defrosting) did not significantly affect the UCP values, I ran a series of control tests. I selected a number of samples that were diluted with the same dilution factor, and these were analysed on 3 consecutive days. UCP values from these control samples were highly significantly correlated with initial analysis after 24 hours (N=39, r=0.763, P<0.001), and after 48h (N=43, r=0.636, P<0.001), and therefore samples analysed within 48h were kept for data analysis.

The sensitivity of the assay was 0.064 ng/ml. Intra-assay coefficients of variation, calculated from repeated measures of high and low concentration quality controls, were High (N=18)=4.7% and Low (N=17)=6.5%. Inter-assay coefficients of variation were High (N=65)=7.0% and Low (N=65)=13.1%. Therefore, values of assay precision were well within the ranges reported in other studies (e.g. Higham et al. 2011b, Girard-Buttoz et al. 2011, Girard-Buttoz et al. 2014).

A number of samples had values that were below C-peptide assay sensitivity. In order to include these samples and reduce sample size by excluding low C-peptide levels, I assigned them a value of half the maximum possible value (i.e. 0.032 ng/ml). A similar approach was used by Girard-Buttoz et al. (2011). In addition, I ran a second analysis in which I excluded all samples with UCP values below the C-peptide assay sensitivity. Since the results of the latter analysis were not different from the analysis including UCP values below C-peptide assay sensitivity, I included in chapter 5 only analyses including UCP values below C-peptide assay sensitivity; the results without such UCP values can be found in Appendix A7.

Creatinine analysis

C-peptide values were indexed to urinary creatinine concentration, determined with a creatinine enzyme assay. Estimating creatinine concentration for each urine sample controls for differences in water content between samples, which affect measured C-peptide urine concentrations (Girard-Buttoz et al. 2011). Each urine sample was diluted in distilled water with a dilution factor of 1:20, expect for a few samples that were diluted at 1:80. Assay procedures followed those described in Bahr et al. (2000); see Appendix A8. Assay sensitivity was 0.1 mg/ml. Intra-assay coefficients of variation were High (N=17)=1.3% and Low (N=16)=2.9% and inter-assay coefficients of variation were High (N=64)=1.4% and Low (N=64)=2.4%.

Indexing C-peptide values to creatinine concentration:

C-peptide concentrations were presented as ng C-peptide/mg creatinine, following the conversion equation below:

$$\text{C-peptide (ng/mg creatinine)} = \frac{\text{C-peptide (ng/ml)}}{\text{(Creatinine (mg/dl)/100)}}$$

2.3.4 Climate data

As the two groups' home ranges were only 2km apart, and had similar habitats, climate data were only collected at TG site. Each hour, climate data were collected, specifically ambient temperature (°C) and relative humidity (%), using a Kestrel 3500 Pocket Weather Meter. In addition, daily rainfall was recorded using a straight-sided cylinder pluviometer located at the tourist site. These data give a rich source of local environmental information relevant to primate activity (Mayes and Pepin 2011).

2.4 General data analysis

In the present chapter, I describe the general data analysis including a summary of data collected on the macaques and on tourists. I also give general information on the statistics I used through this thesis. Detailed descriptions of data analysis and statistics are provided in chapters 4 and 5.

2.4.1 Summary of data collected on Barbary macaques

A total of 222 days of data was collected in the tourist group (TG) from the 9th of February to the 29th of December 2012. A total of 79 days of data was collected in the green group (GG) from the 10th of March to the 29th of December 2012. A summary of all data collected on macaques from TG and GG and used for analysis is presented in Tables 2-10 and 2-11.

Table 2-10 Summary of data collected on macaques for the Tourist Group (TG) from January 2012 to December 2012.

		Number of scans			Total hours	Number of samples	
ID	**Sex**	**Hourly scans (type 1)**	**30 min scans (type 2)**	***Ad libitum* scans (type3)**	**Continuous focal sampling (h:min:s)**	**Faeces**	**Urine**
Ba	F	863	1843	73	39:02:51	42	34
Ch	M	695	1560	62	33:57:09	43	30
Ci	F	749	1573	59	38:18:04	47	32
Do	M	983	1997	78	36:17:18	43	34
Fi	M	997	2072	79	37:22:29	42	34
Ga	M	997	1984	73	38:27:36	45	36
Ki	M	863	1728	62	37:28:45	44	33
Le	F	1003	2036	69	37:45:37	46	36
Ly	F	995	1902	60	37:52:39	46	38
Ma	F	802	1689	60	35:49:57	42	39
Nu	M	730	1362	65	31:38:56	32	22
Ol	F	1118	2266	70	38:39:58	46	35
Pa	F	612	1254	44	35:46:49	47	32
Pe	M	678	1411	54	37:53:23	45	27
Sa	F	1043	1996	54	35:50:27	44	29
Te	F	693	1354	48	35:00:32	42	29
Tw	M	895	1920	64	38:20:50	44	31
Total		2009	4130	739	625:33:20	740	551
Mean		865.65	1761.59	63.18	69:30:22	43.53	32.5
SD		152.98	298.57	9.86	0.08	3.45	4.34

Table 2-11 Summary of data collected on macaques for the Green Group (GG) from March 2012 to December 2012.

		Number of scans	Number of samples	
ID	**Sex**	**Hourly scans (type 1)**	**Faeces**	**Urine**
An	F	367	34	22
Ar	M	340	33	18
Da	F	372	34	15
Ge	M	189	26	18
He	F	319	36	16
Jo	F	359	32	22
Ke	F	342	35	19
Le	M	304	32	15
No	M	322	33	15
Oz	M	356	30	24
Re	F	305	33	21
Total		520	358	205
Mean		325	33	19
SD		50.98	2.7	3.23

2.4.2 Climatic data

Three main types of climatic data were collected (see page 74): rainfall, temperature and humidity. All three climatic variables were correlated with each other (Figure 2-5). Daily rainfall was negatively correlated with average daily temperature (N= 212, r_S=-0.467, P<0.001) and positively related to average daily humidity (N= 212, r_S=0.600, P<0.001). Average daily temperature was negatively associated with average daily humidity (N= 212, r_S=-0.830, P<0.001).

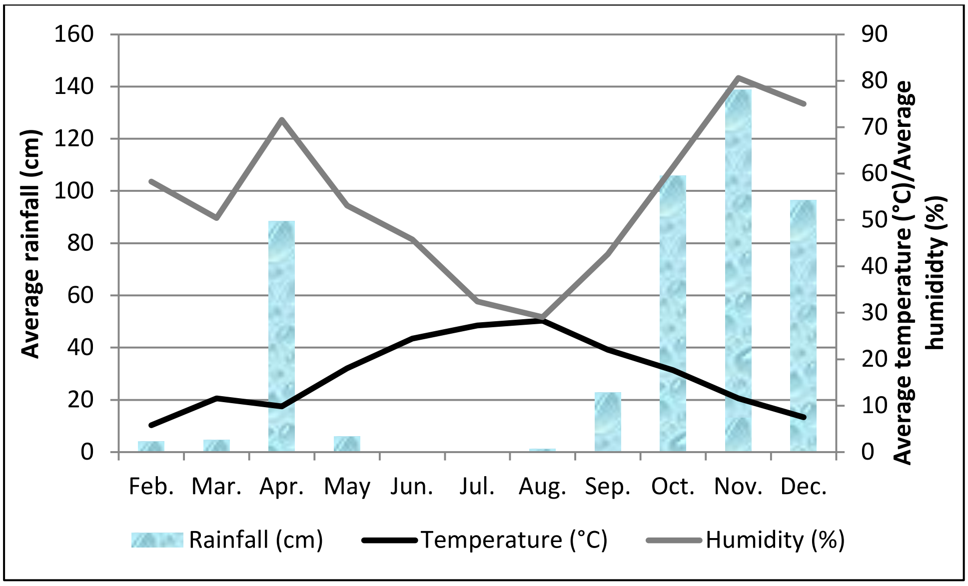


Figure 2-5: Variation in monthly average rainfall, temperature and humidity 2012 recorded at the tourist site.

2.4.3 General statistics

GLMMs

General linear mixed models (GLMMs) were used to analyse the relationships between macaques' behavioural responses and tourist pressure in chapter 4, and the relationships between health measures and provisioning in chapter 5. This approach is more powerful than multiple regression because GLMMs allow the analysis of the simultaneous effect of a series of independent variables (i.e. predictors) on a dependent variable (i.e. continuous or binomial), while controlling for the non-independence of the data points using random factors (e.g. identity of the macaques) (Pinheiro and Bates 2000). A number of other factors were also included in the models as independent variables (e.g. ecological conditions, social factors) in order to control for their effects when appropriate, and are described in further detail in each chapter section on data analysis.

GLMMs were conducted in R 2.14.0 (R Development Core Team 2011) using the function lmer of the R package lme4 (Bates and Maechler 2010). Depending on the nature of the dependent variable data (i.e. continuous or binary), GLMM were fitted with Gaussian or Binomial error structure. To determine the relationships between each independent variable and the dependent variable, log-link function and likelihood ratio tests were calculated using the R function ANOVA. Significance of the individual fixed effects was determined based on the χ^2- and p-values provided by lmer. The lmer function takes into account sample variation within individuals, so this is not included as a separate random factor.

When running GLMM analyses, several assumptions must be taken into consideration before running the models, as well when interpreting the results. In each model, multi-collinearity between independent variables was checked in order to avoid including within the same model two independent variables that were highly correlated. This test was conducted using variance inflation factors (Field 2005), and the VIF function of the R-package car (Fox and Weisberg 2010) was applied to the full linear model excluding the random effect (e.g. macaque ID). VIF values greater than 10 indicate that the two predictors are highly collinear (Field et al. 2012), corresponding to a high correlation coefficient ($r > 0.6$), and therefore the one of the highly correlated predictors that had the lower likelihood ratio tests after running the model was removed from the final model (Field et al. 2012). Furthermore, Cook's distance was measured in order to identify if there were outliers, which would influence the model (Field et al. 2012). To be accepted, Cook’s distance must be lower than 1 (Field et al. 2012). In the present study, Cook’s distance was always lower than 1.

For each model (i.e. Gaussian and binomial), the significance of the full final model was compared to the corresponding null model using a likelihood ratio test (R function ANOVA with argument test set to "Chisq") (Bolker et al. 2009). The null model corresponds to the full model excluding all independent variables, which are replaced by the value 1 in the model. The significance of each individual predictor included in the model was accepted only if this likelihood ratio test was significant and assumptions were met. I used the full model to test the effects of individual predictors and not the “best fit model” as recommended by Mundry and Nunn (2009). In the ‘best fit model’, independent variables which are not individually significant are discarded; however these predictors might still have an influence in the model and therefore arguably they should still be taken into account. In order to avoid this issue, the predictors were kept in the full model even when they did not have a significant effect. Using this method also enabled consistent analysis of the data, using the same model for the different dependent variables tested.

In addition, for the Gaussian model only, the assumptions of normally distributed and homogeneous residuals were checked by visually inspecting a q-q plot where the residuals were plotted against fitted values (Field et al. 2012). The model was accepted if the q-q plot was close to linear. However when the assumption of normality was not met, i.e. the q-q plot was not linear, the dependent variable was Log_{10} transformed in order to tend to achieve the normal distribution of the residuals. P-values for each test were derived using the functions pvals.fnc and aovlmer.fnc of the R package languageR (Baayen 2010) and were based on Markov Chain Monte Carlo sampling (Baayen 2008).

For binomial models only, the over dispersion of the data was also tested and to accept this assumption, the result must be equal to 1. The binomial models were fitted with a binomial error structure. Logit link function and likelihood ratio tests were calculated using the R function ANOVA. The maximum likelihood estimation in the mixed model (argument REML of the function lmer set to FALSE) was used (Field et al. 2012). The significance of the individual fixed effects was determined based on the z- and p-values provided by lmer (Bates and Maechler 2010).

Standard parametric and non-parametric tests

Throughout chapters 4 and 5, a number of standard parametric and non-parametric statistical tests were used, including Mann-Whitney U tests, Kruskal Wallis tests and Wilcoxon matched paired tests. All these tests were performed using SPSS software (version 21). Prior to analysis, the distribution of the data was tested using a Kolmogorov-Smirnov test. If data followed a normal distribution, parametric tests were used. If the data were not normally distributed, the data were either log-transformed to reach normality or non-parametric tests were used. All tests are two-tailed and the level of significance was set at $P < 0.05$. Sequential Bonferroni corrections were used in the present study to control for type I error rates associated with multiple testing (Rice 1989).

Chapter 3

Feeding monkeys as a tourist experience in Morocco

The nature of the human/animal interactions in the context of primate tourism is complex, and unique to each individual site. The type of tourists, cultures of the local community, the ecosystems and primate species involved all characterise the specific character of primate tourism at each place where it occurs. A key component of primate tourism, however, is the tourist experience while viewing or interacting with animals. Interactions between tourists and primates, such as feeding or taking pictures, are driven by different motivations. In order to better understand why these interactions occur, it is essential to look closely at the different types of tourists and their motivations for engaging in interactions with primates. To do this for my study site in Morocco, in this chapter I first describe the tourist site itself, the types of tourists involved, and the behaviours of these tourists towards the macaques. I then explore the different motivations of tourists for engaging in the most common human/primate interaction, namely feeding of monkeys. Understanding the motivations which drive tourists' behaviour - and thus shape their experience - may be important for developing realistic and implementable recommendations to improve primate tourism at this site and at others.

3.1 Description of primate tourism at the tourist site in Morocco

3.1.1 The tourist site

The tourist site in this study is locally named 'Moudmam' (meaning *hawthorn* in the local Imazighen language) and is located on National Road number 13, in Ifrane National park. It is on the edge of an open area where hawthorn bushes are present in large numbers. Sellers of souvenirs and fossils are located at the site, in several 5 m^2 wooden shops in front of a car park (Figure 3-1.). As well as selling, these people are also in charge of the tourists' parking. On the extremity of the parking area, there is a museum called Cedar house, which has been under construction since 2006. On the opposite side of the road is the forest, where there are picnic tables, barbecues, rubbish bins, and in general, tourists. On the corner of this area, several horse riders wait for tourists and offer them horse rides for the cost of a few Dirhams. In addition, there is a peanut seller who lives at the tourist site in a small wooden shack, and a museum keeper who adopts the role of horse rider during the day and sleeps in the semi-derelict museum at night. All these people earn their daily living directly from tourism at the site. Although the souvenir sellers have been asked to keep the site clean by the authorities, tourism at the site is otherwise completely unregulated. A group of macaques (named the Tourist Group) is present at the site. This group is commonly spread throughout the forested areas near to the souvenir shops. The tourists come to the site by car or bus and generally park either in the car park or at the side of the road. National Road 13 links the Imperial city of Fes to Errachidia in the direction of the Sahara desert. Tourists often stop at the site on their way to Fes or to the desert for a brief opportunistic stop, in what I term 'quick look' tourism. They typically spend a few minutes at the site, on approximately 15 min, to see the monkeys and to interact with them. Some tourists, generally those from outside Morocco, also stop at the site to visit the souvenir shops, which are easily visible from the road.

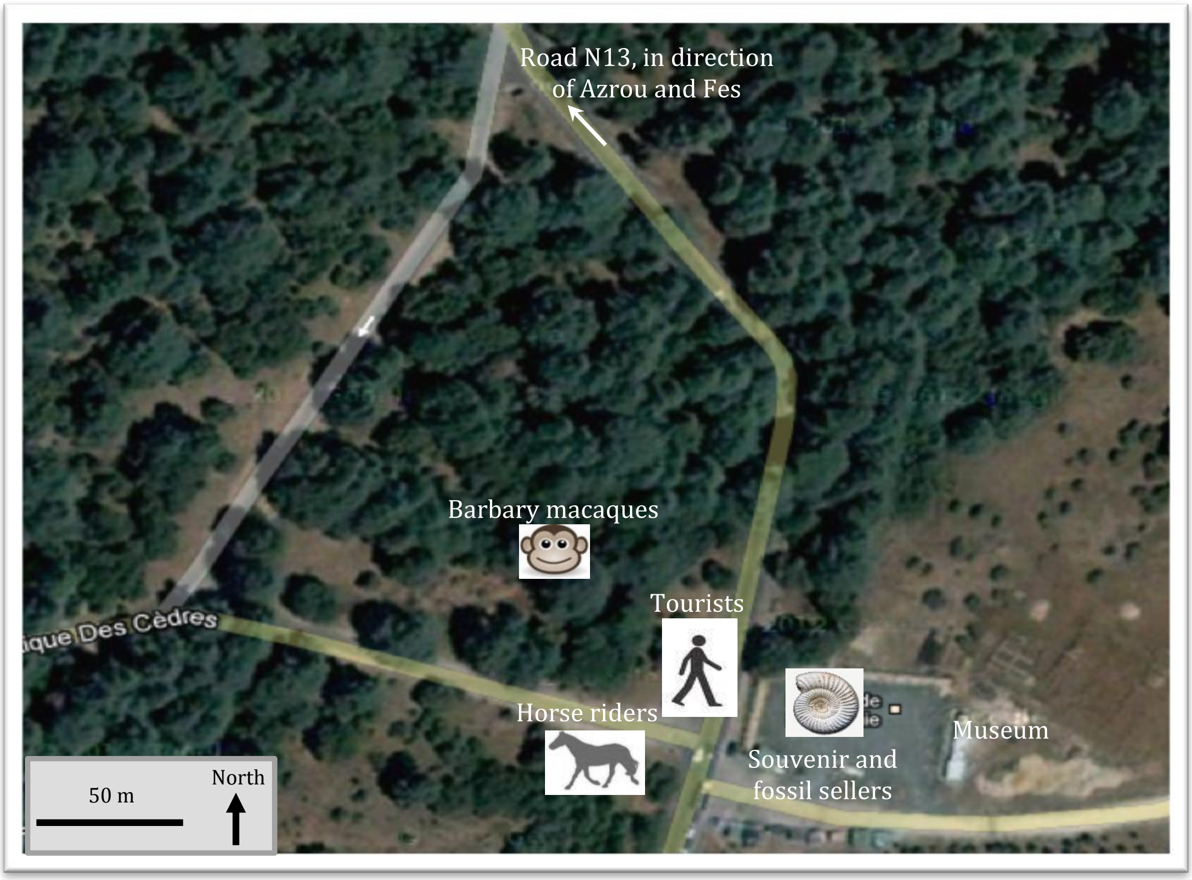


Figure 3-1: Map of the tourist site, Moudmam, close to Azrou in Ifrane National Park, Morocco, indicating the general areas where the monkeys and different groups of people are usually found. GPS: N33° 25'; W005° 10', map source: Google-Maps (2014).

3.1.2 Type of tourists

National tourists

Moroccan visitors make up the majority of the tourists at the site. The Moroccan tourists are quite difficult to define and classify; the site attracts poor and rich people, countryside and city-dwellers, families and solitary travellers. Nevertheless, I describe four main tourist categories.

Toilet break tourists

A large number of visitors use this area solely as a toilet stop on the national road, in a similar way to a highway station. However, there are no toilet facilities available at the tourist site, so people hide behind trees to urinate or defecate. They usually stop for no more than 15 minutes in total. If the monkeys are at the tourist site, these tourists often take the opportunity to take a few pictures and to feed them, but they generally do not appear to stop there primarily to see the monkeys, or for any other tourist activities. This kind of visitors mostly consists of families or lorry drivers. The latter frequent the site all the year around, but there is an increase in family visits during school holidays. Every summer, emigrant Moroccan families who live in Europe travel back to Morocco to visit their families. They cross Europe and Morocco with their cars full of presents and equipment and often pass through the tourist site for a break on their journey.

Regional tourists

Regional tourists are not present all year around, but mostly visit the site during weekends and holidays. They often come when they have relatives visiting, in order to show them the monkeys and enjoy some time in the forest. They often bring barbecues, on which they cook a tajine for lunch. They spread carpets on the ground to eat more comfortably, and to have a nap in the afternoon. When they arrive at the site, the women prepare the food and place the carpets down, while the men and children go to find and interact with monkeys. When the tajine is ready, all the family sit around and eat. The dogs and any monkeys present at the tourist site surround them, hoping to get some food. The tourists often throw food for the animals, but if the dogs or monkeys are too close or insistent, they chase them away. This occurs repeatedly until the tourists finish their meal. After lunch, the children often play football while the older tourists talk or sleep.

School trips

On Wednesdays and at weekends during the school year, many school buses stop at the tourist site. Often these buses arrive in groups and in total several dozens or even hundreds of children arrive at the site. Within minutes of their arrival, the site is transformed into a playground where children scream, play and run around. A few adults, teachers and parents generally come along to look after the children and to control their behaviour. They often stop to eat at the site where the picnic tables are. Once they finish their lunch, the children play and interact with the monkeys that are attracted by the children's food. Teachers sometimes organise games to entertain the children but usually they are left to play by themselves.

When children arrive at the site, the monkeys generally disappear into the trees, presumably because of the noise, but they reappear when the visitors start to eat. The children feed the monkeys with food from their picnic, which consists primarily of bread and apples. When there is no food left to give, or when the children get bored because the monkeys do not approach them, or do not take the food offered, the children often play by throwing rocks or branches at the monkeys. The children also climb the trees or scare the monkeys with threatening gestures. This greatly amuses the children, who laugh and become very excited. After one or two hours at the site, the children get back into their buses and continue their trip. They often leave behind a large amount of rubbish around the picnic tables, and the monkeys then forage for food amongst the litter.

City-dwellers

Ifrane National Park is located just a few hours drive from the main Moroccan cities which are the economic core of Morocco, including Casablanca (4.5 hours), Rabat (4 hours), Fes and Meknes (1 hour). In early 2000, Morocco experienced an expansion in economic development which may have modified certain aspects of Moroccan life-style including leisure activities (Cherkaoui and Ali 2007). This new wealth may have facilitated the internal tourist industry in Morocco. There are currently two main city-dweller categories who visit the site: wealthy families who arrive in their own cars and less wealthy tourists who visit on bus tours.

Wealthy city-dwellers often spend their weekends and/or holidays in Ifrane and the surrounding region. They take the opportunity to explore the surrounding forests where the monkeys are a particularly popular attraction; they come to the tourist site to interact with the macaques. These tourists generally spend between 30 min and 2 hours at the site, often feeding the monkeys with peanuts bought from the peanut seller, or with food that they have brought with them. They spend their time taking pictures of themselves and the monkeys or the horses. They also often explore around the tourist site and occasionally go deeper into the forest to find the monkeys if they are not visible close to the road.

In winter, bus tours are very popular for middle class Moroccan city-dwellers and these trips provide them with an opportunity to see snow, often for the first time in their lives. Several dozen buses leave in the early morning from big cities such as Rabat, Casablanca, Tangier, Fes or Meknes, and drive toward tourist sites to see the snow. These sightseeing tours often cover a number of sights in one day. Moudmam is generally the first stop of this journey and they usually finish in Michelifène, a popular ski resort located at few kilometres away from the site. These tourist groups normally spend between 15 minutes and 1 hour at the tourist site, usually playing loud music, playing in the snow, feeding monkeys, riding horses and taking pictures.

International tourists

International tourists represent less than the 20% of the visitors at the site. Most of these tourists come from Europe, and the majority are French and Spanish. I have sub-divided international tourists into 3 different types: tourists on guided tours, those in 4x4 convoys, and retired people with camper-vans.

Guided tours

Guided tours generally stop at the site for ‘quick look’ tourism, where tourists view and interact with monkeys for just a few minutes, averaging 15 min (Personal observation). This stop at the tourist site is not included in the ‘official’ tours which operate from the major cities. There are two types of guided tours: group tours and private tours. In the group tours, tourists travel in mini-buses or coaches depending on the price and type of excursion. Each bus usually contains tourists from different countries including France, Spain, Germany, England, Poland, and Brazil. The private tour is reserved for wealthier tourists, as it is a rather more expensive way to travel than the group tours. Private tours are usually composed of couples or families.

When the guided tour vehicles stop at the tourist site, the tourists and the guides go in the direction of the monkeys to interact with them. Tourists are often quite shy and do not know if they should approach or feed the monkeys. As time is often very limited, guides usually encourage the tourists to interact with the monkeys by buying peanuts from the peanut seller and attracting the monkeys with the food. They show the tourists how to feed the macaques, explaining that they do not need to be afraid, and encourage them to get close to the monkeys for a picture. After a few peanuts have been given to the monkeys, tourists become more comfortable with the interaction, and appear to enjoy the experience very much. Guides have a limited knowledge of the monkeys but it is rare that the tourists ask for much information, except perhaps which kind of monkeys they are.

4x4 convoys

Another type of tourist group is the 4x4 convoys, which come mainly from Spain or Portugal. In spring and autumn, especially during the Easter and All Saints holidays, many Spanish families, typically couples on their own or couples with children, drive in convoys of 4x4 vehicles toward the desert for a week or so. Generally each convoy is composed of between 10 to 20 vehicles. The families do not necessarily know each other before the trip but a friendly relationship seems to link those in the convoy. It is not always clear if there is a guide paid to organise the trip or if the person in charge is simply someone who is more experienced in that particular location. It is also not always clear if they stop at the tourist site because of the monkeys or because of the souvenir sellers, as these tourists often spend as much time in the souvenir shops as with the monkeys. Some of them do not even seem to realise that there is a group of macaques nearby. When they do interact with the monkeys, they usually try to take a picture of each person in the group feeding one or two macaques. They rarely go very far into the forest to try to find the monkeys who may be hiding in the trees; instead, they mostly focus on the ones that are easily visible and accessible on the ground.

Retired people with camper vans

In spring and autumn, another type of tourist is frequently present at the tourist site; these are retired people who travel in camper vans. The majority are retired French couples who come to spend between 3 to 6 months, from autumn until spring, in the hot regions of Morocco. On their way to the desert, or on their way back to France, some of these tourists travel through the Middle Atlas and stop at the tourist site. There is no typical length of time for this group to stop; some can spend a few minutes at the site and others spend the night. The flexibility of their schedule and the nature of their accommodation make these tourists less predictable. This group are the most reliant on guide book advice. These tourists stop at the tourist site mainly because of the monkeys and to see the forest, either because the location was advised in their guide book or because they have visited the same place for many years. They often take time to explore the surroundings, especially if the macaques are not at the tourist site but are further away in the forest. The behaviours of these tourists towards the monkeys also varies greatly, from close interactions including feeding, to taking pictures and keeping a reasonable distance from the animals. Interestingly, I would suggest based on my personal observation that people who go deeper into the forest to find the monkeys are also more likely to keep some distance from them once they have found them.

3.2 Interacting with monkeys as a tourist experience

Although the tourists visiting the site are diverse in terms of their nationalities, age, culture, social background, and although they come to the tourist site for a variety of different reasons (e.g. for a toilet break, to see the monkeys, or the snow, or the forest) tourists do tend to have similar interactions with the monkeys. The two main activities that tourists engage in are feeding the monkeys and taking souvenir pictures. In the following section, I investigate in detail the tourist interaction of feeding the monkeys, and explore tourists' different motivations for doing so.

As previously described, feeding monkeys is the main monkey-related activity that tourists engage in when they are at the site and thus this plays a key role in shaping their experience. This is common in primate tourism (Bali: Fuentes 2010; Japan: Knight 2011) as well as in wildlife tourism more broadly (Orams 2002). Feeding animals was, until recently, also a very popular attraction for visitors to zoos. Until wildlife tourism began to expand rapidly a few decades ago, feeding of animals was restricted to captive individuals and groups which were dependent on food provisioning to survive. The desire to be closer to the wild world in a more naturalistic environment may explain why wildlife tourism is increasingly popular (Mallpur 2013). In order to facilitate viewing of wildlife for research and/or tourism purposes, the provisioning of wild animals has become much more common. The examples of Barbary macaques in Gibraltar, long-tailed macaques in Bali and Japanese macaques in Japan provide useful illustrations of the development of primate tourism via food provisioning.

Barbary macaques in Gibraltar

Although the origins of the Barbary macaque colony in Gibraltar are still subject to discussion, Modolo (2006) found that this population is genetically linked to North Africa, suggesting that these animals were introduced by humans from Morocco and Algeria. The Gibraltar population was under management from 1915 until 1990s by the British army in charge of the macaques, provisioning them and controlling population size (Perez and Bensusan 2005, Modolo 2006, Shaw and Cortes 2006). Currently, the monkeys are managed by the Gibraltar Ornithological and Natural History Society (GONHS), and provisioning is employed as a management strategy to avoid macaques raiding for food in the town (Perez and Bensusan 2005). Unauthorised feeding began to cause problems as early as the 1900s, and a law was passed prohibiting feeding by non-official authorities (Perez and Bensusan 2005). As Fuentes (2006a) described, it was in 1960 that increased and regular human interactions with the macaques began as a tourist attraction.

Semi-free ranging macaques are kept in the Upper Rock Nature Reserve, where visitors pay an entrance fee to come to see them (Perez and Bensusan 2005). Illegal provisioning by tourists, taxi drivers and tour guides, has increased with the growing popularity of the monkeys as a tourist attraction. In 2002, a substantial increase in fines for feeding macaques was imposed and a number of signs were erected, in an attempt to enforce the law. Despite this management effort, illegal provisioning still causes problems, including posing a nuisance for local people, occurrence of aggression to tourists and locals, and problems for the macaques' health (Perez and Bensusan 2005).

The majority of tourists who visit the Upper Rock Nature Reserve in Gibraltar to see the monkeys are international tourists. Large cruise ships stop at Gibraltar as a part of their itinerary. Buses and taxi drivers then drive the tourists up the rock to see the macaques. The total duration of these visits varies between a few hours to a full day, leaving time for tourists to visit the city as well as the nature reserve.

Long-tailed macaques in Bali

Macaques and humans in Bali have co-existed for centuries, sharing spaces and forming complex relationships, with monkeys being seen in different ways, for example as objects of religious worship, as economic commodities or pests (Wheatley 1999, Fuentes 2013). Many temples in Bali have become significant tourist attractions since the mid-1990s, where tourists come to see monkeys as well as the temples themselves (Fuentes et al. 2006). Tourists often must pay a fee to enter these temples or to purchase food for the macaques, which increases the income of the local community (Fuentes 2013). Domestic and foreign tourists are present at the different sites, travelling via tour guide companies or in individuals' vehicles (Fuentes et al. 2006, Fuentes 2010).

Provisioning constitutes 50-70% of the diet of macaques at Padangtegal temple, one of the largest temple and primate tourism attractions in Bali (Fuentes et al. 2011). Macaques receive daily food from the temple staff committee, from tourists and from temple offerings. Warning signs are erected at the site to inform tourists that feeding monkeys can be dangerous, and requesting that visitors do not do so (Fuentes et al. 2006). In addition, staff members intervene and warn visitors who try to feed the monkeys, but despite these efforts, feeding interactions are still very frequent (Fuentes et al. 2006).

Japanese macaques in Japan

Japanese macaques were intensively hunted until the mid-twentieth century, and were subsequently very wary of humans, making study of these animals in their natural setting very challenging (Knight 2011). Japanese primatologists suggested that provisioning wild macaques would facilitate the observation of these monkeys. In the 1950s successful provisioning started, and soon after a number of sites began provisioning to attract and to tame wild monkeys for scientific and tourism purposes (Knight 2011). Nowadays, monkey parks are very popular in Japan, and there are at least 41 spread all over the country. Provisioning is mainly carried out by park staff that lure habituated groups of macaques to an open feeding station at the core of the park. Visitors come to see the monkeys and pay a fee to enter the park (Knight 2010, 2011).

Tour party visits are very popular in Japan, and monkey parks are often on the itinerary of sightseeing tours (Knight 2010). Buses stop typically for 40 minute periods, which enable tourists to see the monkeys for few minutes before heading off again. Wild monkeys must therefore be present and visible at the feeding site for this 'ready–to-view' wild monkey experience, and provisioning is therefore used every half-an hour to "fish monkeys outside of the forest" (Knight 2010). Large warning signs indicate to visitors not to feed monkeys, and staff members monitor the interactions between tourists and macaques and intervene when rules are not respected (Knight 2011).

Barbary macaques in Morocco, at the site of the present study

Barbary macaques, like most wild animals, have a natural fear of humans. At the study site, this may have resulted from, or been reinforced by, agonistic encounters with Moroccan people, including poaching, chasing and hunting (Majolo et al. 2013). Several older local tourists at the site, during interviews with me, reported stories of their teenage years, explaining that they used to chase monkeys for fun in the forest by displaying yogurt pots to attract monkeys, and hiding, waiting for the monkeys to eat the yogurt. As the monkey got his hand stuck in the pot and could not climb up the tree, they were easier to chase. Other locals related similar stories but instead of yoghurt, they used bread and alcohol. It cannot be established if these stories were of their own activities, or if they had heard them from others; however several locals narrated similar stories. These games were also described as forming part of the poaching technique. The poaching of Barbary macaques for the pet trade is a common occurrence in the forest surrounding Azrou, with infant

Barbary macaques caught and sold to tourists as pets, or for entertainment purposes in Marrakech (van Lavieren 2008). The other threat to the monkeys comes from shepherds' dogs, which have been observed attempting to catch (and actually catching) infant and juvenile Barbary macaques. In addition to these practices which are ongoing, a former forest ranger also reported that intensive hunting of macaques took place in the 1970s, as it was believed that the macaques were destroying the forest by stripping bark from the trees for food. He recalled that during these hunts, a large number of monkeys were killed; however Barbary macaques have never been hunted for food in Morocco (Majolo et al. 2013). To summarise, humans may be perceived as dangerous by wild Barbary macaques, and non-habituated macaques generally avoid people where possible, fleeing when they encounter people (Personal observation). This situation is comparable to the one in Japan where the non-habituated monkeys generally avoid human encounters. Habituation is therefore necessary in order to get close to wild Barbary macaques.

Sites where the provisioning of monkeys has successfully led to a lucrative tourist business - such as in Gibraltar, Bali and Japan - are now internationally well known. These examples may encourage other countries and sites to try a similar approach. In the late 1990s, encouraged by the successful attraction of a group of Barbary macaques at the Cêdre Gouraud site near Azrou, souvenir sellers set up their stalls at a crossing point on the National road 13, which has now become the tourist site of the present study. Local souvenir sellers recalled that one year in the late 90s, during a serious summer drought, they observed that the macaques were looking for water. They saw the drought as a perfect opportunity to start attracting monkeys by providing monkeys with a place to drink. For this, they provided a tyre cut in half filled every day with water. With daily water and food provisioning from souvenir sellers and tourists, it was not long before the monkeys were well habituated to human presence. Today, the feeding of monkeys by the souvenir sellers is no longer needed in order to habituate the animals, but is instead used solely as a way to ensure that monkeys continue to show up reliably at the tourist site. So, although souvenir sellers used to provision the macaques regularly, the monkeys now obtain their food almost entirely from tourists, and only very occasionally from the local sellers. Locals provide water in dry summers or disperse a few peanuts on the ground to attract the monkeys when they are not at the tourist site. Horse riders and souvenir sellers reported that provisioning monkeys by tourists was the only way to ensure their presence at the site, and if the macaques were not coming any more, their business would suffer.

The tourism context at this site differs from the examples of Gibraltar, Bali or Japan in that tourists do not pay fees to visit the site, and the majority of tourists do not come purposely to see the monkeys. Rather, the tourists' presence at the site is more opportunistic or incidental, in a similar situation to that seen for howler monkey tourism in Belize described by Grossberg et al. (2003).

3.3 Tourists' motivations

Currently, macaques are mainly fed by tourists at the site, Moudmam. For tourists, feeding monkeys is clearly not done for economic reasons as was the case when the locals initially did it; tourists therefore may have different motivations for feeding monkeys, and these may be related to people's perception of macaques. Exploring American preferences for a range of animals, Kellert (1996) found that aesthetically appealing animals were one of the most preferred animal categories. Moscardo and Saltzer (2004, p.10) similarly found that *"there were preferences for large, cute, furry and non-threatening species. Similarly, when asked of the most memorable animal, visitors provided a mix of very different animals, but again highlighting the importance of 'cute and cuddly' and larger size."* In addition, tourists appear to be highly attracted to animals presenting special features such as similarity to humans, and to those which are rare or endangered (Newsome et al. 2005). Barbary macaques would fall into the 'most preferred' category of Kellert (1996) and Newsome et al. (2005) because of (according to tourists' comments at the tourist site) their cute, fluffy, relaxed and human like appearance, and due to the fact that they are classified as an endangered species. Their attractive cute aesthetic may explain why Barbary macaques are a very popular tourist attraction in Gibraltar and in many animal parks across Europe. The emotional motivation of tourists for interacting with animals is likely to be related to their aesthetic value. In fact, Serpell (2004) suggested that attitudes toward animals could be categorised into two primary motivational considerations: affect and utility. According to his definition, affect represents people's emotional responses to animals, whereas utility represents animals' instrumental value. As no utilitarian value might be conferred upon Barbary macaques from the point of view of tourists, I would suggest that tourist motivation for feeding these animals is associated with Serpell's concept of affect. Their loveable appearance, in addition to the emotional motivation of tourists, may underlie tourists’ fascination and keenness to interact with the macaques.

Sharing food with animals is a complex interaction, often involving a range of different motivations, ranging from cultural and religious reasons to emotional bases. Orams (2002, p.287) stated that *“the sharing of food is more complex and fundamental for humans than simply a means of getting close to animals. The sharing of food is a fundamental part of human nature…”* Feeding monkeys, therefore, either by hand or by throwing food, is a personal act which might be driven by diverse motivations. In the following sections, I explore these different possible motivations for this behaviour; it is important to note that these are not mutually exclusive.

The merit of sharing food

In wildlife tourism, the attitudes of tourists towards animals may be driven by emotional responses, and can therefore be classified as affect, as described by Serpell (2004). The feeding of wildlife is often underpinned by emotional responses such as pity or a need to care for animals. These emotions are transferred into a compassionate attitude or behaviour, often leading people to believe that feeding wildlife is an altruistic act. This presumed altruistic behaviour has the effect of increasing the self-worth of the tourist (Orams 2002) and may lead to psychological health benefits (Curtin 2009). Emotional responses associated with feeding wildlife might also be triggered for reasons including empathy and identification, a sense of responsibility, or cultural and religious influences (Orams 2002). There are a number of possible reasons why tourists may think that feeding Barbary macaques is a generous gesture, and these are discussed below.

Empathy/Identification:

Emotional responses might be linked to empathy/identification with animals that live in challenging conditions. Barbary macaques at the tourist site would fit this representation of poor animals living in a harsh environment. In fact, a number of tourists stated that the monkeys had nothing to eat in this forest, and pointed out the surroundings of the tourist site, showing the degraded soil, where no grass was growing anymore, the surrounding trees where no fruit was visible, rocks as well as rubbish lying around. It is true from a human perspective that this environment may appear very poor, without much that is edible food available. Indeed, provisioning seemed to increase in the summer and winter periods when the vegetation was dry or covered with snow. It seems that tourists projected their own interpretation of animal needs, leading to empathy/identification with the animals' need for food. Tourists often asked what monkeys ate when there were no tourists around, and I answered that Barbary macaques were omnivores and mostly eat grass, acorns, leaves, insects or small vertebrates. After hearing the macaques' natural diet, some tourists grimaced and stated that if they were a monkey themselves they would also prefer human food to their natural diet. This displays a clear identification with the animals, and with these words, tourists justified the need for feeding the monkeys.

Similar perceptions by tourist were described by Russell (1995) when reporting how volunteer eco-tourists perceived orphan orang-utans: the majority of tourists perceived orang-utans as childlike. In addition, Knight (2011, p.196) pointed out that: *"the conservation motif is also prominent in accounts of the provisioning of monkeys on the Shimokita Peninsula in northern Japan… But it is claimed that provisioning was also an expression of villagers' concern for the monkeys. Maruyama Yasushi has suggested that the onset of regular food handouts at Kusodomari should be understood as an act of villager compassion for the starving monkeys living nearby… Maruyama has also claimed that, in helping monkeys in need, the villagers simply extended their own tradition of solidarity and mutual assistance to the monkeys... Takahashi Kinzo also sees provisioning at Kusodomari in altruistic terms, as related to 'the development of a wild monkey protection movement in which the village thinks of the wild monkeys as our children and our friends'."* As seen in the examples in Morocco and in Japan, people often express empathy for wild animals in order to explain their provisioning; this act is also associated with identification.

Sense of responsibility linked with animal dependence/domestication

The emotional responses of the tourists at Moudmam seemed also to be triggered by an apparent feeling of responsibility towards 'domestic' monkeys. The majority of tourists referred to the macaques present at the tourist site as 'domestic', as compared with the 'wild' monkeys further away in the forest. Defining what they meant by 'domestic' they answered for example that *"domestic ones were the nice* *ones who you could give food to".* Others answered that the *"domestic ones depended on human food while the wild ones did not".* When informed that they should not feed the monkeys, many tourists replied that without food from humans, the monkeys would not be able to feed by themselves any more, and were now entirely dependent on humans for food. This may show a feeling of responsibility for the animals. In the minds of tourists, the acceptance of food from humans by the macaques seems to make them domestic animals, which in turn brings a responsibility to continue to provide food for animals which can no longer survive without this human support. This feeling is reinforced by the fact that the monkeys were, in their view, clearly waiting to get fed by tourists, and tourists rarely saw the monkeys outside of the tourist site eating natural resources by themselves, so the feeling of dependence is strong.

Orams (2002, p.284) introduced a similar idea, stating that some animals lose the ability to find food by themselves especially when provisioning occurs in the long term. *"When an animal does less of this, they quite simply become less efficient at it… Eventually, if an animal is fed so frequently that it no longer needs to forage for itself, it may lose the ability or skills to do so and become dependent on the human handouts."* Similar views were also expressed in interviews with tourists visiting marmosets in a city park in Brazil (Leite et al. 2011). The majority of people believed that the animals were starving and needed to be fed by managing authorities, although the study provided evidence that the animals were healthy. Leite et al. (2011) explained that people seemed to perceive the wild marmosets in the park as pets or zoo animals, which needed to be looked after. In Japanese monkey parks, similar comments were made first by primatologists (Knight 2011, p.450): *"Monkey parks are 'natural zoos' or 'wild monkey parks' in name only, because they run in such a way that monkeys end up losing their 'wild'* character (Mizuhara 1967 in Knight 2011)… This decline in the 'wild' status of provisioned monkeys is sometimes represented as a form of domestication." In addition, in his article *"Monkey mountain as a megazoo: analysing the naturalistic claims of 'wild monkey parks' in Japan",* Knight (2006, p.245) points out that the claim by monkey parks to display wild and free monkeys is controversial because of the way that provisioning changes monkey behaviour by reducing and focussing the range of previously more nomadic animals.

Culture/religion:

The vast majority of tourists who were present at the site of this study and who fed the monkeys were Moroccans. Most thought that feeding monkeys was a good thing for these animals, but some also stated that to be good for the monkeys, the food must be healthy. Some of the tourists also stated that feeding monkeys was a generous act *"because the monkeys need this food in the same way that humans need charity"* or *"feeding monkeys was a donation, a charitable act and that God rewards charitable actions."* Sharing food with monkeys may therefore be underpinned by religious beliefs. Charity is a renowned and key part of Moroccan culture, which is generally closely linked with the Muslim religion. One of the main principles of Islam is generosity toward less fortunate people, especially in relation to food. The Qur'ān (Al-'Insān 76:8, p.605) states: *"And they give food, in spite of their love for it (or for the love of Him), to the poor, the orphan, and the captive.''*

Orams (2002) discussed how peoples' motivations for feeding wildlife vary according to the differing human/wildlife relationships seen in different philosophies. He gave as an example the Judeo-Christian perspective of seeing animals as subordinate to humans; the sharing of food with animals as an act of charity relies on the animals' inferior position to humans. Animals are seen as poor creatures which need to receive charity from humans in order to survive. It seems that this Judeo-Christian view may also be shared by the Muslim faith. Zhao (2005) and Fuentes et al. (2006) also mention that the religious beliefs found in Buddhism and Hinduism influenced tourists' feeding interactions with macaques, with food seen as a charitable offering.

Sharing food to facilitate the creation of a relationship between the monkeys and the tourists

In unregulated primate tourism, if the feeding of wildlife is not strictly forbidden and the interaction appears safe, then the majority of tourists may be willing to feed the monkeys. Fine (1992) stated that there is an unmediated and intensely personal relationship between the person and the natural word. Tourists might therefore seek the creation of such intimate relationships with wild animals, which may be a representation of the natural world. Markwell (2001, p.51) described an encounter between a tourist and a young orang-utan: *"the interests of the animal were apparently subsumed by the tourist's desire for a physical, personal and* *somewhat unique experience with an exotic animal."* The opportunity to experience an intimate relationship with wildlife is greatly appealing for the majority of tourists. In addition, Horwitz (2011, p.1) suggested that pet owners found feeding their pet to be associated with bonding: *"For many owners feeding their pet is a bonding experience associated with love and caring. They like to show their pet how much they care, and providing the pet with delectable food, treats, and special titbits symbolize love."* Horwitz (2011) states that feeding wildlife facilitates creating a relationship with the animal. I suggest that, at this study site, the first feeding encounter may also greatly influence the tourists' subsequent relationship to other monkeys.

Observing tourists feeding a monkey for the first time, it became clear that this act was the key which determined the connection between each tourist and the macaques. The following is a description of an encounter which was very typical of what generally occurred during first feeding interactions at this tourist site. This is taken from my field notes:

> A young Moroccan woman, encouraged by her group of friends, approached a juvenile monkey with a peanut in her hand. Her approach was hesitant, and she looked back to her friends for support. Her emotional state appeared to be that of anxiety, fearful of the reaction of the macaque. But she also showed excitement; she was smiling and nervously laughing. The monkey approached her in order to reach the peanut she was offering. Suddenly the young woman withdrew her hand and emitted a little scream of fear just as the young macaque was about to take the peanut. She turned back to her friends, who were all laughing. She then attempted

to feed the macaque a second time. This time she did not panic and the young macaque quickly grabbed the peanut from her hand. She had a big smile on her face, and turning back to her friends she exclaimed: *"look what I have done, he is so cute, and he took it from my hand very nicely. Give me another peanut I will try again…"* She then went straight back to the young macaque to give him more peanuts, and after a few tries with the same monkey, she went on to feed several other monkeys surrounding her.

Knight (2011) described a similar experience of Hazama Naonosuke when he succeeded in feeding a monkey for the first time. Knight (2011, p.163) reported the particular and intimate experience of Hazama's first feeding interaction:

> "One morning after I had set out in the dark for the national forest as usual, I was sitting in the second temporary feeding station just created when a large monkey came up close to me and stared at me… As I talked quietly, I rolled an apple over to it to see what would happen. When I did this, he picked it up without hesitation and went over to a nearby tree where, appearing relaxed, he started to eat it. At that time, as well as feeling a deep affection for this first one of them to directly accept food from me, without thinking I exclaimed to myself in my heart, "right, now provisioning will succeed". The reason for this was that when a top class large monkey like this comes up this close, it means that most of the others will come to trust me too."

Sharing food represents a means to facilitate and secure an intimate relationship with animals. Humans infer that, by accepting food, animals consent to this relationship. From this implied agreement between tourists and monkeys, a trustful relationship can be built. As described in the two examples above, feeding monkeys enables tourists to create a trusting, intimate relationship with them. This trust is perceived to be mutual. On the one hand, as Hazama pointed out, if one monkey took food, others will be likely to imitate him and accept food as well. On the other hand, tourists need to be reassured that interacting with macaques is safe. Once the first interaction has been successful, the tourist is generally much more confident and willing to closely approach and/or feed the macaques.

Education and/or a 'rite of passage' for children

A number of parents justify feeding monkeys because of their children. They claim that children enjoy feeding animals and that it is important that they experience the contact with the monkeys. According to a number of parents I spoke to, children prefer more interactive experiences with animals, rather than merely observing them. It is obvious from many observations that the first interactions between children and macaques are frequently initiated and/or encouraged by the parents. Parents seem to gain a great joy and pride in helping their children overcome their fear of the monkeys. Here, I observed the following:

> A little boy, aged around 5 years old came along with his father toward an old macaque that was sitting on the ground relaxing. The child was carrying a bag of peanuts and, encouraged by his father, he presented some peanuts to the macaque. The monkey grabbed a few peanuts and ate them immediately. The child looked at his father smiling, looking clearly proud of himself while his father congratulated him for conquering his fear of the monkey.

In some cases, however, the interactions with macaques do not seem to be a pleasant experience for the children but their parents quite often encourage or even force them to interact with macaques regardless of their fear. I often observed parents forcing crying children to hand a peanut to a monkey. After such interactions, often parents claimed: *"You see, nothing happened. There is nothing to be scared of."*

From these examples, it seems that parents encourage their children to have new experiences, and the feeding of wild monkeys is a prime example of this. It is quite difficult to interpret whether parents feel that children must experience a relationship with animals in order to build their confidence or whether they are proud because their child has been brave in a fearful situation. Shepard (1996, p.332) stated that animals may provide a *"first lesson in otherness*", and this might explain why parents want to provide their children with this particular life experience. Furthermore, Mithen (1999, p.195) said: *"People have a remarkably rich and varied set of relationships with animals… we use them to entertain and to educate us."* Leite et al. (2011, p.191) described that *"Most adults considered the presence of marmosets in the park important, because they provided "entertainment", especially for children who may have little opportunity to interact with wild animals."* Endenburg and Baarda (1995) described how parents perceive a child's contact with pet animals to be very important for their child's development. It seems likely that this perception could also apply to their child's contact with wild animals, as suggested by Leite et al. (2011).

I will make a parallel between feeding monkeys and the experience described by Markwell (2001, p.47) of a tourist who had climbed a mountain, a challenging experience which she was proud to have accomplished: *"I will always remember the fuckin' mountain. I am glad I did it. I felt elated."* Markwell (2001, p.48) stated that *"the boundary between tourist and the wild was, to some extent at least, transcended during the final stage of the ascent. A certificate is given to each successful climber and this becomes a symbolically important way of confirming their experience."* In the same way, when children are encouraged by their parents to feed a wild monkey, a picture is generally taken in order to immortalise the proud moment. In this case, the picture might have the same symbolic representation as the certificate in Markwell's example, confirming the tourist's experience and achievement.

Sharing food as an instrument of control over animals

One of the major motivations for people to feed animals is to gain control over them. In Japan, monkey park staff use food to control macaques' movement patterns, and to attract them to the feeding station where they can be seen by the tourists. As stated by Knight (2011, p.289): *"The food handouts in the monkey park are, in the first instance, an instrument of control over animal movement rather than a substitute animal diet."*

In Morocco, local people at the tourist site try a similar strategy to that used in Japan by occasionally baiting macaques with food. This strategy is generally used in spring and autumn when monkeys appear less frequently at the tourist site. The majority of the food is nevertheless now provided by tourists rather than locals. In contrast with local people and park staff in Japan, tourists do not use food to ensure the presence of macaques but they rather use it as an instrument to control animal's behaviour when they are already present at the site. From my year of observations at the tourist site, I identified two main motivations for controlling animals: to enable the tourist to get closer to the animals, and for the tourists' entertainment.

Getting closer to the monkeys

Orams (2002, p.281) stated: *"The feeding of wildlife has become a popular means by which tourists and tourism operators can facilitate close observation and interaction with wildlife in the wild."* One of the main reasons why people tend to feed wild animals is to enable them to get closer in order to facilitate the observation of the animal. Orams (2002, p.287) stated: *"There are a wide variety of reasons – certainly the provisioning of wildlife allows the close viewing of animals which may otherwise be inaccessible for tourists."*

In the article *Ready to view wild monkeys,* Knight (2010, p.744) describes how *"the parks render macaques instantly viewable for time-pressed tourists through the practice of food provisioning".* In Japan, tourist attractions are generally scheduled to be time efficient, in order to view as much as possible within a limited time frame. Wild monkey parks ensure the reliable presence of macaques by baiting them with food at a specific feeding station. The feeding stations are often an open space in the middle of the forest, allowing tourists to have a better view of the overall monkey troop. Knight (2011, p.80) described these feeding stations: *"In essence, the monkey park is a small clearing surrounded by a large forest. The challenge for the park staff is to lure the monkey troop out of the forest and into a clearing at the start of the day and then to get it stay in the grounds of the park until closing time."* In addition, staff lure the monkeys to the clearing in order to encourage the visibility of the whole troop, in order to show the social relationships and the range of behaviour associated with the entire group. Knight (2011, p.44) reported an interview with Mitsuji of the Takasakiyama Park, who said: *"If there were only ten of them, it would not be a troop. That's what I think…. But at Takasakiyama we have the concept of showing troop monkeys. Therefore ten monkeys would be no good! There have to be babies, there have to be females, and there has to be a leader and so on. I think that the original mission is to show the whole thing."* Knight (2011, p.45) also added: *"The visitor experience of the monkeys as a troop is intensified by the practice of feeding the troop… When staff dispenses large amounts of food, the hitherto dispersed troop becomes concentrated in the centre of the park to form a dense monkey crowd."*

In the context of Barbary macaques at my study site, which are already tamed by years of provisioning and are visible from a few metres distance, it seems that tourists are willing and keen to get even closer. By contrast, however, with Japanese parks, tourists do not seem to look for the whole troop experience but rather they seek more of a one-to-one interaction with a single monkey. One of the tourists pointed out to me: *"If we do not give them food, they (monkeys) will never approach us and we could not see them like this."*

Frequently at this site, tourists attracted macaques with food in order to get them down from the trees and onto the ground so that they could get closer to them. They also tried to bait them further away from bushes, to get them into open spaces, or make them climb up onto a rock where they were more clearly visible. This control of monkey positioning enables tourists to better observe, and interact more closely with the macaques. It also helps for the composition of the pictures, by which tourists wish to remember their experience. They move the animal in order to fit with the image they would like to capture. They often try to position the wild monkey close to a relative. Tourists often tried to pose by the side of a monkey, handing them a peanut to ensure the monkey’s cooperation. If the light or background setting were not adequate, they baited the monkey to move a bit further away where the conditions were better for the photograph.

Another reason why tourists feed wildlife is to get closer in order to initiate an interaction such as playing, or petting the animal, as described by Shackley (1996) and Orams (2002). As previously suggested, tourists are keen to create a relationship with macaques, which often then progresses into actual interactions with the animals. Giving food to animals generally facilitates the approach and the subsequent interactions.

Entertainment

Monkeys are widely used for entertainment, and this is a very powerful image in people’s minds. When I asked a Moroccan policeman (who was regulating the traffic at the tourist site) what he thought people think about the monkeys, he replied: *"Monkeys are like clowns for people; like visual theatre, the same as in Marrakech. They do not know that they misbehave."*

A Barbary macaque performance in Jemaa el-Fnaa square in Marrakech is indeed a well-known tourist attraction which is advertised in a number of tourist guides (Humphrys 2012), and also on Moroccan TV. Many tourists, therefore, have a perception of 'monkey acrobats' that perform some shows to entertain them. At the study site, the most common interaction was feeding monkeys for something that appeared to lie somewhere between entertainment and training purposes. Tourists often deceived macaques, pretending to hand them food and then retrieving the food before the macaque could get it. This greatly amused the tourists, with the aim of the 'game' apparently to see who was the quickest between the tourists and the monkey. After several attempts, the monkey often became frustrated and either showed aggressive behaviour toward the tourists or moved away. However, to ensure the cooperation of the monkey, tourists generally gave the bait food to the monkey as a reward after a few tries; if they could not gain the cooperation of the monkey, tourists often threw rocks or branches at it. Another entrainment interaction associated with food occurs when tourists get the macaques to grab the food from different positions. For example, they often present the food so that the monkey had to stand on its feet, or jump to get it.

3.4 Problems caused by unauthorised feeding and why tourists do not stop feeding animals

Problems caused by unauthorised feeding

A number of serious problems have been found to be associated with unregulated and unauthorised feeding of primates, in particular for the animals' health (Honess et al. 2005, Maréchal et al. 2011). Disease transmission between humans and macaques has been shown to be a real threat for the welfare of animals (Engel et al. 2002). Fuentes (2006a) stated that a number of disease outbreaks in the Barbary macaque population of Gibraltar were suggested to have been due to pathogens transmitted from humans to the macaques. In addition to disease transmission, macaques' health may be greatly compromised by over-feeding, which can lead to animals becoming apparently overweight and unhealthy (Perez and Bensusan 2005).

Unauthorised feeding may also greatly increase the risk of poaching and traffic accidents. Poaching is the main threat to Barbary macaque population survival in Morocco (van Lavieren 2008). A number of colleagues at the tourist site observed tourists occasionally trying to grab and take away in their car an infant monkey that they had lured with food. In addition, feeding may increase the risk of traffic accidents. At the study site Barbary macaques spend a large amount of time on the edge of the very busy National Road N13. The traffic there is reasonably heavy and constant, and the speed limits and driving rules are rarely respected. Consequently, every year a number of macaques are injured or killed in traffic accidents (Personal observation). Unfortunately, collisions with wildlife are rarely reported to authorities and therefore no accurate data are currently available on the real impact of traffic accidents on the macaque population.

Finally, unregulated feeding may increase the risk of crop raiding and town raiding. Gibraltar provides a perfect example of the problems of town raiding by Barbary macaques, which causes some very serious issues for the local community (Perez and Bensusan 2005). In Ifrane National Park, some locals have reported occasional crop raiding and house invasion by Barbary macaques, but these events have not yet become widespread.

Why tourists do not stop feeding monkeys when asked to do so

In order to eliminate tourist provisioning of macaques, a number of tourist sites - for example in Gibraltar, Bali and Japan - have erected large signs to inform tourists that feeding primates is forbidden (Perez and Bensusan 2005, Knight 2011). In some places, substantial fines are charged to limit unregulated feeding by tourists (Gibraltar: Perez and Bensusan 2005). A sign has also been erected in the middle of the tourist site in Morocco, written in French and Moroccan Arabic, and including an illustration instructing people not to feed the macaques. Unfortunately, these measures to prevent such feeding are often unsuccessful (Perez and Bensusan 2005, Fuentes 2006a, Knight 2011, Maréchal et al. 2011); it is important therefore to understand why tourists continue to feed wildlife despite knowing that it is banned.

During my conversations with tourists, I raised the issue that feeding monkeys was prohibited, and asked them why they continued to do so. The large majority of tourists looked quite surprised on hearing this, and admitted that they had no idea that feeding the monkeys was forbidden. Most of them had not read or even noticed the sign where information about the monkeys was displayed. Others looked around and said that *"others are feeding the monkeys and nobody bothers them, so we thought it was not a problem."* During these exchanges, some tourists were surprised about the feeding ban, and asked the reasons for it. It is obvious that the information provided and the public's comprehension of the risks of feeding monkeys were insufficient at this site. Based on this starting point, I explained the different risks and potential consequences associated with tourist provisioning, and placed particular emphasis on the health issues such as disease transmission and risk of attacks/injuries. Despite their concern on hearing this, the majority of tourists were observed to continue feeding the monkeys, just a few minutes after our conversation. Therefore I attempted to understand why they persisted in feeding the monkeys after being informed about the negative consequences. In the following sections, I explore possible explanations of their behaviour; once more, these are not mutually exclusive.

Long term and abstract effects

The problems caused by tourist provisioning do not have an immediately visible effect, and therefore ideas of harm are perhaps quite abstract for tourists. When interviewed, many tourists pointed out that *"giving one or two peanuts to a monkey would not kill it!"* While it is true that one or two peanuts may not cause harm, the hundreds of tourists regularly feeding the monkeys may have a severe cumulative effect. Over a long period of time this may cause serious health issues for the monkeys. Unfortunately tourists seemed to really struggle to understand this idea, and so did not take responsibility for their part in causing these problems. In addition, other tourists replied that the *"monkeys do not look sick and we are not sick either, so I am sure it is fine!"* If none of the monkeys or tourists presents physical sign of sickness, people do not easily understand that an individual they are interacting with might potentially be contagious or have health issues, or that they themselves might be passing on diseases to the animals. From my experiences, the majority of tourists could not, or would not, understand the information given to them, and therefore they simply ignored the possible negative consequences linked with provisioning. Reyna (2004) suggested that when making a decision in relation to risk, people use a dual-process based on memorising and reasoning. They make a decision based on their representation of the risk. It seems likely, therefore, that feeding monkeys is perceived by tourists as a low risk activity, since the majority continued to feed the macaques after being informed of the potential health risks for both macaques and themselves.

Affective association

As previously described, according to Serpell (2004), animals are perceived in terms of utility or affect. In the tourist context, is has been suggested that people perceive animals in terms of affect (Newsome et al. 2005). Tourists have emotional motivations to interact with wild animals, and this would certainly seem to be the case at this study site. Tourists said for example that *"the monkeys are so cute that* *they could not resist feeding them."* and that *"feeding monkeys pleases the children, so we could not forbid it because they looked so happy."* In these two examples, feeding monkeys triggered emotional responses which influenced tourists' behaviour; this is linked to their affective perception of the animal itself or to the affective desire to please a child. Damasio (1994) and Bechara et al. (1999) draw comparisons with the somatic marker hypothesis, which proposes that *"emotional responses guide decision making in risky and uncertainty situations."*(Boyer 2006, p.306). Mittal and Ross (1998, p.321) suggested that *"motivational aspects of affective states are more likely to be influential in risk behaviour",* implying that emotional states, whether positive or negative, influence a person's ability to undertake decisions in situations involving risk. The relationships between affect and risk-taking have been shown to be complex (Islen and Patrick 1983, Boyle 2006). In gambling risk-taking, *"individuals who had reason to be feeling elated bet more than control subjects on a low-risk bet, but wagered less than controls on a high-risk bet"* (Islen and Patrick 1983, p.194). I would suggest that tourists find that the emotional reward from feeding monkeys outweighs the perceived low-risk of actually doing so.

Social contagion

When observing tourists coming into contact with wild monkeys for the first time at the study site, I noticed that they were often quite scared and did not seem to know if they should approach and feed the monkeys or not. After observing other tourists interacting with monkeys and with some encouragement from their guides, the newly arrived tourists also began to interact with, and to feed the monkeys. I suggest that this behaviour may be due to the phenomenon of social contagion (Colman 2014). Social contagion involves individuals adopting the attitudes and behaviours of others through imitation and conformity (Colman 2014). When I asked the tourists why they continued to feed the monkeys after I had given them information on the possible risks and negative consequences of such feeding, a typical reply was: *“Others are feeding the monkeys, so I do not see why I cannot do the same. And it is certainly not so risky if everybody is doing it!”* Here, the tourists express how the social context of the situation influenced and reduced their perception of the risks.

3.5 Impact of feeding wild monkeys on tourists’ experience

Moscardo and Saltzer (2004, p.10) reported that *“the three most important features sought [by tourists] in a wildlife experience were: seeing wildlife in its natural environment, seeing wildlife behaving naturally and seeing rare, unique or unusual wildlife. The least important was being able to touch/handle wildlife.”* A study on whale watching described similar views, suggesting that tourists were seeking to see wildlife in its natural setting, displaying natural behaviours (Stamation 2008). Markwell (2001, p.39) described how the wildlife tourism industry advertised *“an encounter with nature to achieve a better understanding and love for nature and how one fits into this cycle.”* Knight (2011) also describes the effort of monkey park staff in Japan to display the group of monkeys in order to show the tourists monkeys’ natural social behaviour. Furthermore, Fuentes et al. (2006, p.1144) describe that when asked about the reasons for visiting macaques *“...>50%*

(275/500) of tourists surveyed at the macaque tourism sites of Padangtegal, Sangeh, Alas Kedaton (Bali, Indonesia), and Gibraltar (Europe) responded with answers such as 'interest in wildlife', 'natural', 'nature education', and 'seeing' the monkeys." In contrast, Grossberg et al. (2003) indicated that incidental ecotourists at a site in Belize did not fit with the ecotourism standard, which predominantly includes the desire to view and learn about the natural location and/or the wildlife. At the tourist site in Morocco, there is a mix of tourists. The majority are opportunistic or incidental tourists, while others come for leisure purposes, which include viewing the forest and the monkeys. These different backgrounds may have an effect on the different aims of the tourists, in wanting to feed and touch the monkeys, rather than just to observe them.

Tourists' perceptions of wildlife influence their behaviour towards wild animals as much as their expectations of the wildlife tourism experience. Wildlife is imagined by tourists as pristine (Russell 1995), which leads to tourists expecting to experience wildlife tourism as a pure and unviolated wild environment, uncontrolled by the human world; Russell (1995) described how volunteers at a rescue centre in Borneo made a clear distinction between ex-captive orang-utans and wild-born orang-utans, valuing more the encounter with wild individuals because the experience was considered as 'pristine'. Russell (1995) described three elements which made the 'pristine story': the first was the purity of the animal breed, i.e. not influenced by humans, such as hybrids. The second was the rarity of the animal. Finally, the setting was an important part of the experience. As Urry (1990, p.42, 45) noted, it is the ecotourist who strives to *"enjoy the unspoiled view* *before the crowds get there"* and who desires *"solitude, privacy and a personal, semi-spiritual relationship with the object of the gaze."*

On the other hand, Markwell (2001) stated that tourist-nature experience is mediated and limited to boundaries which shape the tourist experience. He argued that *"these boundaries separate, both spatially and symbolically, tourists from nature, operating for example at the edges of walking trails and paths, at fences at lookouts and viewing platforms. The boundaries formalize the relationship between nature and tourists and serve to reinforce nature as the 'other', as the object of the tourist gaze. "* (Markwell 2001, p.42)

Primate tourism in Morocco is unregulated; no boundaries constrain the tourists at this, or any other, tourist site where macaques are found. No officials are present at the site in order to regulate the tourist experience. Markwell (2001, p.54, 55) argued that *"the tourist experience is not only an occular one, but truly corporeal. Nature is constructed, presented, re-presented, interpreted and consumed through particular experiences and discourses (Urry 1990, Wilson 1972). Within this framework, particular ways of seeing, feeling, experiencing and knowing nature structure the tourist experience."* In the context of my study site, the feeding of the monkeys clearly shapes the tourist experience. This lack of boundaries, this *'intimate rendez-vous with wildlife'* as described by Markwell (2001, p.39) might be preventing tourists from experiencing nature in a way which allows them to gain a real and beneficial understanding of the natural world. Therefore, tourists' experience at this site is strongly shaped by feeding interactions between visitors and monkeys. Although there may be some superficial benefits to tourists in the feeding interactions, these encounters mean that tourists miss an important and arguably more valuable experience of wildlife. Baker (2001, p.1) commented that *"recent books on animal representation acknowledge the extent to which human understanding of animals is shaped by representations rather than by direct experience of them".* Marvin (2005, p.1) emphasised that *"such representations emerge in the main, however, from a direct experience of – or a direct encounter with - an embodied living animal, that begins with looking."* While feeding monkeys, tourists see the animal and even look at it. They often take a picture to keep as a souvenir. However, they generally miss watching (defined as continuous and attentive viewing - Marvin 2005) or observing these animals (defined as a concentrated, attentive viewing guided by a particular interest - Marvin 2005). At this site the vast majority of tourists miss out on observing the natural behaviour of Barbary macaques, the social interactions between animals and the connection between the animal and its environment. By feeding monkeys, tourists momentarily disconnect the wild animal from its social and environment normality. The main important features of the wildlife experience reported in Moscardo and Saltzer (2004) are therefore not met because of the influence of provisioning on the wild animals' behaviour.

Curtin (2009, p.451) found evidence that watching wildlife has important well-being benefits for people, and can *"initiate an emotional response of awe, wonder and privilege that unlocks ecocentric and anthropomorphic connections to wild animals and a feeling that is 'beyond words'. So watching wildlife can provoke a feeling of connectedness with the whole of nature"*. By feeding monkeys, tourists force the animal to enter into a human world. They create a relationship based on giving food in exchange for the opportunity to take a picture or to be entertained. So the emotional response associated with a connectedness with nature is diminished by bringing the monkeys into the tourists' comfort zone and by tourists controlling the situation. The pristine nature of the encounter may therefore be ruined by the tourists' influence on the macaques' behaviours.

3.6 Conclusion

Orams (2002) closely examined the complex reasons for feeding wildlife and highlighted the controversial implications of such tourist activity for the animals involved. The causes of this behaviour are thought to be closely linked with how tourists perceive the animal that they feed. In this context, habituated Barbary macaques have all the criteria (i.e. aesthetic, rare, human like) that attract people, and this facilitates feeding interactions with tourists. In addition, a range of tourists' motivations such as the wish to do a good deed, the desire to create a connection with wild animals, or to take control over the animal, are important in the process of feeding monkeys. Feeding primates may have negative impacts on the welfare of the animals, and potentially also for conservation; these are factors which are often ignored or disregarded by tourists in order to satisfy their desire to share food with, and have a close encounter with such appealing animals. Finally, provisioning monkeys may greatly alter the tourist experience by changing the context of the encounter from involving wildlife to something more resembling a human-pet relationship. The expectation and reality of seeing wild monkeys behaving ‘naturally’ in their ‘natural’ environment is biased and distorted by their interactions with humans.

Chapter 4

Behavioural responses of wild Barbary macaques to tourist pressure

4.1 Introduction

An animal's survival and wellbeing rely on its ability to cope with challenges from its environment (Romero et al. 2009). In order to alleviate the potential detrimental effects of such challenges, animals use behavioural responses called coping mechanisms, which are defined by Wechsler (1995) as responses to aversive situations.

Concern has recently been raised regarding the disturbances (or aversive stimuli) created by tourism in an animal's environment (Constantine et al. 2004, Maréchal et al. 2011). As primate tourism is a growing industry and has potential benefits for conservation, understanding how animals respond to tourism is crucial in order to inform management decisions which accommodate primate tourism, while minimising the welfare costs to the animals involved (Maréchal et al. 2011, Majolo et al. 2013).

Previously, anxiety and physiological stress levels of adult male Barbary macaques were investigated in a tourist exposed group in the Middle Atlas Mountains of Morocco (Maréchal et al. 2011). These males showed an increase in self-scratching rates, an index of anxiety, when interacting with tourists, whatever the type of interactions (feeding, aggressive, others). In addition, males had higher faecal glucocorticoids (FGC) levels, a measure of physiological stress, after days when they interacted aggressively with tourists at higher rates. There was no apparent effect on either anxiety or physiological stress levels of simply being in the presence of very high tourist numbers, or of tourists being present for long periods. This apparent lack of impact of high tourist numbers or exposure time was suggested to be due to these animals using a range of behavioural mechanisms to cope effectively with the associated potential stress (Maréchal et al. 2011). A similar idea that animals exposed to tourism have a range of coping strategies to deal with the associated stress has also been suggested by Muehlenbien et al. (2012) in their study of orang-utans, and by Aguilar-Melo et al. (2013) in their study of mantled howler monkeys (*Alouatta palliate)*.

In the current chapter, I aim to understand how Barbary macaques might use behavioural responses to cope with tourist pressure, assessed through measures of tourist presence and of the occurrence of tourist-macaque interactions. I explore in detail a range of behaviours classified under three main potential coping responses: spatial positioning, seeking social support and displacement behaviour. Previous studies have also attempted to understand the impacts of tourists on animals' behaviour (Hill 1999, Hsu et al. 2009, Ruesto et al. 2010, Majolo et al. 2013); however, these were generally focusing on one or a few behaviours and did not take into consideration the fuller range of behavioural responses that animals might use to cope with tourist pressure. Additionally, very few studies have explored the impacts of different aspects of tourist pressure, such as the presence of tourists in the area *per se* and the occurrence of interactions between animals and tourists; exploring these different aspects of tourism is important for understanding tourist effects on animals' behaviour (Maréchal et al. 2011). Furthermore, social context such as dominance rank or the presence of conspecifics might strongly influence animals' behavioural responses (Castles et al. 1999, Majolo et al. 2009), particularly where there is provisioning (Hill 1999, Majolo et al. 2013); therefore I explore the impact of tourists on potential coping mechanisms while taking into account potential social factors that may shape how animals respond.

4.1.1 Environmental stress

The stress response is a set of adaptable mechanisms that helps animals to cope with challenges in their environment by adjusting responses according to the intensity of the stressor perceived (Romero et al. 2009). Hence, estimating variations in stress response in animals is a very useful means of evaluating how they respond to environmental challenges. Three main indicators have generally been proposed and used to evaluate stress levels in animals: anti-predator behaviours such as fleeing or vigilance (Frid and Dill 2002), behavioural indices of emotional state such as anxiety (e.g. displacement activity, Maestripieri et al. 1992), and measures of physiological stress levels (e.g. faecal glucocorticoid metabolite concentrations: Heistermann et al. 2006, Higham et al. 2009).

In an animal's environment there are many possible causes of a stress response. Environmental conditions such as temperature (Beehner and McCann 2008, Chollet and Teaford 2010), predation (Sheriff et al. 2009), human disturbance (Barja et al. 2007, van Meter et al. 2009) and risky social situations (Sapolsky 1983, Abbott et al.

2003, Bergman et al. 2005) are all factors that might elicit a stress response. Amongst these environmental factors, human disturbance is suggested to be an important stressor in certain situations (Creel et al. 2002, Barja et al. 2007, van Meter et al. 2009), and in particular tourism is of growing concern in relation to animal welfare (Maréchal et al. 2011, Russon and Wallis 2014). Furthermore, social interactions between conspecifics are also influenced by tourism and this can lead to stress occurring (Majolo et al. 2013).

Tourist-related stress

Tourists might cause a great deal of direct or indirect disturbance by their presence and interactions with animals (Orams 2002, Constantine et al. 2004). Many tourist related factors have been proposed to affect animals, such as human presence, their proximity or the noise they make (Mitchell et al. 1991, Hosey 2000, Birke 2002, Ruesto et al. 2010). In addition, animals' sensitivity toward tourism may depend on a number of characteristics such as species, sex, age, rank and health (Muller et al. 2004). Understanding the impact of tourism on the animals involved is therefore complex, due to the large number of factors which might influence how animals respond to tourists.

In order to evaluate the impacts of tourism, most previous research has quantified behavioural changes in the animals involved. It has been shown that animals of many species express behavioural changes in relation to tourist presence or interactions. For instance, large mammals in Borneo appeared to change their activity periods and to avoid some areas because of human traffic (Griffith and van

Schaik 1993), and wild Asian rhinoceroses increased vigilance time when tourist density increased (Lott and McCoy 1995). Provisioning, which is often associated with wildlife tourism, has also been found to affect animals' behaviour. For example, evidence was found that provisioning influences activity budgets, reducing the time spent grooming in male Barbary macaques (Majolo et al. 2013), and also increasing intraspecific aggression rates in four macaque species (Hill 1999, Hsu et al. 2009, Majolo et al. 2013). In Barbary and Tibetan macaques, individuals' self-directed behaviour rates were positively related to the proximity of tourists (Maréchal et al. 2011, Matheson et al. 2007). Evidence from previous studies suggests therefore that tourists might influence behavioural responses in many animal species; however in a number of other studies or mesures no such effect was seen (Ruesto et al. 2010, Maréchal et al. 2011, Usui et al. 2014). Self-scratching rates in male Barbary macaques were not found to be related to tourist number in the area (Maréchal et al. 2011), and no relationships were found between tourist number and self-directed behaviour or aggressive behaviour in Tibetan macaques (Ruesto et al. 2010, Usui et al. 2014).

Social stress

An animal's social status and environment may affect its stress responses (e.g. Abbott et al. 2003, Bergman et al. 2005). For example, social status might influence individual physiological stress levels, as has been suggested to occur in olive baboons (*Papio anubis*: Sapolsky 1983). In a tourism context, the presence of tourists or, more likely, the interactions between tourists and an animal, may increase social stressors by increasing the risk of aggression between conspecifics (Altmann 1992, Hill 1999, Berman et al. 2007). For example in baboons, during provisioning, high value food resources were concentrated in limited spaces, increasing the competition between individuals (Altmann 1992). A similar effect was also seen in rhesus and Japanese macaques (Hill 1999). In male Barbary macaques, feeding on human food was associated with significantly higher intraspecific aggression rates compared to feeding on natural food (Majolo et al. 2013). Higher ranked individuals might try to monopolise food resources by threats and aggression towards subordinate individuals, as found in Japanese macaques (Hanya 2004), which might explain this increased intraspecific competition during provisioning. In this context, proximity to a more dominant individual could therefore be considered as a social stressor. In fact, it has been shown that rhesus macaque females' heart rate increased when a dominant approached, suggesting that close proximity to a dominant individual was stressful (Aureli et al. 1999). Therefore, social context appears to be an important parameter to take into consideration when attempting to better understand animal stress responses to tourism.

4.1.2 Types of coping mechanisms

In order to modulate the impact of stressors, including environmental stressors, animals may use different behavioural coping strategies. A wealth of studies have looked at how individuals cope with stressful situations; "fight or flight" (Cannon 1915) and "fight, freeze, flight" (Engel and Schmale 1972) were the first terms describing coping mechanisms associated with survival strategies (Korte et al. 2005). More recently, a number of displacement behaviours have also been proposed to act as coping mechanisms, as they seem to mediate the impacts of physiological stress responses (Maestripieri et al. 1992, Taylor et al. 2000, Koolhaas 2008).

Spatial positioning

Physical avoidance of stressors is a well-known behavioural coping mechanism (Korte et al. 2005, Stankowich and Blumstein 2005). Animals might opt for different ways to avoid aversive stimuli. One of the first strategies described was flight; simply keeping an appropriate distance from a stressor might act as a coping strategy. For example, prey animals flee when they perceive a predator (e.g. Fernández-Juricic et al. 2001b, Frid and Dill 2002, Stankowich and Blumstein 2005). A study of predator avoidance in Juvenile Coho salmon (*Oncorhynchus kisutch*) found evidence that individuals with higher avoidance levels had a shorter recovery period, meaning their plasma corticosteroids levels returned faster to baseline after a mild stressor than was the case for those with low avoidance levels (Olla et al. 1992). In humans, a negative relationship between avoidance behaviour and stress-induced cortisol responses was found (Roelofs et al. 2005). Therefore, anti-predator behaviour such as keeping distance from a stressor, measured via flight distance for example, might be a key factor to investigate when considering the impacts of tourists on animals, as humans may be perceived as potential predators (Frid and Dill 2002, Blumstein 2014). In the case of non-human primates, when they are threatened by a predator, they usually seek refuge in a tree if one is available (Stanford 1995).

Another coping strategy used by animals to deal with stressful stimuli is maintaining proximity to a potential escape route, which might be enough to modulate the impact of a stressor (Weiss 1968). Evidence of such an effect in primates is provided by studies of baboons, rhesus macaques and ring tailed lemurs, in which proximity of overhead tree cover reduces the flight distance between an animal and a potential threat, such as a human (Rowell 1966, Menzel 1966, Klopfer and Jolly 1966); in other words, these primates allow humans to approach closer when they themselves are closer to tree cover. According to Wilson (1972), this may be due to the greater availability of an effective escape route. Escape seems to be an important coping strategy; an animal's spatial positioning in relation to an aversive stimulus could therefore reflect the expression of a coping mechanism. Keeping some distance from the aversive stimulus, climbing up a tree, or being in close proximity to a potential escape route are all tactics that might be used to cope with stressful situations. Proximity to refuges, as well as actual use of refuges, can thus reflect adoption of spatial coping strategies.

Social support

Animals may cope better with stress when a socially bonded partner is present, a phenomenon which is known as "social buffering" (Sachser et al. 1998). The presence of a socially bonded partner (or partners) enables an individual to modulate the impact of stressors on homeostasis (Cohen and Wills 1985), such that physiological and behavioural stress responses are reduced. Evidence for this effect has been provided by studies of many species of social mammals (Guinea pigs, *Cavia porcellus*: Sachser et al. 1998; farm animals: Ishiwata et al. 2007, Rault 2012; non-human primates: Mendoza et al. 1978, Engh et al. 2006a,b; and humans: Thorsteinsson et al. 1998, Rosal et al. 2004). The first evidence of social buffering in non-human primates was provided by a study of mother-infant bonding in squirrel monkeys (*Saimiri sciureus.:* Mendoza et al. 1978). When an infant was separated from its mother, its physiological stress levels increased but this increase was lower when it was placed in a familiar social environment with known conspecifics. Adult squirrel monkeys exposed to stressful stimuli such as foot shock showed no elevation in cortisol levels if in a social housing condition; by contrast isolated individuals showed an increase in cortisol levels (Stanton et al. 1985). Social support appears to be an important coping mechanism in a range of gregarious species; however, to my knowledge no study has looked at how social support may be used by animals to cope with tourists.

Displacement responses

Displacement behaviours are characterised by their lack of apparent relevance to the context in which they occur (Tinbergen 1952, Anselme 2008). Recent studies that have investigated displacement behaviours suggest that several of these behaviours can act as coping strategies in mammals, amongst them: self-directed behaviour (Maestripieri et al. 1992, Gustison et al. 2012), restlessness (Ohl et al. 2008, Duboscq et al. 2014), redirected-aggressive behaviours (Koolhaas 2008) and affiliative behaviours (Taylor et al 2000, Cheney and Seyfarth 2009). The four types of displacement behaviour are defined, and examples of their occurrence described below.

Self-directed behaviour

Self-directed behaviours (SDB) are defined as behaviours which are self-oriented, and often body care activities, and it has been proposed that SDB might help animals to cope with aversive situations (McFarland 1966, Maestripieri et al. 1992, Higham et al. 2009). Pharmacological studies of long tailed macaques provided evidence that the frequencies of SDB increased when an anxiogenic drug was administered and decreased when an anxiolytic was used (Schino et al. 1996). Further behavioural research lends additional support to the idea that SDB reflect a response to the emotional state of an individual. Studies show an increase in individuals' SDB when in close proximity to a dominant individual (e.g. olive baboons: Castles et al. 1999), following aggression with a conspecific (e.g. Japanese macaques: Majolo et al. 2009) or when exposed to anthropogenic noise (e.g. giant panda, *Ailuropoda melanoleuca*: Powell et al 2006). Self-scratching is the most frequently reported self-directed behaviour in non-human primates, and also the one most often used to determine emotional states (Maestripieri et al. 1992; Gustison et al. 2012). Two previous studies have quantified self-scratching to investigate the impacts of tourists on anxiety levels in macaques (Matheson et al. 2007, Maréchal et al. 2011), and the results suggested such behaviour was related to certain aspects of tourist pressure but not to others. Further research is therefore needed to better understand the complex relationships between self-scratching and tourist pressure.

Restlessness

Restlessness (or in extreme cases, hyperactivity) is defined as a frequent change in an individual's behaviour and has been reported to be a coping mechanism in a range of species (Ohl et al. 2008). In lab and farm animals, restlessness rates were positively related to corticosteroid increase, suggesting that restlessness may be used as a coping mechanism (Palit et al. 1998, Ohl et al. 2008). For instance, chronic stress in lab mice (*Mus musculus*) induced an increase in hyperactivity (Strekalova et al. 2005), suggesting restlessness is positively associated with physiological stress levels and may serve to modulate such levels. However, the potential coping role of restlessness has rarely been explored in wild animals. In primates, only a few recent studies have used restlessness as an index of anxiety (Palit et al. 1998, Arnold and Aureli 2006, Higham et al. 2011a, Duboscq et al. 2014). In rhesus macaques, it was found that lower ranking males had higher restlessness rates than higher ranked males during both the birth and mating seasons, two periods with high levels of competition and social tension, especially for lower ranking males (Higham et al. 2011a). Furthermore, the receipt of aggression was associated with an increase in restlessness in different primate species (Arnold and Aureli 2006, Duboscq et al. 2014). Although evidence has been found that restlessness might act as a coping mechanism, to my knowledge, no previous study has investigated the impacts of tourists on animals' restlessness.

Aggressive behaviour directed towards conspecifics

Redirection of aggressive behaviour toward other individuals has also been indicated to act as a coping behaviour in stressful situations. Evidence has been found that bystander-directed aggression is used as a coping mechanism in a number of non-human primates, especially in the genus *Macaca* (Kazem and Aureli 2005). Commonly, in a socially living species, the target of the aggression is a subordinate within the group or a relative, both of which present a “safe” target (Cheney and Seyfarth 1989, Kazem and Aureli 2005). In howler monkeys, males showed an increase in aggressive behaviour directed toward an intrusive solitary male within their territory, but showed no increase in physiological stress levels, suggesting they might use an active aggressive coping style; by contrast females adopted a more passive, non-aggressive style and did show an increase in physiological stress levels (Cristóbal-Azkarate et al. 2007). In spotted hyenas, *Crocuta crocuta,* a cascade of redirection of agonistic interactions towards lower rank animals has often been observed during a kill (Zabel et al. 1992), and this may serve to mediate tension between individuals. A number of studies have found evidence that provisioning increases aggression between conspecifics in primates (Hill 1999, Berman et al. 2007, Majolo et al. 2013); however, it appears difficult to determine if this increase in aggression is a coping mechanism to mediate tension between individuals, or rather is due to high intraspecific competition.

Affiliative behaviour

In addition to the simple presence of a conspecific (i.e. social support), positive interactions with conspecifics (i.e. affiliative behaviour) have been proposed in a number of studies to act as a coping mechanism. In humans, the “tend-and-befriend” hypothesis proposes that women would be more likely to use affiliative behaviour as a coping strategy than men (Taylor et al. 2000). This hypothesis was supported by recent evidence from a number of primate species (Cheney and Seyfarth 2009). For example, Engh et al. (2006a) found that chacma baboon (*Papio ursinus*) females increased both grooming frequencies and the number of grooming partners following the loss of a close relative. Most of these findings are based on quantifying affiliative behaviour through grooming frequency; however grooming may not be an appropriate measure in a tourist context, as provisioning might disrupt this activity. In male Barbary macaques, a decrease in grooming rates was found when in proximity to tourists, supporting this idea (Majolo et al. 2013). Short affiliative behaviours (short term positive social behaviours such as embracing or teeth chattering, but excluding grooming, see Table 2-6, pp. 41-42) might also act as a coping mechanism in males and females, but have rarely been explored; where they have, the results present an inconsistent picture. A study of female bonnet macaques (*Macaca radiata*) found that short affiliative behaviour rates decreased during provisioning compared to foraging on natural items (Ram et al. 2003), while a study of male Barbary macaques found that short affiliative behaviour rates increased when tourists were in close proximity (Maréchal 2010).

Overall, previous studies have suggested that tourists might influence a range of behavioural responses in animals. However, studies of tourism impacts have often focused on only a few behavioural responses, and different factors such as different aspects of tourist pressure and social settings have rarely been taken into consideration. A more integrative approach is needed in order to better understand the multidimensional spectrum of behavioural responses that animals might use to cope with tourist pressure.

4.1.3 Chapter aim

I aim to understand if and how tourists influence macaques' behaviours, in particular their spatial positioning, their seeking of social support, and their displacement behaviours. To address this main goal, I test predictions from three hypotheses:

Hypothesis 1: Barbary macaques adjust their position to cope with tourists.

Here, three predictions about macaque spatial positioning are tested:

Prediction 1i: The probability of macaques being off the ground is positively related to tourist pressure.

Prediction 1ii: The probability of macaques being under tree cover is positively related to tourist pressure.

Prediction 1iii: The distance between macaques on the ground and tourists is positively related to tourist pressure.

Hypothesis 2: Barbary macaques use social support to cope with tourists.

Prediction 2: The probability of macaques having a socially bonded partner in close proximity is positively related to tourist pressure.

Hypothesis 3: Barbary macaques use displacement behaviours to cope with tourists.

Here I explore four types of displacement behaviour potentially influenced by stressful stimuli:

Prediction 3i: Macaques' rate of self-scratching is positively related to tourist pressure.

Prediction 3ii: Macaques' rate of restlessness is positively related to tourist pressure.

Prediction 3ii: Macaques' rate of aggression toward conspecifics is positively related to tourist pressure.

Prediction 3iv: Macaques' rate of affiliative behaviour is positively related to tourist pressure.

4.2 Methods

4.2.1 Behavioural data collection

The methods for collection of behavioural data and the definitions of the behaviours included in this chapter are provided in the field and lab methods chapter (chapter 2). Behaviours analysed in this chapter were extracted from scan sampling (i.e. spatial positioning and social support) and continuous sampling (i.e. displacement behaviours).

4.2.2 Variables

In order to investigate if and how Barbary macaques respond to tourist pressure, I used two aspects of tourist pressure: tourist presence and tourist-macaque interactions (TMI). Tourist presence is defined as tourists being within 100 m of the core of the macaque group, and was measured by assessing the number of tourists in the area and tourist noise levels. In order to assess behavioural responses used during tourist-macaque interactions (TMI), I used variables which either directly influence the interactions between a macaque and tourists (e.g. number of tourists in the nearest tourist group, distance from the nearest tourist group) or reflect the type of actual tourist-macaque interactions (e.g. feeding, agonistic, others). It is important to differentiate these two measures of tourist pressure (i.e. tourist presence and TMI) as they might trigger different responses in Barbary macaques.

In addition to tourist pressure variables, I included social variables as control factors in the GLMM analyses, as provisioning increases conspecific competition in primates (Hill 1999, Berman et al. 2007). Here, I included rank, presence of a more dominant individual within 5 m, number of conspecifics involved in the interaction and social season as control social factors.

4.2.3 Statistical analysis

In order to analyse if and how tourists might influence Barbary macaques' behavioural responses, I used two complementary approaches: pairwise comparisons and GLMMs.

Pairwise comparisons

I ran pairwise comparisons to assess whether animals were more frequently (a) on the ground or off the ground, (b) under or not under tree cover, and (c) in the presence or not in the presence of a closely bonded social partner (Table 4-1). These analyses were run separately for females and for males.

Occurrence of a behaviour Yes vs. No: When tourists were present in the area, I first calculated the total number of scans in which each behaviour occurred for each individual macaque and I compared one condition against the other using pairwise comparisons. For example, I calculated the number of scans an animal was on the ground (i.e. condition 1) vs. off the ground (i.e. condition 2), under a tree cover (i.e. condition 1) vs. in open space (i.e. condition 2). Also I calculated the number of scans in which a socially bonded partner was present (i.e. condition 1) vs absent (i.e. condition 2) in close proximity to the focal animal.

Tourist presence without TMI vs. TMI: Then I compared the frequency of animals' behavioural responses during tourist-macaque interactions (i.e. condition 1) against the frequency of animals' behaviours when tourists are present, excluding when they are interacting with them (i.e. condition 2).

Finally, for the four displacement behaviours, I calculated the average rates of each behaviour per hour for each individual macaque during tourist-macaque interactions (i.e. condition 1) and during matched control periods (i.e. condition 2). Then I compared the average rates of behaviour between these two conditions, for each sex separately. For instance, I calculated the average rates of self-scratching per hour during tourist-macaque interactions which I compared to the average rates of self-scratching during matched controls.

Generalized linear mixed models (GLMM)

In order to examine if and how tourist presence and tourist-macaque interactions influence macaques' behaviour, I ran a number of separate mixed model analyses for each sex, each using a different dependent variable (defined in Table 4-1) and a specified set of predictor variables (defined in Table 4-2) for each prediction for all three hypotheses. For analyses related to spatial position (i.e. hypothesis 1) and social support (i.e. hypothesis 2), dependent and predictor variables were extracted from scans. For analyses linked to the displacement behaviours (i.e. hypothesis 3), dependent and predictor variables were extracted from continuous sampling, with one exception, the number of tourists in the area, which was determined by averaging values for the two scans occurring before and after each focal observation.

In addition, for displacement behaviours only, I analysed separately and in different ways how tourists may influence Barbary macaques' displacement behaviour for (a) tourist presence and for (b) tourist-macaque interactions.

For the analysis of tourist presence, as tourists were present in the area almost all the time, I investigated the variations in rates of displacement behaviour in relation to the predictor variables only when tourists were present in the area.

For tourist-macaque interactions (TMI), I investigated how tourists might influence macaques' displacement behaviour during TMI compared with a matched control (see Chapter 2, p.59). Rates per hour of each displacement behaviour were determined during TMI and matched control periods (MC). A matched control was collected within a week of the TMI, and it was defined as when the focal monkey had no TMI 10 min prior to and during a focal observation. Analyses were carried out in order to determine if higher displacement behaviour rates during TMI compared to MC may be influenced by interactions with tourists.

Table 4-1: Description of dependent variables included in GLMMs to test the relationships between Barbary macaques' behavioural responses (dependent variables) and measures of tourist pressure (independent variables).

Dependent variables		**Description**	**measures of tourist pressure (independent variables)**
Spatial positioning	**Elevated position**	Position of the macaque i.e. on the ground or off the ground (binomial variable Y/N).	Tourist presence and Tourist-macaque interaction
	Tree cover	Macaques positioning under or not under a tree (binomial variable Y/N).	
	Distance from tourists on the ground	Distance from the tourists on the ground (in meters, log transformed).	
Social support	**Partner**	Presence or absence of a closely socially bonded partner in close proximity (binomial variable Y/N). The CSI (Composite index of sociality) score was calculated for each same sex dyad following methods from Silk (2006). The 3 highest CSI score partners were considered as closely socially bonded partners.	Tourist presence and Tourist-macaque interaction
Displacement behaviours	**Self-scratching**	Rate of self-scratching per hour (log transformed).	Tourist presence
	Restlessness	Rate of restlessness per hour.	
	Aggression toward conspecifics	Rate of aggression towards conspecifics per hour (log transformed).	
	Affiliative behaviour	Rate of short affiliative behaviour per hour (log transformed).	
	Self-scratching (TMI/MC)	TMI had higher self-scratching rates compared to MC (binomial variable Y/N).	Tourist-macaque interactions
	Restlessness (TMI/MC)	TMI had higher restlessness rates compared to MC (binomial variable Y/N).	
	Aggression toward conspecifics (TMI/MC)	TMI had higher aggression rates toward conspecifics compared to MC (binomial variable Y/N).	
	Affiliative behaviour (TMI/MC)	TMI had higher affiliative behaviour rates compared to MC (binomial variable Y/N).	

Table 4-2: Description of the independent variables (or predictor variables) included in GLMMs to test the relationships between Barbary macaques' behavioural responses (dependent variables) and measures of tourist pressure (independent variables).

Independent variables		Description
Tourist variables	**Number of tourists in the area**	Number of tourists present in the area, surrounding the core macaque group (within 100 m) taken during each 30 min scan. For the four displacement behaviours collected during continuous focal sampling, number of tourists in the area corresponds to the average number of tourist present during two 30 min scans (z-transformed, Schielzeth 2010).
	Number of tourists in the nearest tourist group	Number of tourists present in the closest tourist group to the focal macaque recorded during 30 min scan. For the four displacement behaviours, the number of tourists was the maximum reported during continuous focal sampling (z-transformed).
	Distance from the nearest tourist group	Distance from tourists in the closest tourist group from the focal subject including when the macaque was off the ground recorded during 30 min scan. For the four displacement behaviours, the closest distance to the nearest tourist group reported during continuous focal sampling (z-transformed).
	Noise	Noise levels scored from 1 to 6 (see chapter 2 p.54, z-transformed).
	TMI (Tourist-macaque interaction)	3 types of interaction: **agonistic** (received or given by the tourist), **feeding** (giving food; which does not necessarily imply that the macaque was eating it) and **others** (any other interactions which excluded agonistic and feeding interactions). As several types of interactions could occur during a focal sampling observation, I organised each type of interaction according to a hierarchical order. When an agonistic interaction occurred, and even if feeding and other interactions occurred as well, I classified the interactions as agonistic. When a feeding interaction occurred without any agonistic interaction but with other interactions, I classified the interaction as a feeding interaction. When neither an agonistic nor a feeding interaction occurred, the interaction was classified as other interaction.
	TMI (Y/N)	Presence or absence of a tourist –macaque interaction (binomial variable Y/N).
Social variables	**Season**	4 social seasons were determined (i.e. pre-birth, birth, post-birth and mating). Mating period lasted from the first complete copulation to the last complete copulation observed. Pre-birth was between the mating and the birth season. Birth season lasted from the first birth to the birth of the last infant. Post-birth was between birth and mating seasons.
	Rank	Defined using David' scores (see chapter 2 p.48-49), z-transformed.
	Presence of dominant	Presence or absence of a more dominant conspecific within 5 m of the focal individual (binomial variable Y/N).
	Number of conspecifics	Number of conspecifics involved in the same tourist-macaque interaction other than the focal individual (z-transformed).

As outlined in Tables 4-3 and 4-4, each GLMM contained a specific set of predictor variables. Each model was run as full model, including all predictors thought potentially to influence the dependent variable, less those that were highly collinear woth others. Definitions of terms can be found in Tables 4-1 and 4-2 above.

Table 4-3: Variables included in GLMMs to test the relationships between Barbary macaques' behavioural responses (dependent variables) and measures of tourist presence (independent variables). - not included in the model and ✓included in the model.

		Dependent variable							
	Prediction number	**1i**	**1ii**	**1iii**	**2**	**3i**	**3ii**	**3iii**	**3iv**
	Predictor variable	Elevated position	Tree cover	Distance from tourists on the ground	Partner	Self-scratching	Restlessness	Aggression toward conspecifics	Affiliative behaviour
Tourist variables	**Number of tourists in the area**	✓	✓	✓	✓	✓	✓	✓	✓
	Number of tourists in the nearest tourist group	✓	✓	✓	✓	✓	✓	✓	✓
	Distance from the nearest tourist group	✓	✓	-	✓	✓	✓	✓	✓
	Noise	✓	✓	✓	-	-	-	-	-
	TMI (Y/N)	-	-	✓	No data	-	-	-	-
Social variables	**Season**	✓	✓	✓	✓	✓	✓	✓	✓
	Rank	✓	✓	✓	✓	✓	✓	✓	✓
	Presence of dominant	No data	No data	No data	✓	✓	✓	✓	✓
	Random factors	**Nested factors: macaque ID/ Date/Scan**				**macaque ID**			

Noise as a predictor variable was excluded from most of the models due to high collinearity with other factors (see Appendix A9). In addition, the presence of a more dominant individual within 5 m was not included in the spatial models because this was not recorded during the 30 min scans. Finally TMI was only used when the variable 'distance from tourists on the ground' was used as the dependent variable. Also the variable 'distance from tourists on the ground' was not included in the model where this variable was used as the dependent variable.

Each line of data was automatically nested by lme4 package within ID for each model.

Table 4-4: Variables included in GLMMs to test the relationships between Barbary macaques' behavioural responses (dependent variables) and measures of tourist-macaque interactions (independent variables). - not included in the model and ✓included in the model.

		Dependent variable							
	Prediction number	**1i**	**1ii**	**1iii**	**2**	**3i**	**3ii**	**3iii**	**3iv**
	Predictor variable	Elevated position	Tree cover	Distance from tourists on the ground	Partner	Self-scratching	Restlessness	Aggression toward conspecifics	Affiliative behaviour
Tourist variables	**Number of tourists in the nearest tourist group**	✓	✓	✓	✓	✓	✓	✓	✓
	Distance from the nearest tourist group	✓	✓	-	✓	✓	✓	✓	✓
	TMI	✓	✓	✓	✓	✓	✓	✓	✓
Social variables	**Season**	✓	✓	✓	✓	✓	✓	✓	✓
	Rank	✓	✓	✓	✓	✓	✓	✓	✓
	Dominant	✓	✓	✓	✓	✓	✓	✓	✓
	Number of conspecifics	✓	✓	✓	✓	No data	No data	No data	No data
	Random factors	**Nested factors: macaque ID/ Date**				**macaque ID**			

The number of conspecifics involved in an interaction was not included in the four displacement behaviour models because this was not recorded during continuous focal sampling. Furthermore, distance from tourists on the ground was not included in the model when this variable was used as dependent variable. Each line of data was automatically nested by lme4 package within ID for each model.

4.3 Results

Here, I present results from different models using tourist and social predictor variables. Each model result is presented in full in an individual table; however only significant results associated with tourist predictors are described in the text. Figures to show raw data for significant relationship can be found in Appendices 10-13. Social predictors were used as control factors and therefore are not considered further in the text or discussion.

4.3.1 Barbary macaques' responses to tourist pressure: (A- tourist presence and B- tourist macaque interactions)

General patterns of the predictors

A- Tourist presence: Tourists were present in the area in 99.8% of the scans. For this reason, in order to evaluate the impact of tourist presence, I only used the behavioural data when tourists were present as a comparison between presence and absence of tourists was not possible. The number of tourists in the nearest tourist group was up to 5 tourists in 72.7% of scans.

B-Tourist-macaque interactions: Interactions of macaques with tourists occurred in 15.3% of scans overall, and these interactions occurred in 90.5% of scans when macaques were within 5 m from tourists on the ground. Feeding interactions accounted for 50.0% of the total interactions, followed by other interactions (44.7%) and agonistic interactions (5.3%). In 68.1% of the interactions, up to 5 tourists were involved and, in 10.0% of the interactions more than 10 tourists were involved. Percentage of scans macaques spent feeding on human food was positively correlated with the number of tourists in the area (N=222, r_s=0.619, P<0.001), and negatively related to the distance between macaques and tourists (N=222, r_s=-0.643, P<0.001).

In 51.4% of the interactions there was no more dominant macaque present within 10 m of the focal animal. When a more dominant individual was present, the distance of the focal macaque from a dominant individual was 3.5 m on average. The total number of conspecifics involved in an interaction was 4.25 including the focal animal.

Prediction 1i: The probability of macaques being off the ground is positively related to tourist pressure.

A-Tourist presence: Macaques were off the ground in 31.9% of the scans when tourists were present and on the ground in 68.1% of scans. All individuals were more often on the ground than off the ground when tourists were present (females: paired t-test: df=8, t=9.932, P<0.001; males: paired t-test: df=7, t=8.984, P<0.001, Figure 4-1).

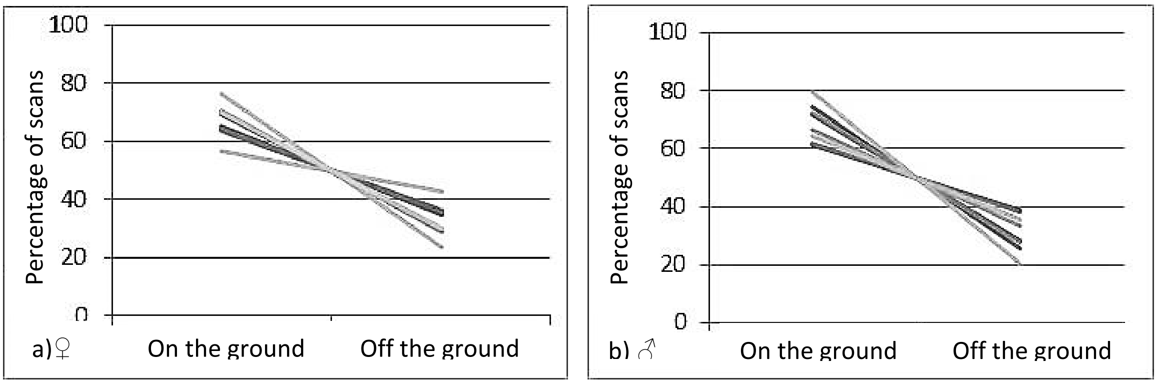


Figure 4-1: Percentage of scans in which (a) females and (b) males were on the ground or off the ground. Each line is a single individual.

Relationships between tourist pressure and the macaques' vertical position

Both female and male macaques were more likely to be off the ground when there were more tourists present in the area, when there were more tourists in the closest tourist group, and when the nearest tourists were further away (Table 4-5, Figures A10-1,2,3 and Figures A11-1,2,3).

Table 4-5: Results of the GLMM testing the relationships between tourist pressure and the macaques' vertical position.

		Females' vertical position				**Males**' vertical position			
	Null vs.	N	df	χ^2	*P*	N	df	χ^2	*P*
	full model	10293	7	1674.2	**<0.001**	9084	7	1410.9	**<0.001**
		Estimate	**±SE**	**z**	***P***	**Estimate**	**±SE**	**z**	***P***
	Intercept	-0.590	0.110	-5.180	**<0.001**	-1.050	0.100	-10.230	**<0.001**
Tourist variables	Number of tourists in the whole area	0.350	0.030	11.960	**<0.001**	0.310	0.030	9.740	**<0.001**
	Noise	0.010	0.030	0.210	0.832	0.000	0.030	-0.030	0.979
	Number of tourists in the nearest tourist group	0.140	0.030	5.290	**<0.001**	0.060	0.030	1.980	**0.048**
	Distance from nearest tourist group	0.770	0.030	27.990	**<0.001**	0.790	0.030	26.560	**<0.001**
Social variables	Rank	-0.210	0.070	-2.990	**0.003**	-0.320	0.030	-10.590	**<0.001**
	Season								
	Birth vs Mating	-0.100	0.100	-0.970	0.331	0.000	0.120	-0.030	0.980
	Birth vs. PostBirth	-0.280	0.100	-2.820	**0.005**	0.150	0.110	1.410	0.159
	Birth vs. PreBirth	-0.580	0.130	-4.560	**<0.001**	-0.070	0.140	-0.500	0.615
	Mating vs. PostBirth	-0.180	0.060	-2.980	**0.003**	0.160	0.070	2.280	**0.023**
	Mating vs. PreBirth	-0.480	0.100	-4.770	**<0.001**	-0.070	0.110	-0.600	0.547
	PostBirth vs. PreBirth	-0.300	0.100	-3.150	**0.002**	-0.230	0.110	-2.140	**0.032**

B-Tourist-macaque interactions: Macaques were off the ground in only 9.1% of the total interactions with tourists, and all individuals were more often on the ground during an interaction than off the ground (females: paired t-test: df=8, t=-22.112, P<0.001; males: paired t-test: df=7, t=-16.014, P<0.001, Figure 4-2).

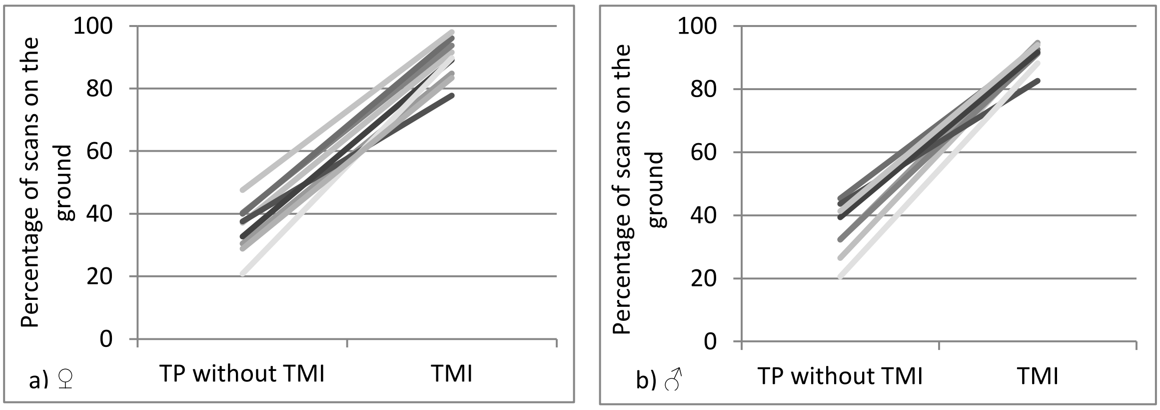


Figure 4-2: Percentage of scans in which (a) females and (b) males were on the ground during TMI and during tourist presence (TP) without TMI. Each line is a single individual.

Relationships between tourist pressure and the macaques' vertical position during an interaction

None of the tourist variables predicted females' likelihood of being off the ground (Table 4-6). Males were more likely to be off the ground when the nearest tourists were further away (Table 4-6; Figure A13-1).

Table 4-6: Results of the GLMM testing the relationships between tourist pressure and the macaques' vertical position during an interaction.

		Females' vertical position during TMI				**Males'** vertical position during TMI			
	Null vs. full model	N	df	χ^2	*P*	N	df	χ^2	*P*
		435	8	0	1	429	8	0	1
		Estimate	**±SE**	**z**	***P***	**Estimate**	**±SE**	**z**	***P***
	Intercept	-3.292	3.121	-1.055	0.292	-3.999	3.126	-1.279	0.201
Tourist variables	Number of tourists in the nearest tourist group	0.201	0.547	0.367	0.713	0.751	0.480	1.564	0.118
	Distance from nearest tourist group	0.475	0.437	1.089	0.276	1.200	0.534	2.249	**0.025**
	TMI								
	Agonistic vs. Feeding	-1.374	1.647	-0.834	0.404	-1.848	2.520	-0.733	0.463
	Agonistic vs. Other	-0.560	1.624	-0.345	0.730	-0.630	2.198	-0.287	0.774
	Feeding vs. Other	0.416	1.005	0.414	0.679	1.037	1.558	0.666	0.506
Social variables	Dominant	-0.813	1.118	-0.727	0.467	-0.228	2.067	-0.110	0.912
	Rank	0.300	0.813	0.369	0.712	-0.083	0.864	-0.096	0.923
	Number of conspecifics involved	-0.491	0.576	-0.854	0.393	-0.784	0.469	-1.673	0.094
	Season								
	Birth vs Mating	0.141	2.939	0.048	0.962	1.124	2.940	0.382	0.702
	Birth vs. PostBirth	0.370	2.600	0.142	0.887	0.122	2.468	0.049	0.961
	Mating vs. PostBirth	-0.084	1.374	-0.061	0.951	-1.187	2.191	-0.542	0.588

Prediction 1ii: The probability of macaques being under tree cover is positively related to tourist pressure.

A-Tourist presence: Macaques were found under the cover of a tree in 90.2% of the scans when tourists were present. All individuals were more often under cover of a tree than in open space when tourists were present (females: paired t-test: df=8, t=17.157, P<0.001; males: paired t-test: df=7, t=21.986, P<0.001, Figure 4-3).

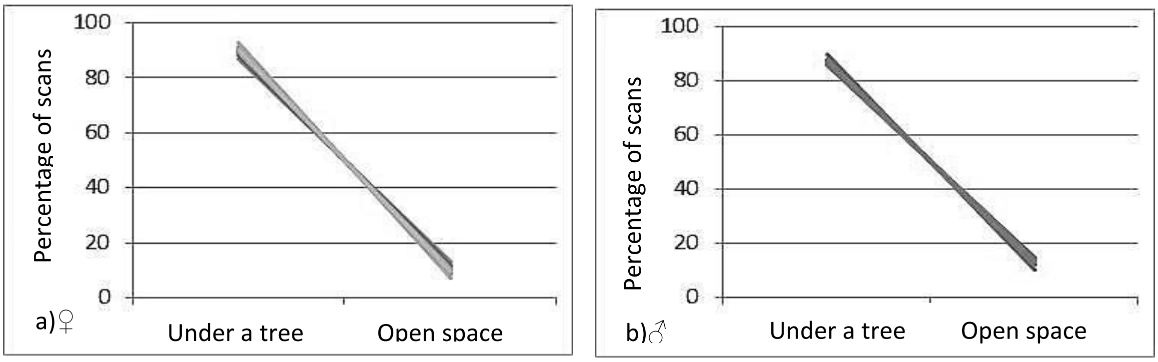


Figure 4-3: Percentage of scans in which (a) females and (b) males were under tree cover or in open spaces. Each line is a single individual.

Relationships between tourist pressure and the macaques' presence under tree cover

None of the tourist variables predicted females' presence under tree cover (Table 4-7). Males were more often under tree cover when the nearest tourist group was further away (Figure A11-4).

Table 4-7: Results of the GLMM testing the relationships between tourist pressure and whether macaques were under tree cover.

		Females' positioning under tree cover				**Males'** positioning under tree cover			
	Null vs. full model	N	*df*	χ^2	*P*	N	*df*	χ^2	*P*
		6805	7	0	1	6238	7	317.7	**<0.001**
		Estimate	**±SE**	**z**	***P***	**Estimate**	**±SE**	**z**	***P***
	Intercept	5.669	0.589	9.617	**<0.001**	5.080	0.480	10.530	**<0.001**
Tourist variables	Number of tourists in the whole area	-0.028	0.276	-0.101	0.920	0.150	0.210	0.710	0.478
	Noise	-0.129	0.249	-0.516	0.606	0.000	0.190	0.030	0.979
	Number of tourists in the nearest tourist group	0.030	0.245	0.122	0.903	-0.070	0.170	-0.420	0.674
	Distance from nearest tourist group	0.137	0.229	0.597	0.550	0.520	0.190	2.750	**0.006**
Social variables	Rank	-0.092	0.221	-0.416	0.678	0.020	0.180	0.080	0.933
	Season								
	Birth vs Mating	1.305	0.715	1.824	0.068	0.890	0.590	1.520	0.129
	Birth vs. PostBirth	2.447	0.710	3.448	**<0.001**	2.000	0.590	3.410	**0.001**
	Birth vs. PreBirth	-0.195	0.719	-0.272	0.786	-1.560	0.580	-2.680	**0.007**
	Mating vs. PostBirth	1.364	0.509	2.678	**0.007**	1.280	0.490	2.620	**0.009**
	Mating vs. PreBirth	-0.855	0.526	-1.627	0.104	-1.980	0.490	-4.080	**<0.001**
	PostBirth vs. PreBirth	-1.850	0.528	-3.505	**<0.001**	-3.060	0.500	-6.100	**<0.001**

B-Tourist-macaque interactions: Macaques were found under the cover of a tree in 78.4% of the total interactions with tourists; however all individuals were more often in open space during an interaction than when such interactions were not taking place (females: paired t-test: df=8, t=-7.107, P<0.001; males: paired t-test: df=7, t=-6.403, P<0.001, Figure 4-4).

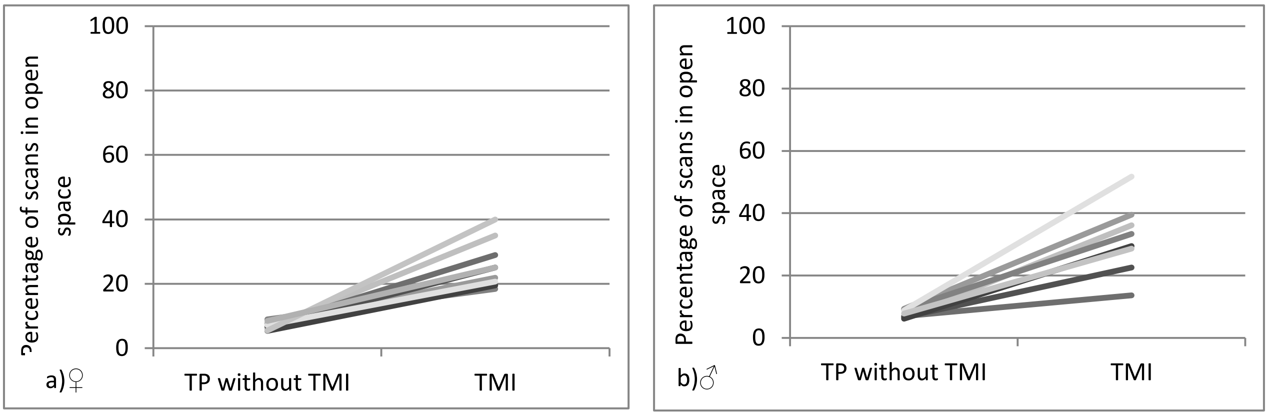


Figure 4-4: Percentage of scans in which (a) females and (b) males were in open space during TMI and during tourist presence (TP) without TMI. Each line is a single individual.

Relationships between tourist pressure and the macaques' presence under tree cover during an interaction

None of the tourist variables predicted females' presence under a tree cover (Table 4-8). Males were less likely to be under tree cover during a feeding interaction than during other interactions (Table 4-8, Figure A13-2).

Table 4-8: Results of the GLMM testing the relationships between tourist pressure and whether macaques were under tree cover during an interaction.

		Females' positioning under tree cover during TMI				**Males'** positioning under tree cover during TMI			
	Null vs.	N	df	χ^2	*P*	N	df	χ^2	*P*
	full model	485	8	14.955	0.06	482	8	30.008	**<0.001**
		Estimate	**±SE**	**z**	***P***	**Estimate**	**±SE**	**z**	***P***
	Intercept	1.237	0.685	1.806	0.071	1.920	0.830	2.300	**0.022**
Tourist variables	Number of tourists in the nearest tourist group	-0.031	0.128	-0.243	0.808	-0.050	0.130	-0.380	0.704
	Distance from nearest tourist group	0.032	0.146	0.221	0.825	0.010	0.140	0.050	0.964
	TMI								
	Agonistic vs. Feeding	-0.446	0.604	-0.738	0.461	-1.160	0.780	-1.490	0.137
	Agonistic vs. Other	-0.062	0.614	-0.100	0.920	-0.360	0.800	-0.450	0.652
	Feeding vs. Other	0.384	0.279	1.378	0.168	0.800	0.290	2.730	**0.006**
Social variables	Dominant	-0.496	0.296	-1.672	0.095	-0.210	0.380	-0.560	0.574
	Rank	0.154	0.140	1.097	0.273	-0.270	0.130	-2.040	**0.041**
	Number of conspecifics involved	0.090	0.110	0.822	0.411	0.010	0.090	0.130	0.894
	Season								
	Birth vs Mating	0.198	0.416	0.476	0.634	0.210	0.450	0.470	0.638
	Birth vs. PostBirth	0.618	0.356	1.735	0.083	0.100	0.320	0.320	0.753
	Mating vs. PostBirth	0.420	0.323	1.301	0.193	-0.110	0.370	-0.290	0.771

Prediction 1iii: The distance between macaques on the ground and tourists is positively related to tourist pressure.

A-Tourist presence:

Relationships between tourist pressure and distance between macaques on the ground and tourists

When on the ground, both females and males were closer to tourists when more tourists were present in the area and/or when an interaction with tourists occurred (Table 4-9, Figures A10-4,5 and Figures A11-5,6). By contrast, both females and males were further away when tourist number in the nearest tourist group increased (Figure A10-6 and Figure A11-7).

Table 4-9: Results of the GLMM testing the relationships between tourist pressure and distance between macaques on the ground and tourists.

		Distance between **females** and the nearest tourist group				Distance between **males** and the nearest tourist group			
	Null vs.	N	df	χ^2	*P*	N	df	χ^2	*P*
	full model	5732	8	3022.6	**<0.001**	5344	8	3515.3	**<0.001**
		Estimate	**±SE**	**z**	***P***	**Estimate**	**±SE**	**z**	***P***
	Intercept	0.070	0.080	0.940	0.399	0.160	0.040	4.450	**0.001**
Tourist variables	Number of tourists in the whole area	-0.110	0.010	-8.770	**<0.001**	-0.080	0.010	-6.920	**<0.001**
	Noise	-0.010	0.010	-1.140	0.207	-0.020	0.010	-1.920	0.132
	Number of tourists in the nearest tourist group	0.070	0.010	6.390	**<0.001**	0.070	0.010	7.360	**<0.001**
	TMI (Yes/No)	-1.510	0.030	-59.130	**<0.001**	-1.490	0.020	-65.330	**<0.001**
Social variables	Rank	0.050	0.020	2.260	0.112	0.040	0.010	3.460	0.498
	Season								
	Birth vs Mating	0.340	0.080	4.370	**<0.001**	0.320	0.040	7.660	**<0.001**
	Birth vs. PostBirth	0.280	0.080	3.560	**<0.001**	0.270	0.040	6.970	**<0.001**
	Birth vs. PreBirth	0.170	0.080	2.190	**0.012**	0.010	0.050	0.300	0.581
	Mating vs. PostBirth	-0.070	0.040	-1.670	0.077	-0.050	0.030	-1.930	0.094
	Mating vs. PreBirth	-0.170	0.030	-6.220	**<0.001**	-0.310	0.040	-7.800	**<0.001**
	PostBirth vs. PreBirth	-0.110	0.040	-2.660	**0.006**	-0.250	0.040	-7.100	**<0.001**

B-Tourist-macaque interactions: Macaques were at 2.60 m on average from tourists on the ground during an interaction with tourists. During feeding interactions, macaques were on average at 1.88 m, during agonistic interactions they were at 2.40 m, and during other interactions, they were at 3.40 m.

Relationships between tourist pressure and distance between macaques on the ground and tourists during an interaction

When on the ground, females and males were nearer to tourists during agonistic and feeding interactions compared to other interactions (Table 4-10, Figure A12-1 and Figures A13-3, 4). In addition, males were more likely to be further away from tourists when there were fewer tourists within the nearest tourist group.

Table 4-10: Results of the GLMM testing the relationships between tourist pressure and distance between macaques on the ground and tourists during an interaction.

		Distance between **females** and the nearest tourist group during TMI				Distance between **males** and the nearest tourist group during TMI			
	Null vs. full model	N	df	χ^2	*P*	N	df	χ^2	*P*
		485	8	76.269	**<0.001**	485	8	91.313	**<0.001**
		Estimate	**±SE**	**z**	***P***	**Estimate**	**±SE**	**z**	***P***
	Intercept	0.870	0.140	6.450	**<0.001**	0.740	0.090	8.090	**<0.001**
Tourist variables	Number of tourists in the nearest tourist group	-0.040	0.030	-1.600	0.115	-0.060	0.020	-2.640	**0.009**
	TMI								
	Agonistic vs. Feeding	-0.090	0.110	-0.790	0.436	-0.060	0.120	-0.520	0.613
	Agonistic vs. Other	0.290	0.120	2.520	**0.015**	0.390	0.120	3.310	**0.001**
	Feeding vs. Other	0.380	0.050	7.000	**<0.001**	0.450	0.050	9.530	**<0.001**
Social variables	Dominant	0.100	0.060	1.670	0.097	0.050	0.080	0.650	0.550
	Rank	0.110	0.040	2.840	**0.036**	0.010	0.020	0.280	0.834
	Number of conspecifics involved	0.070	0.020	3.180	**0.001**	0.030	0.020	1.580	0.099
	Season								
	Birth vs Mating	-0.120	0.090	-1.260	0.205	0.010	0.090	0.110	0.928
	Birth vs. PostBirth	0.030	0.080	0.350	0.743	-0.030	0.060	-0.460	0.623
	Mating vs. PostBirth	0.140	0.070	2.130	**0.037**	-0.040	0.070	-0.530	0.574

Prediction 2: The probability of macaques having a socially bonded partner in close proximity is positively related to tourist pressure.

A-Tourist presence: A closely socially bonded partner was present within 5 m of the focal macaque in 40.8% of scans. It was significantly less likely that a socially bonded partner was present within 5 m of the focal macaque than absent (females: paired t-test: df=8, t=-3.275, P=0.011; males: paired t-test: df=7, t=-6.735, P<0.001, Figure 4-5).

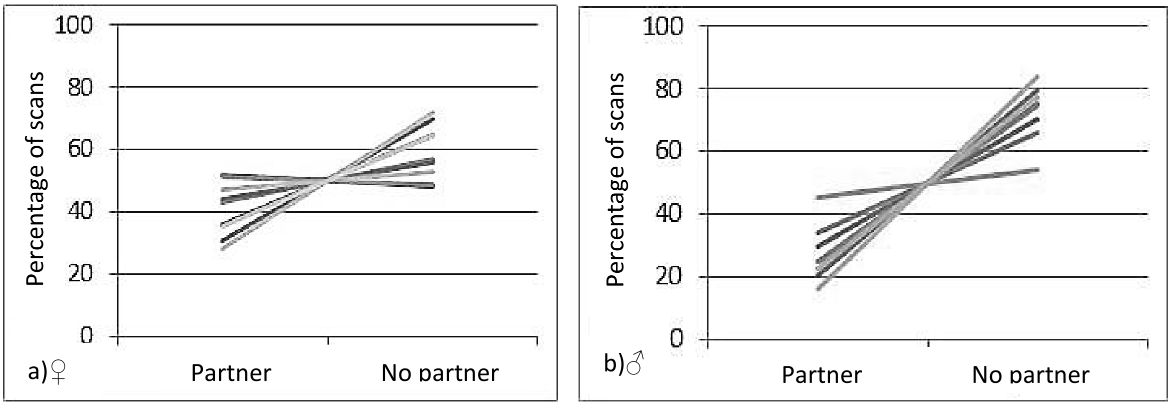


Figure 4-5: Percentage of scans in which (a) females and (b) males had a socially bonded partner present or absent. Each line is a single individual.

Relationships between tourist pressure and the presence of a socially bonded partner within 5 m

Both females and males were more likely to have a socially bonded partner present when there were fewer tourists in the area (Table 4-11, Figure A10-7 and Figure A11-8). In addition, males were more likely to have such a partner present when the number of tourists within the nearest tourist group was higher and when the distance between males and this group was shorter (Figures A11-9,10).

Table 4-11: Results of the GLMM testing the relationships between tourist pressure and presence of a socially bonded partner within 5 m.

		Presence of a partner within 5 m of **females** (Y/N)				Presence of a partner within 5 m of **males** (Y/N)			
	Null vs.	N	df	χ^2	*P*	N	df	χ^2	*P*
	full model	7874	7	594.35	**<0.001**	6708	7	922.7	**<0.001**
		Estimate	**±SE**	**z**	***P***	**Estimate**	**±SE**	**z**	***P***
	Intercept	-0.250	0.120	-2.080	**0.037**	-0.490	0.110	-4.480	**<0.001**
Tourist variables	Number of tourists in the whole area	-0.060	0.030	-2.290	**0.022**	-0.070	0.030	-2.410	**0.016**
	Number of tourists in the nearest tourist group	0.020	0.030	0.870	0.385	0.100	0.030	3.490	**<0.001**
	Distance from nearest tourist group	0.000	0.020	0.090	0.931	-0.060	0.030	-2.250	**0.024**
Social variables	Dominant	0.180	0.050	3.790	**<0.001**	1.730	0.100	16.960	**<0.001**
	Rank	-0.270	0.080	-3.440	**0.001**	-0.240	0.060	-4.270	**<0.001**
	Season								
	Birth vs Mating	-0.490	0.100	-4.810	**<0.001**	-0.570	0.110	-5.230	**<0.001**
	Birth vs. PostBirth	-0.020	0.100	-0.240	0.808	0.010	0.100	0.070	0.945
	Birth vs. PreBirth	-0.260	0.120	-2.240	**0.025**	0.170	0.130	1.380	0.169
	Mating vs. PostBirth	0.460	0.060	7.630	**<0.001**	0.010	0.100	0.070	0.945
	Mating vs. PreBirth	0.220	0.090	2.410	**0.016**	0.170	0.130	1.380	0.169
	PostBirth vs. PreBirth	-0.240	0.090	-2.800	**0.005**	0.740	0.110	7.020	**<0.001**

B-Tourist-macaque interactions: Out of 1064 interactions, a closely socially bonded partner was present within the same interaction of the focal macaque in only 25.8% of scans, and when the close partner was present, the partner was more dominant in 58% of the interactions. A partner was less likely to be present during an interaction than when such interactions were not taking place (females: paired t-test: df=8, t=5.828, P<0.001; males: paired t-test: df=7, t=9.145, P<0.001, Figure 4-6).

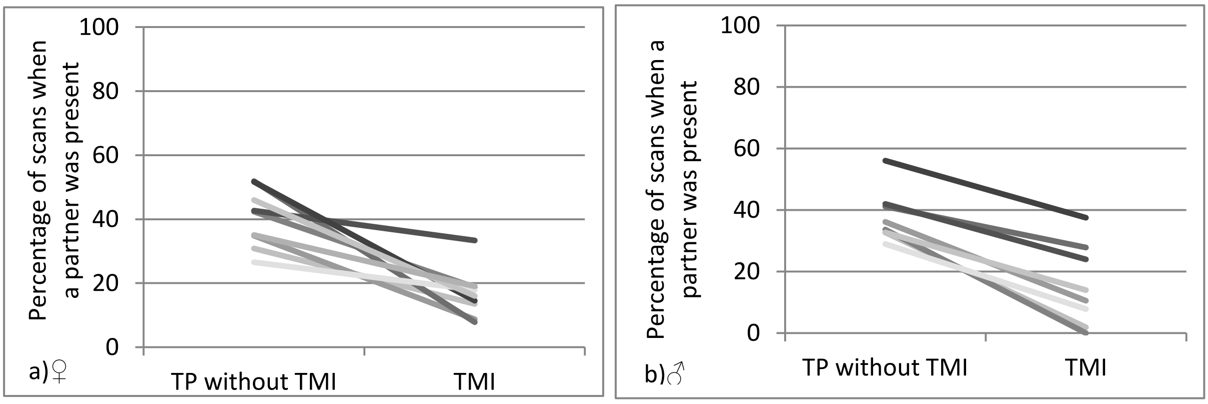


Figure 4-6: Percentage of scans in which (a) females and (b) males had a socially bonded partner present during TMI and during tourist presence (TP) without TMI. Each line is a single individual.

Relationships between tourist pressure and the presence of a socially bonded partner during an interaction

None of the tourist variables was significantly associated with the presence of a socially bonded partner during a tourist-macaque interaction for either sex (Table 4-12).

Table 4-12: Results of the GLMM testing the relationships between tourist pressure and the presence of a socially bonded partner during an interaction.

		Presence of a partner during a TMI for **females** (Y/N)				Presence of a partner during a TMI for **males** (Y/N)			
	Null vs.	N	df	χ^2	*P*	N	df	χ^2	*P*
	full model	535	8	21.331	**0.006**	529	8	47.005	**<0.001**
		Estimate	**±SE**	**z**	***P***	**Estimate**	**±SE**	**z**	***P***
	Intercept	-2.960	0.730	-4.050	**<0.001**	-3.670	1.110	-3.300	**0.001**
Tourist variables	Number of tourists from the nearest tourist group	0.200	0.130	1.500	0.134	0.030	0.170	0.160	0.872
	Distance from nearest tourist group	0.170	0.140	1.210	0.226	0.110	0.200	0.540	0.591
	TMI								
	Agonistic vs. Feeding	-1.040	0.580	-1.790	0.074	-0.020	0.960	-0.020	0.987
	Agonistic vs. Other	-0.940	0.580	-1.620	0.105	-0.210	0.970	-0.220	0.826
	Feeding vs. Other	0.100	0.320	0.330	0.746	-0.200	0.400	-0.490	0.628
Social variables	Dominant	-0.350	0.320	-1.090	0.277	3.530	0.590	6.010	**<0.001**
	Rank	0.300	0.230	1.290	0.197	-1.450	0.310	-4.650	**<0.001**
	Number of conspecifics involved	0.630	0.120	5.220	**<0.001**	0.290	0.110	2.590	**0.010**
	Season								
	Birth vs Mating	-0.580	0.580	-0.990	0.324	-1.770	0.900	-1.980	**0.048**
	Birth vs. PostBirth	0.390	0.460	0.830	0.405	-0.230	0.440	-0.540	0.590
	Mating vs. PostBirth	0.960	0.440	2.210	**0.027**	1.540	0.840	1.840	0.066

Prediction 3i: Macaques’ rate of self-scratching is positively related to tourist pressure.

A- Tourist presence:

<u>Relationships between tourist pressure and macaques self-scratching rates</u>

Both females and males had higher self-scratching rates when the distance from the nearest tourist group was shorter (Table 4-13, Figure A10-8 and Figure A11-11).

Table 4-13: Results of the GLMM testing the relationships between tourist pressure and macaques’ self-scratching rates.

		Females‘ self-scratching rates				**Males**‘ self-scratching rates			
	Null vs. full model	N	df	χ^2	*P*	N	df	χ^2	*P*
		1184	8	120.19	**<0.001**	986	8	104.71	**<0.001**
		Estimate	**± SE**	**t**	***P***	**Estimate**	**± SE**	**t**	***P***
	Intercept	1.720	0.150	11.770	**<0.001**	18.720	2.570	7.270	**<0.001**
Tourist variables	Number tourists in the whole area	-0.010	0.040	-0.310	0.770	-0.640	0.530	-1.220	0.229
	Number of tourists from closer tourist group	-0.030	0.040	-0.770	0.443	-0.630	0.540	-1.170	0.257
	Distance from nearest tourist group	-0.280	0.040	-7.050	**<0.001**	-4.880	0.560	-8.750	**<0.001**
Social variables	Dominant	0.300	0.090	3.380	**<0.001**	1.740	1.280	1.360	0.190
	Rank	0.100	0.060	1.700	0.176	1.350	1.490	0.910	0.659
	Season								
	Birth vs Mating	0.020	0.140	0.130	0.887	0.110	1.960	0.060	0.887
	Birth vs. PostBirth	0.370	0.130	2.790	**0.006**	2.170	1.840	1.180	0.994
	Birth vs. PreBirth	0.050	0.160	0.330	0.748	-2.870	2.300	-1.250	0.243
	Mating vs. PostBirth	0.350	0.080	4.270	**<0.001**	2.060	1.210	1.700	0.994
	Mating vs. PreBirth	0.040	0.120	0.290	0.778	-2.970	1.870	-1.590	0.084
	PostBirth vs. PreBirth	-0.310	0.120	-2.660	**0.008**	-5.040	1.730	-2.920	**0.005**

B-Tourist-macaque interactions: As temperature and humidity can both potentially influence animals' self-scratching rates (Ventura et al. 2005), a Wilcoxon test was run in order to check there was no significant temperature and humidity difference between days when a tourist-macaque interaction occurred and matched controls (MC). There was no significant difference in average daily temperature or humidity (Wilcoxon, N=955, temperature: z=-0.298, p=0.766, humidity: z=-0.175, p=0.861) between such days.

Macaques' self-scratching rates were not significantly different during TMI and during MC (females: paired t-test: df=8, t=1.592, P=0.150; males: paired t-test: df=7, t=1.795, P=0.116, Figure 4-7).

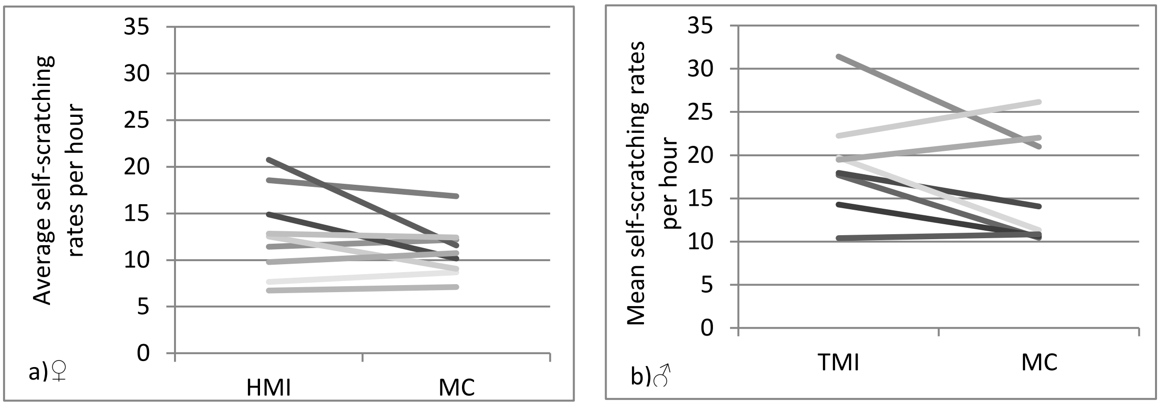


Figure 4-7: Mean self-scratching rates in (a) females and in (b) males per hour during TMI and MC. Each line is a single individual.

Relationships between tourist pressure and whether macaques’ self-scratching rates were higher during TMI compared to MC.

None of the tourist variables predicted higher females’ self-scratching rates during TMI compared to MC (Table 4-14). Males had higher self-scratching rates in TMI than in MC when tourists were closer (Figure A13-5).

Table 4-14: Results of the GLMM testing the relationships between tourist pressure and whether macaques’ self-scratching rates were higher during TMI compared to MC.

		Females’ higher self-scratching rates during a TMI compared to MC				**Males**’ higher self-scratching rates during a TMI compared to MC			
	Null vs. full model	N	df	χ^2	*P*	N	df	χ^2	*P*
		463	10	14.829	0.138	435	10	31.052	**< 0.001**
		Estimate	**± SE**	**z**	***P***	**Estimate**	**± SE**	**z**	***P***
	Intercept	-1.285	0.494	-2.603	**0.009**	-0.310	0.370	-0.820	0.412
Tourist variables	Number of tourists	-0.035	0.118	-0.293	0.770	0.020	0.100	0.220	0.830
	Distance from tourists	-0.265	0.136	-1.946	0.052	-0.670	0.170	-3.940	**< 0.001**
	TMI								
	Agonistic given vs. Agonistic received	-0.207	0.356	-0.580	0.562	-0.240	0.370	-0.650	0.519
	Agonistic given vs. Feeding	-0.108	0.262	-0.411	0.681	-0.430	0.250	-1.710	0.087
	Agonistic given vs. Other	-0.004	0.332	-0.011	0.991	-0.050	0.320	-0.150	0.880
	Agonistic received vs. Feeding	0.099	0.362	0.274	0.784	-0.190	0.360	-0.530	0.595
	Agonistic received vs. Other	0.203	0.412	0.493	0.622	0.190	0.410	0.470	0.641
	Feeding vs. Other	0.104	0.335	0.310	0.757	0.380	0.310	1.240	0.216
Social variables	Dominant	0.235	0.259	0.907	0.364	-0.010	0.240	-0.040	0.965
	Rank	-0.065	0.156	-0.418	0.676	0.250	0.120	2.050	**0.041**
	Season								
	Birth vs Mating	-0.438	0.628	-0.698	0.485	-0.040	0.370	-0.110	0.910
	Birth vs. PostBirth	0.041	0.346	0.118	0.906	-0.180	0.350	-0.520	0.602
	Birth vs. PreBirth	-0.495	0.527	-0.940	0.347	-0.460	0.480	-0.980	0.330
	Mating vs. PostBirth	0.479	0.547	0.876	0.381	-0.140	0.250	-0.560	0.573
	Mating vs. PreBirth	-0.057	0.664	-0.086	0.932	-0.420	0.410	-1.030	0.304
	PostBirth vs. PreBirth	-0.536	0.428	-1.251	0.211	-0.280	0.390	-0.730	0.465

Prediction 3ii: Macaques’ rate of restlessness is positively related to tourist pressure.

A- Tourist presence:

Relationships between tourist pressure and macaques’ restlessness rates

Females had higher restlessness rates when there were fewer tourists in the nearest tourist group (Table 4-15, Figure A10-9). In addition, females and males had higher restlessness rates when this group was closer (Figure A10-10 and Figure A11-12).

Table 4-15: Results of the GLMM testing the relationships between tourist pressure and macaques’ restlessness rates.

		Females’ restlessness rates				**Males**’ restlessness rates			
	Null vs. full model	N	df	χ^2	*P*	N	df	χ^2	*P*
		1184	8	126.07	**<0.001**	986	8	153.16	**<0.001**
		Estimate	**± SE**	**t**	***P***	**Estimate**	**± SE**	**t**	***P***
	Intercept	39.330	2.180	18.030	**<0.001**	39.810	1.680	23.680	**<0.001**
Tourist variables	Number tourists in the whole area	-1.960	1.000	-1.970	0.050	-1.420	1.010	-1.410	0.156
	Number of tourists from nearest tourist group	-2.020	1.000	-2.030	**0.041**	-0.060	1.020	-0.060	0.954
	Distance from nearest tourist group	-7.040	1.070	-6.610	**<0.001**	-8.450	1.070	-7.910	**<0.001**
Social variables	Dominant	12.750	2.360	5.410	**<0.001**	5.450	2.440	2.230	**0.027**
	Rank	0.580	0.960	0.600	0.636	-4.220	1.250	-3.380	**0.003**
	Season								
	Birth vs Mating	14.080	3.660	3.840	**<0.001**	22.200	3.740	5.940	**<0.001**
	Birth vs. PostBirth	8.240	3.510	2.350	**0.020**	5.030	3.530	1.420	0.154
	Birth vs. PreBirth	3.010	4.320	0.700	0.476	3.750	4.390	0.850	0.381
	Mating vs. PostBirth	-5.830	2.180	-2.680	**0.009**	-17.170	2.300	-7.460	**<0.001**
	Mating vs. PreBirth	-11.060	3.300	-3.360	**0.001**	-18.460	3.490	-5.290	**<0.001**
	PostBirth vs. PreBirth	-5.230	3.140	-1.660	0.103	-1.290	3.280	-0.390	0.723

B-Tourist-macaque interactions: Both male and female macaques' restlessness rates were significantly higher during TMI than MC (females: paired t-test: df=8, t=12.136, P<0.001; males: paired t-test: df=7, t=11.057, P<0.001, Figure 4-8).

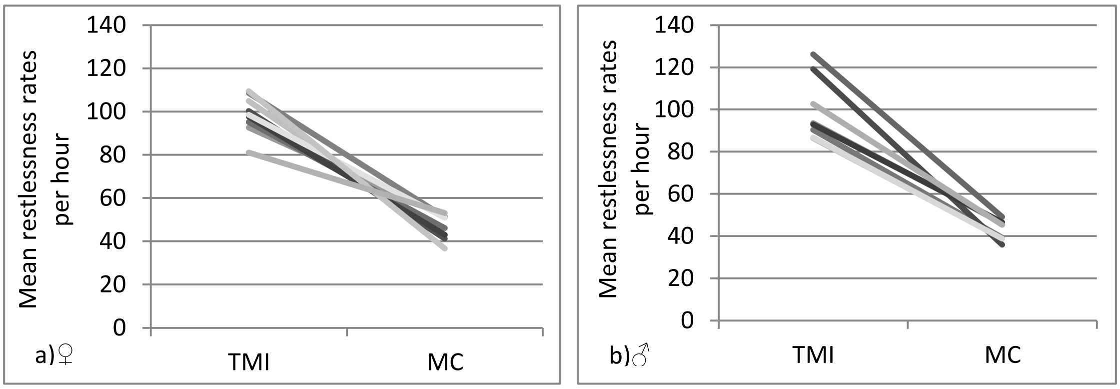


Figure 4-8: Mean restlessness rates in (a) females and in (b) males per hour during TMI and MC. Each line is a single individual.

Relationships between tourist pressure and whether macaques' restlessness rates were higher during TMI compared to MC

Both females and males were more likely to have higher restlessness rates in TMI than in MC during interactions with aggression given by tourists and feeding interactions, compared to other interactions (Table 4-16, Figure A12-3 and Figure A13-6).

Table 4-16: Results of the GLMM testing the relationships between tourist pressure and whether macaques' restlessness rates were higher during TMI compared to MC.

		Females' higher restlessness rates during an TMI compared to MC				**Males**' higher restlessness rates during an TMI compared to MC			
	Null vs. full model	N	df	χ^2	*P*	N	df	χ^2	*P*
		463	10	37.57	**< 0.001**	488	10	34.666	**< 0.001**
		Estimate	**± SE**	**z**	***P***	**Estimate**	**± SE**	**z**	***P***
	Intercept	0.980	0.400	2.440	**0.015**	1.120	0.380	2.920	**0.004**
Tourist variables	Number of tourists	0.020	0.100	0.160	0.873	-0.030	0.100	-0.300	0.766
	Distance from tourists	-0.160	0.110	-1.510	0.131	-0.190	0.100	-1.930	0.054
	TMI								
	Agonistic given vs. Agonistic received	-0.150	0.340	-0.430	0.667	-0.590	0.360	-1.650	0.099
	Agonistic given vs. Feeding	0.020	0.260	0.080	0.940	-0.020	0.260	-0.060	0.951
	Agonistic given vs. Other	-0.790	0.300	-2.630	**0.009**	-1.060	0.300	-3.560	**< 0.001**
	Agonistic received vs. Feeding	0.170	0.340	0.480	0.629	0.580	0.350	1.640	0.101
	Agonistic received vs. Other	-0.640	0.370	-1.750	0.080	-0.470	0.370	-1.260	0.209
	Feeding vs. Other	-0.810	0.300	-2.660	**0.008**	-1.050	0.280	-3.690	**< 0.001**
Social variables	Dominant	0.460	0.230	2.010	**0.044**	0.040	0.250	0.160	0.869
	Rank	-0.200	0.100	-1.910	0.056	-0.090	0.110	-0.860	0.389
	Season								
	Birth vs Mating	-0.680	0.390	-1.760	0.078	-0.420	0.380	-1.110	0.266
	Birth vs. PostBirth	-0.180	0.380	-0.480	0.634	0.210	0.360	0.580	0.561
	Birth vs. PreBirth	-0.710	0.480	-1.470	0.141	-0.190	0.460	-0.410	0.683
	Mating vs. PostBirth	0.500	0.230	2.180	**0.030**	0.630	0.250	2.570	**0.010**
	Mating vs. PreBirth	-0.030	0.380	-0.070	0.941	0.230	0.380	0.610	0.539
	PostBirth vs. PreBirth	-0.530	0.360	-1.470	0.143	-0.400	0.360	-1.100	0.271

Prediction 3iii: Macaques’ rate of aggression toward conspecifics is positively related to tourist pressure.

A- Tourist presence:

<u>Relationships between tourist pressure and macaques’ aggression rates toward conspecifics</u>

Both females and males were more likely to have higher aggression rates towards conspecifics when the nearest tourist group was closer (Table 4-17, Figure A10-11 and Figure A11-13).

Table 4-17: Results of the GLMM testing the relationships between tourist pressure and macaques’ aggression rates.

		Females’ aggression rates (log transformed)				**Males**’ aggression rates (log transformed)			
	Null vs.	N	df	χ^2	*P*	N	df	χ^2	*P*
	full model	1184	8	217.85	**<0.001**	986	8	217.2	**<0.001**
		Estimate	**± SE**	**t**	***P***	**Estimate**	**± SE**	**t**	***P***
	Intercept	0.690	0.090	8.020	**<0.001**	0.740	0.120	6.180	**<0.001**
Tourist variables	Number tourists in the whole area	0.040	0.030	1.200	0.225	-0.050	0.040	-1.270	0.214
	Number of tourists from nearest tourist group	-0.050	0.030	-1.620	0.102	-0.040	0.040	-1.020	0.296
	Distance from nearest tourist group	-0.340	0.040	-9.740	**<0.001**	-0.450	0.040	-12.000	**<0.001**
Social variables	Dominant	0.520	0.080	6.610	**<0.001**	0.340	0.090	4.020	**<0.001**
	Rank	-0.050	0.040	-1.100	0.354	-0.150	0.040	-4.040	**0.005**
	Season								
	Birth vs Mating	0.140	0.120	1.130	0.252	0.360	0.130	2.740	**0.009**
	Birth vs. PostBirth	-0.050	0.120	-0.450	0.657	0.020	0.120	0.170	0.857
	Birth vs. PreBirth	-0.300	0.140	-2.090	**0.039**	-0.050	0.150	-0.340	0.749
	Mating vs. PostBirth	-0.190	0.070	-2.620	**0.007**	-0.340	0.080	-4.200	**<0.001**
	Mating vs. PreBirth	-0.430	0.110	-4.000	**<0.001**	-0.410	0.120	-3.370	**<0.001**
	PostBirth vs. PreBirth	-0.250	0.100	-2.370	**0.021**	-0.070	0.120	-0.630	0.520

B-Tourist-macaque interactions: Macaques' aggression rates toward conspecifics were higher during TMI than MC (females: paired t-test: df=8, t=4.537, P=0.002; males: Wilcoxon sign rank test: df=7, z=-2.521, P=0.012, Figure 4-9).

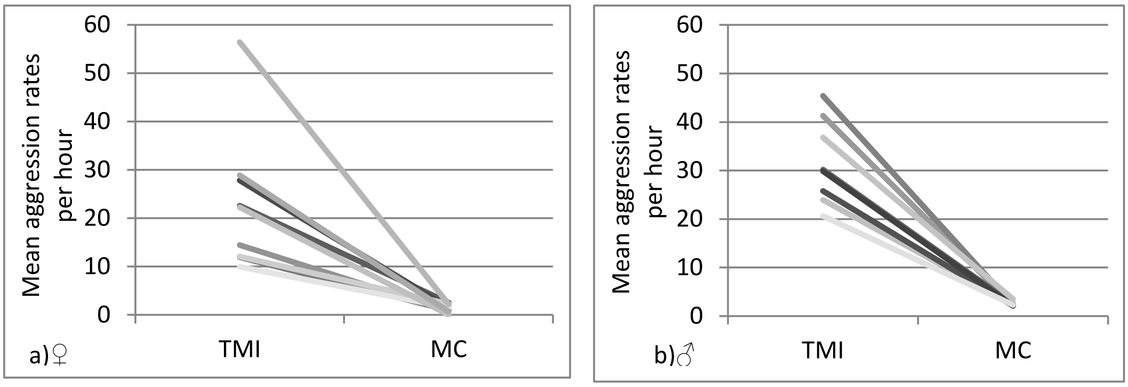


Figure 4-9: Mean aggression rates in (a) females and in (b) males per hour during TMI and MC. Each line is a single individual.

Relationships between tourist pressure and whether macaques' aggression rates toward conspecifics were higher during TMI compared to MC

Both females and males were more likely to have higher aggression rates in TMI than in MC when tourists were closer, and during both types of agonistic interactions (given to and received from tourists) compared to other interactions (Table 4-18, Figure A12-4 and Figure A13-7, 8). For males only, higher aggression rates were seen during TMI compared to MC, during feeding interactions compared to other interactions.

Table 4-18: Results of the GLMM testing the relationships between tourist pressure and whether macaques' aggression rates toward conspecifics were higher during TMI compared to MC.

		Females' higher aggression rates during a TMI compared to MC				**Males**' higher aggression rates during a TMI compared to MC			
	Null vs. full model	N	df	χ^2	*P*	N	df	χ^2	*P*
		488	10	44.704	**< 0.001**	488	10	43.049	**< 0.001**
		Estimate	**± SE**	**z**	***P***	**Estimate**	**± SE**	**z**	***P***
	Intercept	-1.690	0.470	-3.590	**< 0.001**	-0.860	0.400	-2.160	**0.031**
Tourist variables	Number of tourists	0.000	0.120	0.030	0.973	-0.170	0.120	-1.410	0.157
	Distance from tourists	-0.710	0.200	-3.530	**< 0.001**	-0.620	0.180	-3.470	**0.001**
	TMI								
	Agonistic given vs. Agonistic received	0.320	0.360	0.900	0.370	0.400	0.350	1.140	0.256
	Agonistic given vs. Feeding	-0.340	0.280	-1.200	0.229	-0.090	0.250	-0.350	0.724
	Agonistic given vs. Other	-0.980	0.460	-2.130	**0.033**	-1.090	0.380	-2.860	**0.004**
	Agonistic received vs. Feeding	-0.660	0.370	-1.790	0.073	-0.490	0.350	-1.410	0.159
	Agonistic received vs. Other	-1.300	0.520	-2.510	**0.012**	-1.490	0.450	-3.330	**0.001**
	Feeding vs. Other	-0.640	0.470	-1.380	0.169	-1.000	0.370	-2.680	**0.007**
Social variables	Dominant	0.220	0.290	0.760	0.445	-0.110	0.250	-0.440	0.663
	Rank	-0.330	0.120	-2.670	**0.008**	-0.120	0.110	-1.040	0.297
	Season								
	Birth vs Mating	0.100	0.450	0.220	0.830	0.290	0.400	0.710	0.477
	Birth vs. PostBirth	0.410	0.420	0.990	0.323	-0.020	0.370	-0.060	0.950
	Birth vs. PreBirth	-0.170	0.610	-0.270	0.785	0.100	0.490	0.200	0.843
	Mating vs. PostBirth	0.320	0.280	1.140	0.256	-0.310	0.250	-1.230	0.220
	Mating vs. PreBirth	-0.260	0.520	-0.500	0.615	-0.190	0.410	-0.450	0.651
	PostBirth vs. PreBirth	-0.580	0.490	-1.190	0.235	0.120	0.390	0.310	0.755

Prediction 3iv: Macaques' rate of affiliative behaviour is positively related to tourist pressure.

A- Tourist presence:

Relationships between tourist pressure and macaques' affiliative behaviour rates

None of the tourist variables was significantly associated with female macaques' affiliative behaviour rates (Table 4-19). Males showed higher affiliative behaviour rates when there were fewer tourists in the area and when the distance from the nearest group was shorter (Figures A11-14, 15).

Table 4-19: Results of the GLMM testing the relationships between tourist pressure and macaques' affiliative behaviour rates.

		Females' affiliative behaviour rates				**Males**' affiliative behaviour rates			
	Null vs. full model	N	df	χ^2	*P*	N	df	χ^2	*P*
		1184	8	123.92	**<0.001**	986	8	148.44	**<0.001**
		Estimate	**± SE**	**t**	***P***	**Estimate**	**± SE**	**t**	***P***
	Intercept	0.780	0.100	7.650	**<0.001**	1.200	0.140	8.400	**<0.001**
Tourist variables	Number tourists in the whole area	-0.060	0.040	-1.640	0.099	-0.090	0.040	-2.300	**0.022**
	Number of tourists from nearest tourist group	-0.020	0.040	-0.640	0.513	-0.010	0.040	-0.150	0.875
	Distance from nearest tourist group	0.000	0.040	0.070	0.953	-0.300	0.040	-7.270	**<0.001**
Social variables	Dominant	0.850	0.090	9.820	**<0.001**	0.580	0.100	6.130	**<0.001**
	Rank	-0.100	0.070	-1.380	0.284	-0.280	0.060	-4.280	**0.006**
	Season								
	Birth vs Mating	-0.230	0.130	-1.690	0.090	0.330	0.150	2.280	**0.019**
	Birth vs. PostBirth	-0.220	0.130	-1.680	0.091	0.050	0.140	0.370	0.690
	Birth vs. PreBirth	-0.600	0.160	-3.810	**0.001**	-0.150	0.170	-0.860	0.387
	Mating vs. PostBirth	0.010	0.080	0.130	0.912	-0.280	0.090	-3.130	**0.002**
	Mating vs. PreBirth	-0.370	0.120	-3.120	**0.002**	-0.480	0.140	-3.510	**0.001**
	PostBirth vs. PreBirth	-0.390	0.110	-3.360	**0.001**	-0.200	0.130	-1.540	0.128

B-Tourist-macaque interactions: Males' but not females' affiliative behaviour rates were significantly higher during TMI than during MC (females: Wilcoxon sign rank test: df=8, z=-1.718, P=0.086; males: Wilcoxon sign rank test: df=7, z=-2.521, P=0.012, Figure 4-10).

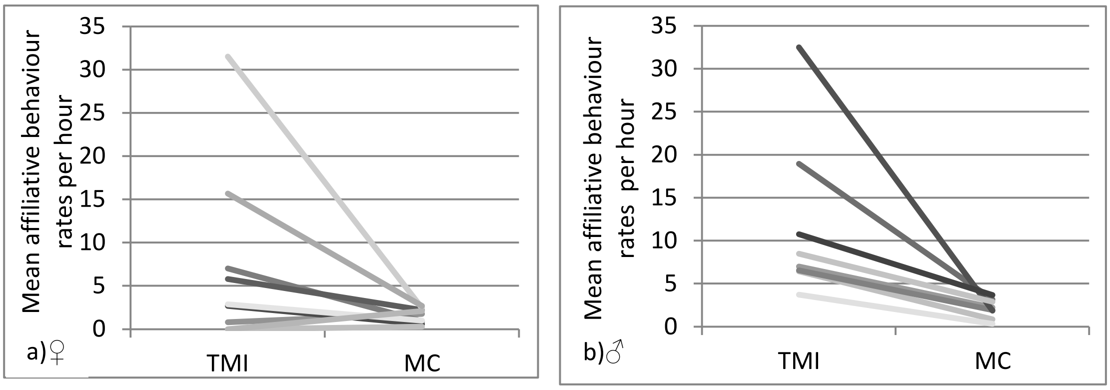


Figure 4-10: Mean affiliative behaviour rates in (a) females and in (b) males per hour during TMI and MC. Each line is a single individual.

Relationships between tourist pressure and whether macaques' affiliative behaviour rates were higher during TMI compared to MC

None of the tourist variables predicted higher male affiliative behaviour rates during TMI compared to MC (Table 4-20). Females were more likely to have higher affiliative behaviour rates in TMI than in MC when the number of tourists in the nearest tourist group was lower (Table 4-20, A12-5).

Table 4-20: Results of the GLMM testing the relationships between tourist pressure and whether macaques' affiliative behaviour rates were higher during TMI compared to MC.

		Females' higher affiliative behaviour rates during a TMI compared to MC (Y/N)				**Males**' higher affiliative behaviour rates during a TMI compared to MC (Y/N)			
	Null vs. full model	N	df	χ^2	*P*	N	df	χ^2	*P*
		476	10	24.58	**0.006**	447	10	17.48	0.064
		Estimate	**± SE**	**z**	***P***	**Estimate**	**± SE**	**z**	***P***
	Intercept	-2.750	0.740	-3.690	**< 0.001**	-1.494	0.539	-2.771	**0.006**
Tourist variables	Number of tourists	-0.930	0.430	-2.180	**0.029**	-0.190	0.164	-1.155	0.248
	Distance from tourists	-0.820	0.420	-1.950	0.051	-0.231	0.179	-1.295	0.195
	TMI								
	Agonistic given vs. Agonistic received	-0.240	0.700	-0.340	0.735	0.001	0.490	0.002	0.998
	Agonistic given vs. Feeding	-0.070	0.540	-0.130	0.895	0.318	0.319	0.998	0.318
	Agonistic given vs. Other	-0.710	0.860	-0.820	0.412	-0.317	0.460	-0.689	0.491
	Agonistic received vs. Feeding	0.160	0.740	0.220	0.825	0.317	0.471	0.673	0.501
	Agonistic received vs. Other	-0.470	0.990	-0.480	0.634	-0.318	0.574	-0.554	0.579
	Feeding vs. Other	-0.640	0.880	-0.720	0.469	-0.635	0.436	-1.456	0.145
Social variables	Dominant	0.090	0.560	0.150	0.878	0.437	0.314	1.392	0.164
	Rank	0.470	0.260	1.790	0.074	-0.318	0.144	-2.203	**0.028**
	Season								
	Birth vs Mating	-0.260	0.610	-0.430	0.671	-0.231	0.435	-0.531	0.595
	Birth vs. PostBirth	-1.260	0.640	-1.970	**0.049**	-0.751	0.408	-1.840	0.066
	Birth vs. PreBirth	0.170	0.840	0.210	0.834	-0.684	0.602	-1.135	0.256
	Mating vs. PostBirth	-1.000	0.540	-1.840	0.066	-0.519	0.322	-1.613	0.107
	Mating vs. PreBirth	0.430	0.770	0.560	0.573	-0.452	0.554	-0.816	0.414
	PostBirth vs. PreBirth	1.430	0.760	1.870	0.061	0.067	0.532	0.126	0.900

4.3.2 Result summary

A-Tourist presence

Table 4-21 provides an overall summary of the results of the GLMMs, organised according to the hypotheses linked with tourist presence.

Hypothesis 1: Evidence was found to support the idea that Barbary macaques adjust their vertical position - by being off the ground - to cope with high tourist numbers in the area and in the nearest tourist group. However, when in close proximity to tourists macaques were more likely to be on than off the ground. In addition, results indicated that Barbary macaques adjust their horizontal position to cope with higher number of tourists in the nearest tourist group, distancing themselves from such groups. Contrary to predictions, however, when tourist numbers in the area were high or when interacting with tourists, the animals were found in closer proximity to tourists. No evidence was found that macaques used tree cover to cope with tourist pressure.

Hypothesis 2: The results indicated that Barbary macaques were less – not more - likely to have a socially bonded partner present when the number of tourists present in the area increased. Also the findings suggested that males, but not females, use social support to cope with the high number of tourists in the nearest tourist group and their proximity.

Hypothesis 3: There was evidence to support the hypothesis that Barbary macaques use displacement behaviours in order to cope with the stress associated with tourist proximity, but not tourist number in the area or tourist numbers in the nearest tourist group. Contrary to predictions, females' restlessness rates were negatively linked to number of tourist in the nearest group and males' affiliative behaviour rates were negatively linked to number of tourists in the area.

Table 4-21: Summary of the results of the GLMMs testing the hypotheses linked with tourist presence. P value: *** <0.001; ** <0.01; *<0.05; Ns=P>0.05 non-significant. - not included in the model. Cases highlighted in light grey indicate results that are opposite to what was predicted. ↗ positive relationship, and ↘ negative relationship. Figures Appendices A10-A11.

A-Tourist presence	Females				Males			
	Number of tourists in the area	**Number of tourists in the nearest tourist group**	**Distance from the nearest tourist group**	**TMI (Y/N)**	**Number of tourists in the area**	**Number of tourists in the nearest tourist group**	**Distance from the nearest tourist group**	**TMI (Y/N)**
Hypothesis 1: Barbary macaques adjust their position to cope with tourists.								
Prediction 1i: The probability of macaques being off the ground is positively related to tourist pressure.	↗ ***	↗ ***	↘ ***	-	↗ ***	↗ *	↘ ***	-
Prediction 1ii: The probability of macaques being under tree cover is positively related to tourist pressure.	Ns	Ns	Ns	-	Ns	Ns	↘ **	-
Prediction 1iii: The distance that macaques keep from tourists is positively related to tourist pressure.	↘ ***	↗ ***	-	↘ ***	↘ ***	↗ ***	-	↘ ***
Hypothesis 2: Barbary macaques use social support to cope with tourists.								
Prediction 2: The probability of macaques having a socially bonded partner present in proximity is positively related to tourist pressure.	↘ *	Ns	Ns	-	↘ *	↗ ***	↗ *	-
Hypothesis 3: Barbary macaques use displacement behaviours to cope with tourists.								
Prediction 3i: Macaques' rate of self-scratching is positively related to tourist pressure.	Ns	Ns	↗ ***	-	Ns	Ns	↗ ***	-
Prediction 3ii: Macaques' rate of restlessness is positively related to tourist pressure.	Ns	↘ *	↗ ***	-	Ns	Ns	↗ ***	-
Prediction 3iii: Macaques' rate of aggression toward conspecifics is positively related to tourist pressure.	Ns	Ns	↗ ***	-	Ns	Ns	↗ ***	-
Prediction 3iv: Macaques' rate of affiliative behaviour is positively related to tourist pressure.	Ns	Ns	Ns	-	↘ *	Ns	↗ ***	-

B-Tourist-macaque interactions

Table 4-22 provides an overall summary of the results of the pairwise comparisons and the GLMMs, organised according to the hypotheses linked with tourist-macaque interactions.

Hypothesis 1: No evidence was found to support the hypothesis that Barbary macaques adjust their position by increasing distance from tourists (horizontally or vertically) or seeking tree cover in order to cope with the stress associated with interacting with tourists. On the contrary, both male and female macaques were more likely to be on the ground, in open spaces or in closer proximity to tourists, when they were interacting with tourists.

Hypothesis 2: No evidence was found that Barbary macaques use social support to cope with tourist interactions. Macaques were in fact less - not more - likely to have a socially bonded partner present during an interaction with tourists.

Hypothesis 3: There was evidence to support the hypothesis that Barbary macaques use displacement behaviours to cope with tourist interactions; however the results also indicated that Barbary macaques seemed to differently use the different types of displacement behaviour during the various interactions with tourists.

Table 4-22: Summary of the results of the pairwise comparisons and the GLMMs testing the hypotheses linked with tourist-macaque interactions. P value: *** <0.001; ** <0.01; *<0.05; Ns=P>0.05 non-significant. - not included in the model. Cases highlighted in light grey indicate results that are opposite to what was predicted. ↗ positive relationship, and ↘ negative relationship. Figures Appendices A12-A13.

B- Tourist-macaque interactions	Females				Males			
	TP without TMI vs. TMI	Number of tourists in the nearest tourist group	Distance from the nearest tourist group	TMI	TP without TMI vs. TMI	Number of tourists in the nearest tourist group	Distance from the nearest tourist group	TMI
Hypothesis 1: Barbary macaques adjust their position to cope with tourists.								
Prediction 1i: The probability of macaques being off the ground is positively related to tourist pressure.	***	Ns	Ns	Ns	***	Ns	↘ *	Ns
Prediction 1ii: The probability of macaques being under tree cover is positively related to tourist pressure.	***	Ns	Ns	Ns	**	Ns	Ns	Feed vs. Other **
Prediction 1iii: The distance that macaques keep from tourists is positively related to tourist pressure.	-	Ns	Ns	Ag. vs. Other * Feed vs Other ***	-	↘ **	Ns	Ag. vs. Other ** Feed vs Other ***
Hypothesis 2: Barbary macaques use social support to cope with tourists.								
Prediction 2: The probability of macaques having a socially bonded partner present in proximity is positively related to tourist pressure.	***	Ns	Ns	Ns	***	Ns	Ns	Ns
Hypothesis 3: Barbary macaques use displacement behaviours to cope with tourists.	TMI VS. MC				TMI vs. MC			
Prediction 3i: Macaques would have higher self-scratching rates due to tourists.	Ns	Ns	Ns	Ns	Ns	Ns	↗ ***	Ns
Prediction 3ii: Macaques higher restlessness rates would be related to tourists.	***	Ns	Ns	Ag. Given vs. Other ** Feed vs. Other **	***	Ns	Ns	Ag. Given vs. Other *** Feed vs. Other ***
Prediction 3iii: Macaques' rate of aggression toward conspecifics is positively related to tourist pressure.	**	Ns	↗ ***	Ag. Given vs. Other * Ag. Rec. vs. Other *	*	Ns	↗ **	Ag. Given vs. Other ** Ag. Rec. vs. Other ** Feed vs. Other **
Prediction 3iv: Macaques higher affiliative behaviour rates would be linked to tourists.	**Trend**	↘ *	Ns	Ns	*	Ns	Ns	Ns

4.4 Discussion

In this study, I examined the relationships between tourists and the behaviour of adult male and female Barbary macaques, focussing on two measures of tourist pressure: tourist presence and tourist-macaque interactions. I investigated whether tourists influenced different aspects of macaques' behaviour, in particular their spatial positioning, seeking the presence of a close social partner and their displacement behaviours.

In this Discussion, I first explore the major findings in relation to how tourist pressure may influence these animals' behaviour; the structure follows the hypotheses and predictions stated in the Introduction. Then, I discuss in more depth how these behavioural responses might reflect coping mechanisms, and also look at sex differences in potential coping strategies. Finally, I discuss some important caveats of this study and directions for future research.

4.4.1 Hypothesis 1: Barbary macaques adjust their position to cope with tourists.

In order to deal with disturbances within its environment, such as those caused by tourists, an animal might use anti-predator strategies, such as adjusting its position to distance itself from the aversive stimulus (Frid and Dill 2002, Blumstein 2014). Primates have the ability to use space along two dimensions - height and ground distances - which therefore offers two potential escape routes; being close to a refuge such as trees facilitates an escape, and may also therefore be used as an anti-predator strategy (Wilson 1972). However, tourists might also be beneficial and attractive to animals, because of the food resources they may offer. Evidence was found in the present study to support the idea that Barbary macaques adjust their position to cope with tourists, according to a trade-off between perceived risk and potential benefit. The following sections examine in depth the results regarding the three types of positioning: elevated position, distance on the ground from tourists and location under tree cover.

Prediction 1i: The probability of macaques being off the ground is positively related to tourist pressure.

Overall, the findings provided evidence in support of the prediction that Barbary macaques use elevated positioning as a strategy to cope with tourist presence, but the results suggest such a strategy is not used during tourist–macaque interactions. High tourist numbers in the area and in the nearest tourist group appeared to increase the likelihood that Barbary macaques were off the ground. No evidence was found in support of the prediction that Barbary macaques would be more likely to be off the ground while interacting with tourists.

A number of coping strategies are used by animals to cope with predators. “Flight-or-fight” coping mechanisms (Cannon 1915, Engel and Schmale 1972) reduce the risk of predation. Recently, it has been suggested that animals cope with human disturbance by using anti-predator strategies, as they might perceive humans as a potential predator (Frid and Dill 2002, Blumstein 2014). Climbing is one of the widely described anti-predator strategies in primate species (Stanford 1995). This strategy is used by animals to avoid a stressor, that is to extract or distance themselves from a stressful situation that they might not otherwise be able to deal with (Stankowich and Blumstein 2005).

Previous studies have provided evidence supporting the idea that primates use anti-predator strategies to cope with tourism. For example, pygmy marmosets (*Cebuella pygmaea*) reduced the use of the lower forest strata when humans were present in the area, suggesting that these animals used active avoidance mechanisms (de la Torre et al. 2000). Similar results have been seen in a study of black howler monkeys, in which it was found that there was a significant positive relationship between the number of humans present and monkeys' height above the ground (Treves and Brandon 2005). The present results similarly indicate that Barbary macaques use escape strategies when very high numbers of tourists are present at the site, and human disturbance increases. Therefore, these current findings provide additional evidence that anti-predator strategies, such as elevated positioning, might be used by animals to cope with human disturbance such as tourism.

Interactions between humans and wild animals often occur as a result of people feeding wildlife (Orams 2002). Attraction to food supplied by tourists has been documented in a wealth of wildlife tourism sites around the world (Orams 2002), and this attraction often changes animals' behavioural patterns (activity budget: Majolo et al. 2013, rates of aggression: Hill 1999) and also reduces animals' fear of humans, leading to encounters and/or interactions between wild animals and humans happening at a much closer distance (Orams 2002, Knight 2011). Previous studies on New World primates found that monkeys were generally in trees during interactions with tourists (black howler monkeys: Peres 1997, marmosets: Leite et al. 2011), while another study on long tailed macaques found that animals spent more time on the ground when close to a location where tourists gave food-handouts, compared to when they were further away from tourists (Patzschke et al. 2000). The present results support the previous findings in long-tailed macaques, and suggest that Barbary macaques are more often on the ground during tourist-macaque interactions, compared to the whole period when tourists are present.

Several factors might explain why interactions between tourists and macaques mostly occur on the ground. First, this phenomenon might be linked to general patterns of substrate use. Indeed, macaques are much more terrestrial than black howler monkeys or marmosets, which are highly arboreal (black howler monkeys: Peres 1997, marmoset: Leite et al. 2011). Barbary macaques, as is the case with many other species in the genus, have been reported by a number of studies to have high dietary plasticity and to be attracted to human food, which facilitates their habituation to tourists (long-tailed macaques: Wheatley 1999, Japanese macaques: Knight 2011). The degree of habituation to tourists shown by Barbary macaques, and macaques in general, might therefore differ from other primate genera (Russon and Wallis 2014). Evidence was found here that Barbary macaques, as has been found in other macaque species, have a strong attraction towards food given by tourists, which may then influence their vertical positioning, such that they are more often on the ground while interacting with tourists, despite the potential risks involved.

***Prediction 1ii: The probability of macaques being under tree cover is positively related to tourist pressure*.**

In the present study, there was evidence that although Barbary macaques spent the majority of time under tree cover, they were more often in open spaces during tourist-macaque interactions compared to the whole period when tourists were present. When investigating which variables influence macaques' likelihood of being under tree cover, no tourist variable was found to be related to females' likelihood of positioning under tree cover, while males were more likely to be in open space during feeding interactions compared to during other interactions.

As described in the previous section, animals with the ability to climb up into a tree often use this as a strategy against terrestrial predators (Stanford 1995). However, in order for this to be an efficient strategy, animals must be able to reach a tree before being caught by the predator, and therefore being in proximity to tree cover might in itself be an anti-predator strategy (Dill and Houtman 1989, Frid and Dill 2002, Cruz et al. 2013, Brotcorne et al. 2014). Wilson (1972) suggested that trees represent objects which structure an animal's environment, such that individuals react towards these objects in a predictable way, locating themselves near to or on the object rather than in an open space, and this would enable them to have a greater availability of escape routes. Evidence to support this idea was found in a study of the koomal (*Trichosurus vulpecual hypoleucus*), an Australian marsupial; individuals stayed in close proximity to trees regardless of predator presence, suggesting that this strategy might be used as first line of defence against predators

(Cruz et al. 2013). A number of other studies have also provided evidence that tree cover functions as a refuge which decreases predation risk. For example, prey animals such as small mammals and birds have been found to have higher vigilance rates when foraging in open spaces compared to when foraging under tree cover (Cassini 1991, Brown and Kotler 2004, Carrascal and Alonso 2006), or have been found to spend more time foraging under brush and tree cover than in open spaces (Newman et al. 1988, Brown and Morgan 1995, Orrock et al. 2004). The present results provide evidence that being under tree cover may be a basic mechanism which enables primates, and arboreal animals more broadly, to cope with perceived risk of predation, including from tourists.

The trade-off between the risks and benefits presented by tourists might explain why animals can sometimes be found in high risk landscapes, such as open spaces (Frid and Dill 2002, Cruz et al. 2013). For example, when predation risk was low, koomal seemed to prefer using open spaces, which was suggested to be associated with benefits such as easier travelling routes and/or better food resources (Cruz et al. 2013). Goshawk (*Accipiter gentilis*) may provide benefits to small nesting birds which nest close to goshawk nests, by protecting them against other nest predators such as corvids, themselves prey of goshawk (Mönkkönen et al. 2007). A similar idea was suggested regarding human observers being apparently used by samango monkeys as a “shield” against predators such as leopards (Nowak et al. 2014).

In the current study, Barbary macaques were more often in open spaces during an interaction with tourists than when tourists were simply present at the site, suggesting that the potential benefits of food might outweigh any risk from being in open spaces perceived by the animal. The present findings therefore provide additional evidence to support the idea that animals may make a trade-off between predator risk and potential benefits; in a tourist context, the benefits are food resources, while the risk is that of aggression from the tourists themselves.

Prediction 1iii: The distance between macaque on the ground and tourists is positively related to tourist pressure.

Evidence was found supporting the prediction that Barbary macaques adjust their horizontal position to cope with tourists; however, the distance between tourists and macaques appeared to be modulated by macaques' attraction for the food tourists may offer. Macaques were found at a greater distance on the ground from tourists when tourist number in the area decreased, and when a larger number of tourists were present in the nearest tourist group. Evidence was also found in support of the idea that tourist interactions with macaques might decrease the distance between tourists and the animals involved.

Keeping distance from a stressor is a primary anti-predator strategy to ensure survival and well-being (Blamires 1999, Fernández-Juricic et al. 2001a, Stankowich and Blumstein 2005). A number of authors have looked at flight initiation distance (FID), defined as the distance at which an individual initiates flight when approached by a potential predator (human or animal) which is perceived as a threat by the animal (Orams 2002, Fernández-Juricic et al. 2009, Blumstein 2014). However, the distance at which the animals perceive flight as an appropriate response toward aversive stimuli might be dependent on factors such as the degree of habituation to these stimuli and/or benefits gained from close proximity, such as food (Berger et al. 2007). For example, animals that are well habituated to tourists might be able to reduce their flight distance. When well habituated, choughs were able to adjust behaviour to cope with tourists, as revealed for example by a reduction of flushing distances (Jiménez et al. 2011). In addition, capuchins demonstrated a habituation to proximity to tourists, such that the distance between them and the tourists can be a metre or less, with close proximity generally shown by capuchins in order to receive food (Sabbatini et al. 2006). Nevertheless, if animals perceive humans as a potential threat (Frid and Dill 2002, Blumstein 2014), anti-predator strategies, such as keeping a safe distance might still occur even in well habituated animals (Fernández-Juricic et al. 2001b, Jiménez et al. 2011).

The present findings indicate that Barbary macaques keep a greater distance when the number of tourists in the nearest group is high, suggesting that an increase in tourist numbers is perceived as a greater threat. Similar results were found in black howler monkeys, where the number of tourists appeared to influence the response of the monkeys, which were more likely to move away when more humans were present (Treves and Brandon 2005). In addition, the present results found that Barbary macaques were further away from tourists when tourist number in the area was lower. As tourist number is positively associated to food opportunities, this suggests that when food opportunity is low, there might be an increase in intraspecific competition to obtain the limited food resources. Therefore in order to reduce the risk associated with high intraspecific competition, Barbary macaques might keep a greater distance from tourists and other conspecifics, as they might perceive it to be a highly risky situation. The present results support the idea that animals might use a perceived appropriate distance to cope with tourists, the distance varying as a function of the intensity of the perceived threat (i.e. degree of habituation, number of tourists, or levels of intraspecific competition) and the perceived benefits (i.e. food).

In a tourist context, animals are generally habituated to tourist presence and their fear of humans is reduced, which allows tourists to approach them at close range and interact (Orams 2002, Knight 2011). This proximity between wildlife and tourists has often been proposed to be due to animals' desire to obtain food from tourists (O'Leary and Fa 1993, Orams 2002, Knight 2011). In a number of studies, animals have been observed to initiate interactions with tourists to acquire food (O'Leary and Fa 1993, Fuentes et al. 2008, Hsu et al. 2009). In the present study, Barbary macaques' proximity to tourists appears to depend on the type of interactions with them. "Other" interactions (e.g. taking pictures) were more likely to occur at greater distance from tourists than agonistic or feeding interactions. The present results therefore provide additional evidence in support of the idea that attraction to food is a very important reason for close proximity between tourists and wildlife.

4.4.2 Hypothesis 2: Barbary macaques use social support to cope with tourists.

Much research has supported the idea of "social buffering", i.e. that the presence of a socially bonded partner helps animals to cope with stressful situations (Sachser et al. 1998, Engh et al. 2006a, Rault 2012). On the other hand, the social environment is also a potential source of stress associated with the risk of aggression from conspecifics (Wechsler 1995). In a tourist context, social support might help animals to cope with the potential risk of aggression from tourists; however when provisioning occurs, intraspecific competition increases, leading to an increase in risk of conspecific aggression (Majolo et al. 2013). Evidence was found to support the idea that male Barbary macaques, but not females, seek social support to cope with tourists, depending on a trade-off between different risks (i.e. from tourists vs. conspecifics) associated with interacting with tourists.

If humans may be perceived as predators by animals (Blumstein 2014), it might be expected that animals seek social support to cope with the associated stress of tourist presence *per se*. In Tibetan macaques, close proximity between conspecifics seen during interactions with tourists was suggested to be due to social reassurance (Pritchard et al. 2014). However, no evidence was found in the present study to support this idea for either sex; in fact the likelihood of having a partner present decreased when the number of tourists in the area was higher. High tourist number was associated with high food availability, which is also related to a higher number of potential interactions with tourists. Food opportunities might be more widely spread when tourist number is high, leading to a reduction in intraspecific competition, including with socially bonded partners. Socially bonded partners might therefore be considered as potential competitors while interacting with tourists, rather than as a support to cope with the associated stress. In fact Barbary macaques did not seem to seek social support during interactions with tourists, as a socially bonded partner was less likely to be present during such interactions than when there was no interaction. This further supports the idea that a socially bonded partner might be considered as a potential competitor during tourist interactions, as previously suggested by Majolo et al. (2013). In order to reduce potential risks associated with intraspecific competition, Barbary macaques might therefore be further away from a socially bonded partner and other conspecifics in general, during these interactions.

Despite the fact that the presence of a socially bonded partner may increase intraspecific competition when tourists offer food, when the number of tourists in the nearest tourist group was higher and when tourists were closer, males (but not females) appeared to seek social support. This suggests that males might seek support from a close social partner when the risk associated with tourists is higher than the risks associated with the presence of such a partner. Interacting with tourists can then be viewed as reflecting a trade-off between different risks (i.e. aggression received from tourists vs. conspecifics). Furthermore, seeking social support during interactions might also provide some benefits (i.e. providing direct support or modulating stress effects) which could counterbalance the risks associated with tourists and other conspecifics. However, it cannot be excluded that two highly socially bonded partners may be in close proximity during interactions with tourists only because both animals may be attracted by the same food, or being already close together and not because they actively seek social support.

Overall, findings of the present study suggest that Barbary macaques do not seek social support while interacting with tourists when the risks associated with intraspecific competition are high, but that a trade-off between costs and benefits of such support may be seen among males. Comparisons with other studies related to social buffering used by animals as a strategy to cope with tourists is very limited as, to my knowledge, no study has explicitly investigated this question.

4.4.3 Hypothesis 3: Barbary macaques use displacement behaviours to cope with tourists.

Displacement activities were first suggested to be generated by situations causing motivational conflicts, thwarting experience and frustration (Tinbergen 1952, McFarland 1966). It was therefore proposed that assessing displacement behaviour could be used as an indicator of animal emotional states, such as uncertainty and anxiety (Maestripieri et al. 1992). More recently, it was suggested that in mammals, fish and birds, these behaviours are generated by stressful stimuli and can act as coping strategies (Koolhaas et al. 2007, 2010). These two ideas about displacement behaviour (i.e. that they provide an index of emotional states, and that they function as coping mechanisms) are not mutually exclusive; one hypothesis refers to cause and one about function. Here I consider that increases in displacement behaviour may be a coping mechanism, which may be associated with animals' emotional state.

The presence of tourists can be viewed as a potential danger - but also a potential benefit - for animals, and interactions with tourists might therefore present a motivational conflict. Consequently, animals might use displacement behaviour to cope with such situations. Overall the present study did not provide evidence supporting the hypothesis that Barbary macaques use displacement behaviours to cope with tourist presence alone. However, evidence was found to support the idea that Barbary macaques use displacement behaviours to cope with the close proximity of tourists, which is often associated with tourist interactions. This suggests that Barbary macaques use displacement activities to cope with emotional conflicts associated with potential risks and benefits of interacting with tourists, but not to cope simply with the presence of tourists. In addition, Barbary macaques seemed to differently use the different types of displacement behaviour during the various interactions with tourists; this does not exclude the possibility that the different displacement behaviours may be used at different points in time during the same interaction.

The following sections examine in depth the results regarding the four displacement behaviours examined here: self-scratching, restlessness, aggression towards conspecifics and affiliative behaviour.

Prediction 3i: Macaques' rate of self-scratching is positively related to tourist pressure.

Overall, the findings provided evidence to support the hypothesis that Barbary macaques use self-scratching behaviour to cope with the emotional conflicts associated with tourist proximity, but not to cope with the stress related to high tourist number or tourist-macaque interactions.

Variations in self-scratching frequencies have been used by a number of studies as an indicator of animal's emotional state (Maestripieri et al. 1992, Maréchal et al. 2011). It has been found, for example, that wild mountain gorillas show higher rates of self-directed behaviour, including self-scratching, during tourist visits compared to before or after these visits occurring (Muyambi 2005), suggesting that tourist presence was stressful. However, studies of two macaque species (male Barbary macaques: Maréchal et al. 2011; Tibetan macaques: Usui et al. 2014) found no relationships between high tourist number and self-scratching rates. It was hypothesised by Maréchal et al. (2011) that animals use other behavioural mechanisms, such as climbing trees, to cope effectively with high tourist number. As expected the present results did not provide evidence to support the idea that self-scratching has a role in coping with the stress associated with tourist presence or number; however the findings on macaques' elevated positioning support the idea of Maréchal et al. (2011) that animals may instead use other behavioural responses, such as being off the ground, to cope with tourist number.

Interacting with tourists could be considered as an excellent example of an emotionally conflicting situation. Therefore it was expected that Barbary macaques would show higher rates of self-scratching while interacting with tourists, and indeed a previous study found that male Barbary macaques had higher self-scratching rates on days when the rates of interaction with tourists were higher (Maréchal et al. 2011). However, although evidence was found in the present study that Barbary macaques had higher self-scratching rates when tourists were in closer proximity (close proximity being associated with interactions), there was no significant difference in self-scratching rates between tourist-macaque interactions and matched control periods. It is difficult to explain the differences in results between these two analyses. One possibility is that proximity to tourists may reflect the whole process of an interaction with tourists: prior to its occurrence, during and after. Self-scratching rates might be higher before or after an interaction, but not during the interaction itself when the animal may be strongly focussed on the tourist. Similar results showing a negative relationship between self-scratching rates and tourist proximity have been found in previous studies (male Barbary macaques: Maréchal 2010, Tibetan macaques: Pritchard et al. 2014).

Prediction 3ii: Macaques' rate of restlessness is positively related to tourist pressure.

Overall, findings suggest that for Barbary macaques, restlessness may play a role in coping with tourist proximity and interactions with tourists (especially during agonistic and feeding interactions), but not with high tourist number in the area.

As previously described regarding self-scratching, I suggest that other behavioural mechanisms are used by animals to cope with the presence of high tourist number in the area. In addition, high tourist number may not represent an emotionally conflicting situation for animals, as defined by Tinbergen (1952), but possibly more a high risk situation only. Displacement behaviours, such as restlessness or self-scratching, might therefore not be an effective behavioural response.

Frustrating situations might elicit higher restlessness, which in turn allows animals to cope with the associated stress (Palit et al. 1998, Ohl et al. 2008). For example, undecided conflicts elicited higher restlessness frequencies in wild female crested macaques (*Macaca nigra*), but levels of restlessness did not vary depending on the intensity of the conflict (Duboscq et al. 2014). This suggested that undecided conflicts may lead to conflicting motivations, and animals may cope with this frustration by expressing higher rates of restlessness. Interacting with tourists might also be a frustrating situation, due to its unpredictability, and might elicit a similar response to the context of an undecided conflict.

The present results provide evidence to support the idea that Barbary macaques use restlessness to cope with tourist proximity and interactions. It is not possible to interpret this result in light of comparable data from animal species, as no other study has been carried out on how restlessness is related to tourist pressure. Understanding such relationships is potentially important as it has been found that restlessness might be energetically costly, which could have negative effects on wild animals' health (Higham et al. 2011a, Girard-Buttoz et al. 2014). In fact, it has been found that non exercise activity such as fidgeting, which is often associated with restlessness, was highly energy costly in overfed humans (Levine et al. 2000). An increase in restlessness rates associated with tourist interactions may therefore potentially have negative impacts on the health of animals.

Prediction 3iii: Macaques' rate of aggression toward conspecifics is positively related to tourist pressure.

The present results provide evidence to support the idea that Barbary macaques use aggression toward conspecifics to cope with tourist proximity and with tourist interactions; however, no evidence was found that Barbary macaques increase aggression toward conspecifics to cope with the stress associated with high tourist number.

Directing aggression towards conspecifics has been suggested to be a coping mechanism, which redirects attention towards a bystander or releases tension (Kazem and Aureli 2005). A number of studies have also suggested that macaques redirected the aggression received from conspecifics towards tourists (Wheatley and Putra 1994, Matheson et al. 2006). Animals might also redirect aggression toward conspecifics to cope with tourists. However, no evidence was found here that Barbary macaques used aggression toward conspecifics to cope with high tourist number, suggesting that other behavioural mechanisms are used instead as previously described. On the other hand, the present results do provide evidence supporting the idea that an increase in aggression toward conspecifics may have a role in coping with the stress associated with tourist proximity and tourist interactions. However, the possibility cannot be excluded that an increase in aggression rates might also be associated with intraspecific competition. In Japanese and rhesus macaques, higher aggression rates between conspecifics have been found in provisioned groups compared to non-provisioned groups (Hill 1999). In Barbary macaques, elevated rates of conspecific aggressive interactions have previously been related to provisioning (Majolo et al. 2013). These two hypotheses suggesting that increases in aggression toward conspecifics may be a coping mechanism or the outcome of high intraspecific competition, are not mutually exclusive; this makes the interpretation of such behaviour complex. Nevertheless, aggression between macaques may have costly consequences for their welfare (Honess and Marin 2006, McFarland and Majolo 2011), and therefore it is important to consider how this might be reduced in a tourism context.

Prediction 3iv: Macaques' rate of affiliative behaviour is positively related to tourist pressure.

Evidence was found that affiliative behaviour may help male Barbary macaques to cope with the stress linked with tourist proximity and tourist interactions, but not high tourist number. By contrast, no evidence was found for these effects in females.

Tourist pressure may cause stress, due for example to the associated elevated levels of competition and consequent threat to social cohesion (Hill 1999, Berman and Li 2002); affiliative behaviour might be used as a coping mechanism to cope with such stressful situations (Cheney and Seyfarth 2009, Rault 2012), and to reduce tension between conspecifics (de Waal 1984). The present results provide evidence supporting this idea for males and are in line with previous results in male Barbary macaques (Maréchal 2010). The present findings also provide evidence that females displayed more affiliative behaviours during tourist-macaque interactions compared to matched control. Contrasting with findings from a study of female bonnet macaques, which showed lower affiliative behaviour rates during provisioning compared to natural foraging (Ram et al. 2003). However, they had lower affiliative rates when the number of tourists during an interaction was higher. These findings provide additional evidence to the idea that females use an increase in affiliative behaviour to cope with stressors (Taylor et al. 2000, Cheney and Seyfarth 2009). However, it cannot be excluded that both animals might be more likely to close togather when they are being fed.

The difference between males and females in terms of the potential use of affiliative behaviour to cope with tourist pressure highlights the way that sex may play an important role in determining the nature of an animal's coping strategies; this theme will be developed in the following section.

4.4.4 Coping mechanisms in wild Barbary macaques

Sex differences in coping strategies

In the present study, the results provide evidence that female and male Barbary macaques often use behaviours similarly to cope with tourists. However, there appear to be some general differences between males and females, with males seeming to take greater risks than females in their apparent use of spatial positioning. In addition, there was an apparent sex difference with respect to seeking social association (i.e. presence of a socially bonded partner and affiliative behaviour) to cope with tourists, suggesting a difference in coping with social tension associated with intraspecific competition during tourist interactions. Here, I explore these sex differences in coping strategies broadly, rather than looking at sex differences in individual behaviours.

Sex difference in perceived risk

Studies have suggested that males generally take greater risks than females, in humans (Byrnes et al. 1999) and in non-human primates (Reader and Laland 2001). Evidence was found in the present study that male Barbary macaques take greater risks than females, probably in order to access food provided by humans: when a larger number of tourists was present, males but not females were more likely to interact with tourists in open spaces, and similarly males but not females were willing to be in closer proximity to the tourists. These results support previous findings that male primates take more risks.

It has been suggested that there is a sex differences in spatial ability, meaning that males and females use their spatial navigation differently, which may affect their risk-taking behaviour (Ecuyer-Dab and Robert 2004). Females might be compelled to favour low-risk navigation strategies, and so stay in known and safe locations (Campbell 1999), while males may be less averse to taking the risks involved in navigating new locations (Gaulin and FitzGerald 1989). In primates, it was suggested that males are more likely to take risks than females in order to access food in novel ways (Reader and Laland 2001). A similar idea was suggested by Sabbatini et al. (2006), who found that male capuchins seemed to take more risks during foraging, while females were more likely to feed on reliable food sources.

Evidence in the present study that males are more likely to take risks to access food than females suggests that there is a difference between sexes in the trade-off between risks and benefits associated with tourists. However, it is difficult to determine with the present results if the apparent sex difference in risk-taking is due to males and females responding differently to the same perceived risk, or rather because they perceive the same situations as posing different levels of risk. It has been suggested that human sex differences in risk taking are associated with the differences in the perception of the benefits and risk, rather than with differences in the response towards perceived risk (Weber et al. 2002). This would suggest that males might perceive risk associated with tourists as lower than do females, therefore changing the trade-off between risk and benefits associated with tourists.

Sex differences in seeking social association: social support and/or social tension reduction

A number of studies have suggested that female humans and other primates tend to cope with stress by seeking social support and/or increasing affiliative behaviour (Taylor et al. 2000, Cheney and Seyfarth 2009). By contrast, males are thought to be more likely to cope with stressful situations by other means, such as through fight or flight responses (Taylor et al. 2002). There is endocrinological evidence to support these ideas. In humans, women secrete more endorphins and oxytocin into the blood stream in response to stress, which are the two main hormones associated with positive social behaviour, and men release more norepinephrine and cortisol, which are more related to a fight or flight response (Taylor et al. 2002). The present results indicate that there is a sex difference in Barbary macaques in the use of social support and affiliative behaviour to cope with tourists, but that both sexes appear to use this general coping strategy; the difference between males and females is potentially due to a difference between the sexes in the perceived risks from tourists and from conspecifics.

During provisioning, there is often unequal food distribution, as it is clumped in a limited space which increases intraspecific competition (Hanya 2004), and creates social tension (de Waal 1984). de Waal (1984) found that male rhesus macaques increased grooming rates with conspecifics during provisioning when food resources were clumped and social tension was high, whereas females showed no significant difference between provisioning and non-provisioning periods. The results of the present study indicate a sex difference in the use of affiliative behaviour to cope with tourist pressure, supporting de Waal’s suggestion that reduction of social tension is particularly important for males.

Low tourist number is associated with lower food availability, which in turn may increase intraspecific competition, creating higher social tension. By increasing affiliative behaviour in such contexts, male Barbary macaques may be able to reduce these tensions. In addition to the idea that males use affiliative behaviour to reduce social tension when interacting with tourists, evidence was also found that males seek social support to cope when more tourists are present in the nearest group and when they are closer. The present results suggest that males were more likely to take risks than females, by being closer to, and tolerating larger numbers of tourists. Seeking the presence of a socially bonded partner in such situations might be a strategy to alleviate the stress associated with this increased risk-taking.

By contrast with males, the present results did not provide evidence suggesting that females seek social support to cope with tourists. However, during tourist-macaque interactions, when more tourists were present in the nearest group females were more likely to have lower affiliative behaviour rates. Previous findings suggested that females would be more likely to seek social support from relatives to cope with stress (Taylor et al. 2000). This “tend-and-befriend” hypothesis, proposed by Taylor et al. (2000), has been supported by a number of studies of female animals (Engh et al. 2006a,b, Cheney and Seyfarth 2009). The present findings support the idea that females might use affiliative behaviour to cope with specific stressful situations associated with tourists, but do not seek social support or increase affiliative behaviour to modulate social tension associated with intraspecific competition.

Overall, the results of the present study indicate that males and females use social associations (i.e. social support and affiliative behaviour) differently to cope with the risks associated with tourists and intraspecific competition. The apparent sex difference in social association may be related to the trade-off between the perceived risk and benefits of provisioning. Males might take more risks to access food compared to females, but they might modulate these risks by using different coping mechanisms such as social support in these situations.

Differential use of coping mechanisms: a new framework to understand how primates cope with tourists by making a trade-off between risks and benefits.

Animals use a range of coping mechanisms to cope with stressful situations. Which mechanism(s) - if any - are used is thought to reflect a trade-off between the costs and benefits (for example, in terms of energy - Frid and Dill 2002) of the alternative options. According to the risk-disturbance hypothesis, animals adapt their behaviour depending on a trade-off between the costs of such anti-predator behaviour (e.g. flight, vigilance) and the perceived predation risk. The costs of anti-predator behaviour, such as flight, are related to the costs of abandoning a resource patch as well as to the increase in energy expenditure due to locomotion (Ydenberg and Dill 1986).

However when the potentially dangerous stimulus also presents potential benefits, animals adapt their behavioural response, and use coping behaviours other than anti-predator behaviour. As previously described, interacting with tourists may pose a number of risks associated with potential aggression from tourists and conspecifics, but also benefits related to the food that tourists may provide. Based on the risk-disturbance hypothesis suggesting that animals cope with human disturbance by making a trade-off directly related to energy gain (Frid and Dill 2002), I propose a new framework to understand how animals adapt their use of coping mechanisms, depending on the trade-off between the perceived threat and attraction (Figure 4-11). This framework focuses on two 2 main coping mechanisms, spatial positioning and displacement behaviour, but not on social support/buffering because this coping mechanism seems to be highly associated with other factors such as sex.

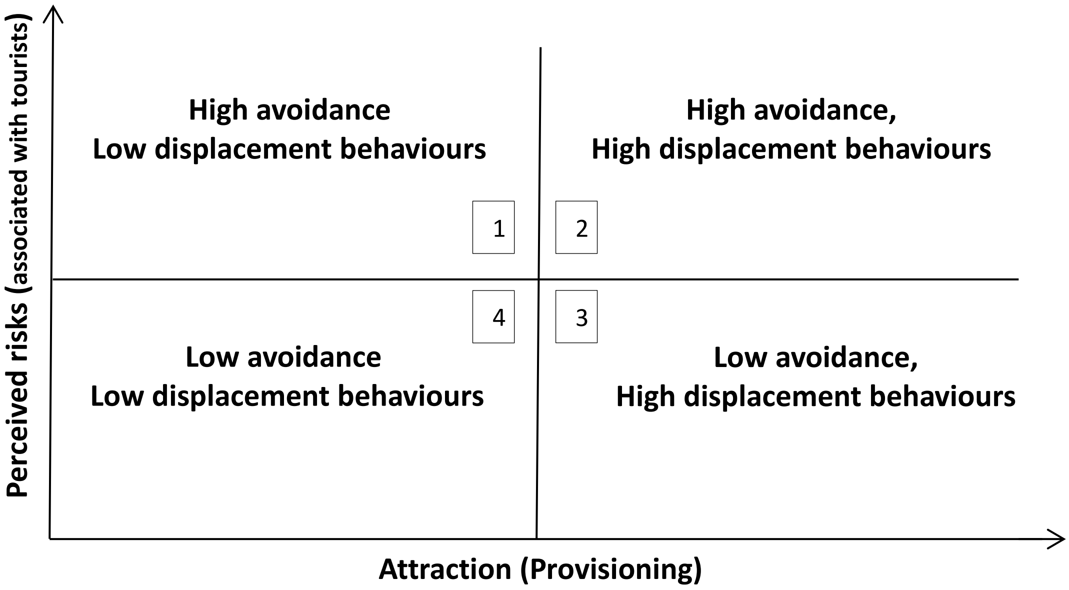


Figure 4-11: Framework of the trade-off for animals between the perceived risks and attraction related to tourists.

When animals perceive high risks associated with tourists but there is little attraction due to no or little provisioning occurring (quarter [1] in Figure 4-11), they are predicted to use an active avoidance strategy. For example, animals might move off the ground or further away to distance themselves from the stressors, or might leave the area. This prediction is supported by results from the present study as well as a large number of previous findings (marmoset: de la Torres et al. 2000, black howler monkeys: Grossberg et al. 2003, Treves and Brandon 2005; animals in general: Frid and Dill 2002).

On the other hand, food is a powerful tool to attract wild animal and provisioning progressively results in the taming of animals that were initially wary toward humans (Orams 2002). Animals well habituated to human presence may perceive tourists as less aversive because of the positive reinforcement provided by the link between human presence and food benefits (Knight 2011). This can be translated into a reduction of flight distance, enabling them to approach or be approached by tourists more closely (e.g. chough: Jiménez et al. 2011, capuchins: Sabbatini et al. 2006, macaques: Priston and McLennan 2013). However, even when well habituated to human presence, animals may modulate their flight distance according to the intensity of the perceived threat; this would then lead to a situation (quarter [2] in Figure 4-11) where high rates of avoidance may occur, but also high levels of displacement behaviour may be used to cope when avoidance is not used.

When the risk is perceived as low and is exceeded by a strong attraction for food (quarter [3] in Figure 4-11) - the distance between animals and tourists may reduce. As a result, animals may not avoid tourists, and may be in close proximity despite the risks associated with potential aggression from tourists or conspecifics, because of the potential benefit, i.e. accessing food. When the distance between animals and tourists reduces, animals may be in an emotionally conflicting situation, which they may cope with by showing displacement behaviours (Tinbergen 1952, McFarland 1966). Evidence was found in the present and previous studies to support this idea (Tibetan macaques: Matheson et al. 2007, Pritchard et al. 2014; male Barbary macaques: Maréchal et al. 2011).

When both the risks and the benefits are perceived as low (quarter [4] in Figure 4-11) animals may not express any avoidance strategy and not show elevated levels of displacement behaviours. A combination of multiple factors must be met to ensure such a situation. For example, the present results suggested that a reduction in tourist number, an increase in distance between animals and tourists, and a limitation or elimination of provisioning may reduce the potential threat and attractions associated to tourists. This configuration of low risks and benefits would potentially reduce the impacts of tourism on animals' behaviour and health.

Overall, evidence was found in the present study suggesting that the relationships between tourists and wildlife may be modulated by the trade-off between animals' perceived risk and perceived benefit. The perceived risk is likely to be affected by the interplay between individual characteristics (i.e. degree of habituation, species, age, sex, temperament, previous experience), and the context (i.e. tourist number, tourist and conspecific behaviour). The perceived benefit is also dependent on a multitude of factors, for example, food preference, amount of food previously consumed, nutritional status and protection against predators. This framework might be extrapolated to assess the range of behavioural responses associated with the trade-off between perceived threat and attraction, within an individual at different times, to compare individuals or sexes, or more broadly to compare species. Finally, this framework may also be used to compare and assess different tourism disturbance and settings.

4.4.5 Caveats and directions for future research

Although evidence was found in the present study that Barbary macaques use a range of mechanisms to cope with tourists, findings must be interpreted with caution due to the number of factors that can be associated with animals' behavioural responses. The present results are based on the relationships between variables, but the observational methods employed do not allow determination of the causal direction of such relationships. For instance, it is difficult to determine if macaques were on the ground during an interaction with tourists because of the interaction itself, or if the interaction occurred because the macaques were already on the ground.

Investigating the impacts of tourism on wildlife has recently become a growing research topic (Ruesto et al. 2010, Maréchal et al. 2011, Borg et al. 2014). Exploring and integrating a range of behavioural responses, as well as investigating other parameters, such as physiological and other individual health measures, is needed to fully understand the variety of effects that tourists might have on the animals involved.

4.4.6 Conclusion

This study has produced novel insights into the potential mechanisms used by Barbary macaques in order to cope with tourists. This is the first study to attempt to explore such a wide range of potential behavioural coping strategies, such as spatial positioning, seeking social support and displacement behaviours. Overall the results suggest a trade-off is made by animals between potential risks and potential benefits associated with tourists. Understanding how animals cope with human disturbances has recently become an increasingly important and popular research area (Frid and Dill 2002, Blumstein 2014); however such coping is still poorly understood, due to the complexity of factors influencing animals' responses. A more integrative approach including a number of behavioural responses, such as in the present study, and careful consideration of the perceived risk and benefits, could lead to greater understanding of how wild animals cope with humans in their environment, which could in turn help management decisions in order to limit negative effects of tourists on animals' welfare.

Assessing behavioural responses can provide a powerful tool for assessing animal welfare, and could help to provide concrete management solutions which could benefit wildlife tourism while reducing the costs for the animals involved. For example, the present results suggest that limiting interactions with tourists, increasing the distance between tourists and animals, reducing the number of tourists in close proximity to the macaques and avoiding interactions when not under tree cover could potentially improve the macaques' welfare.

Finally, this study provides a basis for better understanding coping mechanisms of wild animals more broadly. The results suggest that researchers should select carefully for investigation the behaviours which could be used to cope with a stressor, as animals might use a range of behavioural responses associated with the trade-off made between their perceived risk and perceived benefits. The new framework described in this study might therefore be usefully adapted to other potentially stressful situations, in which there are motivational conflicts between perceived risks and benefits.

Chapter 5

Impacts of tourist provisioning on the health of wild Barbary macaques

5.1 Introduction

With the dramatic growth in wildlife tourism, serious concerns have been raised regarding its impacts on the animals involved, in particular in relation to tourists' feeding of wildlife (Orams 2002). There are numerous potential negative effects of feeding wildlife, such as disease transmission, poaching and traffic risk, and increased conflicts with local human populations via crop and/or town raiding. All of these may negatively affect, directly or indirectly, the health of the animals involved. In this chapter, I explore the impacts of tourist provisioning on the health of wild Barbary macaques by using a range of non-invasive health measures to compare two groups of animals, one experiencing high levels of provisioning and the other relying on natural foraging.

5.1.1 Provisioning wild animals

Maintaining a healthy energy balance is a key factor for fitness (i.e. survival and reproduction), and requires balancing energy intake and energy expenditure. In a natural environment, fluctuations in energy balance are often caused by seasonal variability in food (Koivula et al. 1995, Harrison et al. 2010). Provisioning may help animals to cope with such ecological variation by supplementing their diet with additional nutrients (Brittingham and Temple 1988, Persson 2005). Therefore, provisioning might in this way be beneficial, as increased nutrient intake can lead to better body condition and immunocompetence (Knapp et al. 2013). In general, evaluating the health of wild animals is complex because of the multiple short and long-term factors, physical and environmental, that may influence their health. In order to evaluate the benefits of provisioning in terms of animals' health, in particular during periods of nutritional stress, most studies have used fitness outcomes as indicators of health (Persson 2005, Harrison et al. 2010, Plummer et al. 2013a). A number of studies in mammals and fish provide evidence that when animals receive supplementary food during winter, breeding success the following season is higher, for example: Arctic fox (*Alopex lagopus*, Angerbjörn et al. 1991); wolverines (*Gulo gulo*, Persson 2005); and plaice (*Pleuronects platessa*, Kennedy et al. 2008).

Since provisioning appears to improve animals' fitness, some conservationists have suggested that provisioning wildlife may represent a means of improving nutritional condition, survival and reproductive success of endangered species (Robb et al. 2008); this approach is thought to help reduce the risks of population extinction linked to environmental stochasticity (Kuehler et al. 2000, Schoech et al. 2008). For instance, supplementary feeding provided as part of conservation management was associated with an increase in fledgling populations of European white stork (Hilgartner et al. 2014) and Hihi (*Notiomystis cincta*, Castro et al. 2003), and therefore it was suggested that provisioning may be a powerful tool to attenuate population losses caused by factors such as habitat alteration or food shortage in winter.

However, a number of studies have suggested that provisioning might also have negative consequences for the conservation of endangered species. For instance, intensive food supplementation has been used to attempt to improve the breeding success of the Spanish Imperial Eagle, a critically endangered species, but it was found that the food provided (i.e. domestic rabbits) contained some antibiotics and antiparasitics; these may have led to the poor health condition of individuals fed with this food supplement, including a depressed immune system and high prevalence and richness of pathogens (Blanco et al. 2011). Provisioning might also bias reproductive sex-ratios toward males, and therefore reduce effective population size (Tella 2001). The hypothesis that provisioning might affect sex-ratio is based on the sex-allocation hypothesis of Trivers and Willard (1973), which predicts that females with the best body condition will tend to produce more male offspring. Therefore, if provisioning improves female body condition, it would be predicted that females produce more males. In order to boost the reproduction of kakapo, a critically endangered bird from New-Zealand, intensive food supplementation was provided over several years. However, a study by Clout et al. (2002) suggested that provisioning had no impact on breeding productivity, but might have affected the breeding outcomes, biasing the sex-ratio in favour of males, which negatively affected conservation efforts (Clout et al. 2002).

Overall, supplementary feeding by conservationists can have positive consequences on the health of wild animals involved and in some cases be beneficial for conservation of endangered species by increasing reproductive success. However it can also present negative effects, which may be unexpected, such as reducing fitness, or indirect and unnoticed, such as modification in parasite loads (Blanco et al. 2011). The range of potential effects of food supplementation on health are generally difficult to identify, and therefore are poorly understood.

Provisioning wild animals, even for conservation purposes, is therefore a controversial topic because the impacts of food supplementation on the health of wild animals are not fully understood; this is particularly true regarding provisioning provided by tourists (Orams 2002). The feeding of wildlife by tourists is, nevertheless, a very popular activity, commonly associated with wildlife tourism (Orams 2002). Evaluating the effects of tourist provisioning is complex because the supplementary food is generally not controlled, making it difficult to know the quantity and the quality of the food provided. Since wildlife tourism is rapidly growing, and wildlife feeding is such a common practice, it is important to understand the full impacts of such activity on the health of wildlife. Recent studies have suggested that tourist provisioning might disturb animals’ energy balance by excessively increasing energy intake and/or reducing energy expenditure, and thus negatively affecting their health (Kemnitz et al. 2002, Borg et al. 2014). Food provided by tourists is often the same that people eat, which is typically very energy-rich, high in fats and carbohydrates. This might contribute to obesity and associated deleterious effects, such as diet-related disease and disorders including diabetes, and cardiovascular disease (Ginsberg 2000, Bauer et al. 2011); however no research has been conducted to determine if tourist provisioning does cause such health problems.

Provisioning might have a negative influence on animals' reproductive success or nutritional status. For example, birds in cities are often fed during winter with energy-rich food that has a high fat content, and this appears to have negative impacts on reproductive fitness, such as reduced birth rate (Plummer et al. 2013a,b). In the northern Bahamian rock iguana, biochemical indicators of nutritional status such as glucose, potassium and uric acid levels were higher in individuals from provisioned groups than in those from non-provisioned groups (Knapp et al. 2013), suggesting that the difference in nutritional intake/source may have negative impacts on their long-term fitness. In baboons, it has been found that groups with high caloric food supplements had much higher serum insulin concentrations and higher levels of cholesterol than groups foraging on natural resources, potentially leading to diet-related disease and disorders in the long-term (Kemnitz et al. 2002).

In addition to the impacts of provisioning on energy balance, supplementary food might have other potentially negative effects on animals' health. For instance, provisioned food tends to be clumped with a limited spatial distribution, which aggregates individuals and may increase intraspecific competition, resulting in higher risk of injuries (Hill 1999, Majolo et al. 2013). This aggregation may also increase the risk of disease and parasite transmission (Becker and Hall 2014). Despite such serious concerns, there are few scientific studies of the negative consequences of tourist provisioning for the health and viability of wild animals. This may be related to the numerous challenges involved in identifying the causal relationships between provisioning and health changes in wild populations (Orams 2002), including the difficulties of measuring the health of free ranging animals.

5.1.2 Assessing animals’ health status

Assessing wild animal health can be crucial, especially in endangered species when the survival of a population depends largely on the health of a few individuals (Wikelski and Cooke 2006). Invasive measures offer good accuracy but may also have high costs in terms of the welfare of the animals involved (MacIntosh et al. 2012). Recently, various non-invasive methods have been developed which can be used to evaluate animals’ health (Kersey and Dehnhard 2014). For example, some physiological measurements can be obtained from faeces, urine or saliva samples (Heistermann 2010, Kersey and Dehnhard 2014), and overall health can be evaluated by visual scoring methods of features such as visible scars and injuries (Regula et al. 2004, Pritchard et al. 2005, Mejdell et al. 2010), and disease symptoms (MacIntosh et al. 2012). In the present chapter, I explore several non-invasive methods to assess animal health, to determine whether provisioning affects the health of wild Barbary macaques.

Reproductive success

Animals’ reproductive success is influenced in particular by their nutritional status. Provisioning might therefore have beneficial effects on the reproductive success of females, increasing the number of offspring produced and their survival (Elowe and Dodge 1985, Persson 2005, Kennedy et al. 2008, Hilgartner et al. 2014). However there are a number of examples in which provisioning had no significant effects on breeding productivity (Clout et al. 2002, Jamieson et al. 2003), and other studies have provided evidence for a negative effect of provisioning on reproductive success (Fa 1984, Plummer 2013). Reproductive success may provide an indirect measure of general health for females because females in better condition tend to produce more and healthier offspring, as suggested by a wealth of studies (Harisson et al. 2010). Reproductive success is generally measured by the number of offspring a female produces over certain period, and the number of offspring that reach breeding age (Mann et al. 2000). Nevertheless, the survival of offspring might be influenced by factors other than the health of the mother, such as environmental conditions (e.g. predation, temperature and poaching), and might therefore not reflect accurately the general health of a female. In addition, long term studies are often necessary to estimate reproductive success, especially in taxa with extended developmental phases such as primates, that make it difficult to investigate the factors that influence an individual’s reproductive success.

Physical injuries

A laceration of the skin may provide an entry point for bacteria and parasites, leading to health complications and potentially the death of the individual. Since provisioning has been shown to increase aggression between conspecifics (Hill 1999, Majolo et al. 2013) and potentially human-animal conflicts (Fuentes 2006), assessing injuries provides an important indicator of animals’ health status. Physical injuries are a major health concern as these can result in increased risk of infection, and reduced mobility, and therefore increased risk of mortality and predation (Chilvers et al. 2005, Demas et al. 2011, Archie 2013). In addition to health problems resulting from physical injuries, it has been suggested that evaluating physical injuries may also be a useful welfare indicator as injuries are associated with agonistic interaction between conspecifics, and therefore social stress (Grandin 2010). In livestock, an objective index of physical injury has been developed in order to assess animal health and welfare (Regula et al. 2004, Pritchard et al. 2005, Mejdell et al. 2010). This index is based on a visual system scoring injuries, scarring and lameness. In primates, few studies have quantitatively recorded the number of injuries, scarring and lameness, but none using any visual scoring system, as potential health and welfare indicators associated with social stress (Archie 2013) or tourism (Westin 2007). In howler monkeys, for example, individuals in a tourist area seemed to have more scars and wounds than did individuals in a non-tourist area (Westin 2007), which suggests that such an index might be a useful tool to determine the impacts of provisioning on the health of animals.

Disease symptoms

Since disease can have deleterious effects on both individual animals and populations, and disease might be directly or indirectly related to interactions with humans, it is important to investigate whether provisioning is related to disease in wild animals. Disease outbreaks, such as polio and respiratory disease, have occurred in chimpanzees, resulting in the death of several individuals, and these were attributed to close contact with humans (Lonsdorf et al. 2006). In Barbary macaques in Gibraltar, disease outbreaks have been reported, including gastroenteritis, and pneumonia, as well as nasal discharge and coughing associated with respiratory pathogens, all of which were suggested to have been transmitted by human contacts via provisioning (Fuentes 2006). In fact, a number of studies have suggested that there is a high risk of disease transmission between humans and primates (Fuentes 2006, Goldberg et al. 2007). Monitoring disease symptoms of animals might therefore be a useful tool to assess the health-related impacts of provisioning on animals' health. For example, consistency of faeces was proposed to be associated with potential digestive disease or disorders in chimpanzees (*Pan troglodytes:* Huffman and Seifu 1989) and coughing and sneezing were suggested to indicate potential respiratory infections in Barbary macaques (Fuentes 2006). Evaluating disease via the assessment of symptoms might also help better understand the role of disease in animal ecology, and animals' health status more broadly (Lonsdorf et al. 2006, Gillespie et al. 2008). Recording of disease symptoms has been used in a few studies to assess wild primates' health non-invasively (Huffman and Seifu 1989, Krief et al. 2005, Lonsdorf et al. 2006, Pebsworth et al. 2006, MacIntosh et al. 2012), but no research has been conducted using systematic disease symptom recording to investigate the impacts of provisioning on the health of tourist-exposed primates.

Body size

Provisioning might increase the body size of an animal by increasing energy intake and reducing energy expenditure. An increased body size in wild animals, which is generally associated with an increase in weight, may reflect good condition of an animal. For example, female kakapos that were fed with supplementary food weighed more than those that did not receive provisioning, and the increased weight in the fed kakapo females was suggested to reflect their improved body condition compared to the non-supplemented ones (Clout et al. 2002). However, an excessive increase in body size may reflect or lead to poor health, with animals potentially suffering from weight-related disease and disorders (Bauer et al. 2011). For example, provisioning by tourists was suspected to have caused an increased body size, even obesity, in Barbary macaques in Gibraltar (Honess et al. 2006), and long-tailed macaques in Bali (Lane et al. 2010), but no further research was conducted to determine if this increase in body size was associated with diet-related problems.

Evaluating the health of an animal by measuring its body size is complex because the optimum body size for an animal is unknown. Previous studies have attempted to determine an index of body condition related to body size, body mass or weight using different measures such as BMI (Body mass index), skinfolds and body measurements (Altmann et al. 1993). Recently, photogrammetry has been used successfully to measure body size non-invasively in wild primates and other mammals (Shrader et al. 2006, Breuer et al. 2007, Higham et al. 2008, Webster et al. 2010, Borg et al. 2014), showing that this method, in addition to other measures, could be useful for assessing the nutritional status of wild primates (Kurita et al. 2012). Although a number of studies have reported the link between provisioning and an increase in body size, only one published study has quantitatively assessed variation in body size associated with tourist provisioning (Borg et al. 2014). That study provides evidence that adult Barbary macaques in a group experiencing high levels of provisioning had larger body size than those in two other groups with no/negligible exposure to tourism. However, since the optimum body size for a healthy animal is unknown, it is not possible to determine if a larger body size in itself reflects poor health; nevertheless, as part of a larger suite of measures, it may be a useful indicator of well-being.

Coat condition: coat quality and alopecia

In domestic and captive animals, assessment of coat condition is widely used as an indicator of health, in terms of general well-being, disease and nutritional status (Marsh 1999, Wolfensohn and Lloyd 2003, Honess et al. 2005). For example, it was found that improving the diet of an animal by increasing nutrients led to better coat condition in sheep (*Ovis aries*), goats (*Capra aegagrus hircus:* Khan et al. 2012), and dogs (*Canis lupus familiaris*: March 1999). Provisioning may therefore positively affect the coat condition of an animal by increasing nutrient intake and balance (Galbraith, 1998, Khan et al. 2012). However there are a multitude of factors in addition to animal’s nutritional status which may influence an animal’s coat condition, such as stress or individual state, e.g. pregnancy (Honess et al. 2005). Recently some studies have used coat condition to assess the impacts of tourism on animals' health (Jolly 2009, Zhang 2011, Borg et al. 2014). Results suggested that coat condition was worse in groups experiencing high tourist pressure, and that therefore animals might have poorer health, compared to groups with little or no tourism.

Coat condition is generally measured in pet, livestock and lab animals using a visual scoring system (Marsh 1999, Wolfensohn and Lloyd 2003, Honess et al. 2005), whereas this method has only been used in a few studies to evaluate wild animals' health status (e.g. Jolly 2009, Borg et al. 2014). It is important to note that coat condition visual scoring systems used previously often combine within one scoring system several characteristics of coat condition such as fur quality, alopecia, softness, and colour. However, each characteristic may be affected differently by different factors (March 1999). For example, fur quality and alopecia were combined within the same visual score to assess coat condition in ring-tailed lemurs (Jolly 2009) and Barbary macaques (Borg et al. 2014). Alopecia is generally related to stress (Honess et al. 2005, Zhang et al. 2011), whereas loss of coat shine is commonly associated with poor diet and lack in nutrients (Marsh 1999, Khan et al. 2012). Therefore, a separate visual assessment should be used for coat quality and alopecia.

Urinary C-peptide levels

C-peptide is derived from proinsulin and synthesized in the pancreas. In healthy individuals, C-peptide and insulin are co-secreted in equal amounts into the circulation during insulin biosynthesis, and therefore C-peptide is an indirect measure of endogenous insulin secretion (Rubenstein et al. 1969). Recently, a number of studies on humans and non-human primates have suggested that urinary C-peptide (UCP) might be used as a reliable index of individual nutritional status, and may reflect primate's energy balance (Kruszynska 1987, Sherry and Ellison 2007). Evidence to support this idea is provided by studies finding that 24h UCP levels were positively related to body weight in rhesus macaques (Wolden-Hanson et al. 1993), to skinfold thickness in rhesus and long-tailed macaques (Girard-Buttoz et al. 2011) and to BMI in bonobos (*Pan paniscus*), rhesus and long-tailed macaques (Deschner et al. 2008, Girard-Buttoz et al. 2011). In addition, it has been shown that UCP levels were higher in obese rhesus macaques compared to non-obese individuals, and UCP levels also decreased during food deprivation for animals in both classes (Wolden-Hanson et al. 1993). Similar results were found in feeding experiments on captive bonobos; UCP levels were lower during fasting and higher during re-feeding (Deschner et al. 2008). Provisioning might increase the urinary C-peptide (UCP) levels of an animal as a result of a change in its energy balance resulting from a combination of increasing energy intake and reducing energy expenditure. An increased UCP level in wild animals may reflect good condition; however in humans high basal UCP levels associated with additional measures (e.g. high BMI) may indicate type II diabetes or other diet-related disease (Welborn et al. 1981), which may cause important health issues, and increase the risk of a premature death (Panzram 1987). In macaques, type II diabetes has been reported in captivity (Kaufman et al. 2007), but no analysis has been conducted with wild macaques to determine if provisioned animals suffer from diabetes. It is important to note that evaluating the health of an animal by measuring its UCP levels is complex because the optimum UCP levels for an animal is unknown, and may vary between individuals. However measuring UCP levels may provide useful information which, interpreted in conjunction with other measures such as body size, may help to understand the impacts of provisioning on animals' health.

Faecal glucocorticoid metabolite levels

The HPA axis is a primary mechanism involved in the neuroendocrine response to stress (Sanchez 2006). When an animal is stressed, the hypothalamic-pituitary-adrenal axis (HPA) is activated which produces glucocorticoid hormones (Selye 1936, Romero and Butler 2007). Sustained high levels of glucocorticoids (GCs) might have deleterious effects on animals' health, leading to a reduction in fitness (Sapolsky et al. 2000, Romero and Wikelski 2001). Such levels might vary depending on energy expenditure, since a principal role of increased GC concentrations is to increase blood glucose, making energy available for tissues such as muscles (Sapolsky et al. 2000). For example, low food availability has been related to elevated physiological stress levels, indicating nutritional stress in a number of species, including African elephants (*Loxodonta Africana:* Foley et al. 2001), red colobus monkeys (*Procolobus rufomitratus:* Chapman et al. 2007), howler monkeys (Behie et al. 2010), and olive baboons (Lodge et al. 2013).

Provisioning, which is generally associated with a reduction in energy expenditure (Kemnitz et al. 2002), might result in a decrease in GC levels, and therefore could be viewed as having positive impacts on the health of animals. However, in addition to food availability, other factors might influence an animal's GC levels, including a wide range of social stressors (Sapolsky 1992), such as loss of a close relative (Engh et al. 2006a), dominance rank instability (Sapolsky 2005), or agonistic interactions with conspecifics (Honess and Marin 2006). Since provisioning might increase intraspecific competition, which presumably increases social stress, it may result in an increase in GC levels in the animals involved. If GC levels become chronically high, this can have negative impacts on health. Although an increase in GC levels may indicate that an animal is more stressed, the threshold levels at which such stress may be detrimental is unknown, and poorly understood.

GC levels can be assessed via different biological material such as faeces, urine, blood, hair or saliva (Heistermann 2010). Measuring GC via faecal samples has been widely used in many species (Palme et al. 2005, Heistermann et al. 2006), mainly due to the easy and non-invasive collection of such samples. Faecal glucocorticoid (FGC) metabolite levels can provide a useful measure of physiological stress (Heistermann 2010). Overall, understanding whether and how provisioning affects an animal's FGC levels is complex because multiple factors can influence these levels. However, despite the need for careful interpretation of variation in FGC levels, measuring such levels has proven to be a useful tool to evaluate the impacts of stressors on the welfare of animals, in particular for conservation purposes (Wikelski and Cooke 2006).

Determining the impacts of provisioning on the health of wild animals is very complex and these impacts are still poorly understood because provisioning might have positive and negative effects, depending on a multitude of factors such as individual state, environmental factors, the quantity and the quality of the food supplied. To date, only a few studies have investigated the impacts of provisioning on the health of wildlife, and they often focused on the effects of provisioning, provided as part of conservation management, on the fitness of animals involved. Considering a range of non-invasive measures to assess the health of wild animals could provide a powerful tool to understand more fully the health of tourist-exposed animals, and these measures are used here to explore the effects of tourist provisioning on the health of wild Barbary macaques.

5.1.3 Chapter aims

In this chapter, I aim to understand the impacts of unregulated tourist provisioning on the health of wild adult male and female Barbary macaques. I used a two level approach to investigate this question. First I directly compare a non-provisioned group (Green Group) with a provisioned group (Tourist Group) for each health measure assessed, and then I explore within the Tourist Group the impacts of provisioning on the different health measures. Since ecological and social factors may be important, and change over time, direct comparison between the groups are done in two different ways: over the 10 months of the study period and per month. I also include ecological and social factors (i.e. rainfall, rank and social season) as control factors in the models exploring the effects of provisioning in the Tourist Group. The following predictions are tested:

Hypothesis 1: **Provisioning of the Tourist Group has negative impacts on their health.**

1. Direct comparison of health measures between the Tourist Group and the Green Group.

I General health measures

Prediction 1i: Females in the Tourist Group have lower birth rates than those in the Green Group.

Prediction 1ii: Animals in the Tourist Group have more lameness, scars, injuries and higher mortality than those in the Green Group.

Prediction 1iii: Animals in the Tourist Group show more disease symptoms than those in the Green Group.

II Body size and condition

Prediction 1iv: Animals in the Tourist Group have larger body size than those in the Green Group.

Prediction 1v: Animals in the Tourist Group have worse coat quality than those in the Green Group.

Prediction 1vi: Animals in the Tourist Group have more alopecia than those in the Green Group.

III Energy status

Prediction 1vii: Animals in the Tourist Group have higher UCP levels than those in the Green Group.

IV Physiological stress

Prediction 1viii: Animals in the Tourist Group have higher FGC levels than those in the Green Group.

2. The relationships between health measure and provisioning in the Tourist Group.

In order to determine if and how provisioning affects the health of animals in the Tourist Group, I tested the relationships between amount of provisioning and health measures in individuals from the Tourist Group, including ecological and social variables as control factors. I also tested the relationships between health measures and ecological and social variables for individuals from the Green Group. The results obtained from the Green Group help the interpretation of the results from the Tourist Group by adding important information on factors that could potentially affect health measures in the absence of provisioning.

I Body size and condition

Prediction 2i: Body size in the Tourist Group is positively related to amount of provisioning.

Prediction 2ii: Coat quality in the Tourist Group is positively related to amount of provisioning.

Prediction 2iii: Alopecia scores in the Tourist Group are positively related to amount of provisioning.

II Energy status

Prediction 2iv: UCP levels in the Tourist Group are positively related to amount of provisioning.

III Physiological stress

Prediction 2v: FGC levels in the Tourist Group are positively related to amount of provisioning.

5.2 Methods

5.2.1 Data collection

The descriptions of behavioural, body condition and endocrinological data collection are reported in the field and lab methods chapter (chapter 2). Behaviours analysed in the present chapter were extracted from scan sampling for both groups (chapter 2, p.54). In the Green Group, all females gave birth. In the Tourist Group, 3 females gave birth and 6 did not. As gestation and lactation might affect the different health measures (e.g. alopecia in non-human primates: Novak and Meyer 2009; FGC levels in baboons: Beehner et al. 2006, rhesus macaques: Hoffman et al. 2011; UCP levels: Emery Thompson and Knott 2008), I conducted the following analyses considering separately females who gave birth and females who did not give birth in the Tourist Group.

5.2.2 Description of variables

In this chapter, a number of variables were used to determine Barbary macaques' health status (Table 5-1), and a number of factors which might affect macaques' health were explored (Table 5-2).

Table 5-1: Description of each measure used to determine macaques' health status.

Measure	Description
Birth rates	Percentage of females who gave birth to one live infant per year and per group. Reproductive success could not be reliably estimated using the survival rates of infants and juveniles because of high poaching pressure.
Scars, lameness and injuries	Scars and lameness were scored once a month and injuries were recorded *ad libitum.* All three were scored visually (see chapter 2 p.66)
Disease symptoms	Disease symptoms (i.e. coughing/sneezing and diarrhoea) were recorded *ad libitum* each day.
Body size	Photogrammetric measures of different body parts were assessed once per month (see chapter 2 p.60). The different body measurements were entered into a PCA, with PCA factor 1 defined as body size.
Coat quality	Coat quality scores (1 to 4) were assessed once per month (see chapter 2 p.63).
Alopecia	Alopecia scores (1 to 4) were assessed once per month (see chapter 2 p.64).
UCP levels	Urinary C-peptide levels (UCP levels) were matched to the same day collected.
FGC levels	Faecal glucocorticoid levels (FGC levels). FGC data were matched with ecological and social data collected 24/48h prior to the collection of the faecal samples (Heistermann et al. 2006), see chapter 2 p.70.

Table 5-2: Description of the key independent variables, provisioning, and the ecological and social variables controlled for in analyses.

Predictor	Description
Provisioning	Percentage of total feeding scans spent feeding on human food.
Rainfall (as an indicator of food availability)	Monthly average rainfall (see chapter 2 p.78). Rainfall is linked with natural food availability (Ménard 2002). In the present study, monthly average body size for all individuals was positively correlated with monthly rainfall in the non-provisioned group (N=10, r_s=0.888, P=0.001), suggesting that rainfall is an indirect measure of natural food availability.
Rank	Defined using David scores (see chapter 2 p.48-49), z-transformed.
Social season	Four seasons were determined (i.e. pre-birth, birth, post-birth and mating). Mating season lasted from the first complete copulation to the last complete copulation observed. Pre-birth was between the mating and the birth seasons. Birth season lasted from the first birth to the birth of the last infant. Post-birth was between birth and mating seasons.

5.2.3 Statistical analysis

Descriptive comparison between groups (Predictions 1i to 1iii)

In order to explore if there was a difference between groups in occasional disease symptoms (i.e. coughing/sneezing and diarrhoea), lameness, death and reproductive success, I present descriptive statistics of such events and measures for each group.

Quantitative comparison between groups (Predictions 1ii, 1iv to 1viii)

Whole study period: For scars, injuries, body size, coat quality, alopecia, UCP and FGC levels, I explored if there was a difference between groups, combining data over the 10 months of the study period for each health measure. I first calculated the mean levels or scores per month and per individual for the different measures, and then I calculated the mean levels or scores over 10 months for each individual. I then ran a comparison between groups (i.e. unrelated samples) using either an independent sample t-test or a Mann-Whitney test.

Per month: I compared the groups per month by running a series of comparison between groups based on the average levels per month per individual for body size, coat quality, alopecia, UCP and FGC levels only. I used sequential Bonferroni tests with an adjustment (k) equal to 10 to control the type I error rate (Rice 1989).

Generalized linear mixed models (GLMM, predictions 2i to 2v)

Using GLMMs, I investigated the relationships between provisioning and different health measures in the Tourist Group while controlling for ecological and social factors. GLMMs were run for the Green Group as well, for comparison and to facilitate the interpretation of the results from the Tourist Group. The models were run as presented in Table 5-3.

Table 5-3: Summary of the GLMMs run in order to test predictions 2i to 2v about the impacts of provisioning on health measures. GLMM analyses were run for the Tourist Group and the Green Group. ✓ variable included in the model.

	Dependent variable				
Prediction number	**2i**	**2ii**	**2iii**	**2iv**	**2v**
Predictor variable	Body size	Coat quality	Alopecia	UCP levels	FGC levels
Gave birth and did not give birth (only included for TG females)	✓	✓	✓	✓	✓
Provisioning (only included for TG)	✓	✓	✓	✓	✓
rainfall	✓	✓	✓	✓	✓
Rank	✓	✓	✓	✓	✓
Social season	✓	✓	✓	✓	✓
Random factor	**macaque ID**			**macaque ID**	
Time scale	Monthly measure			Daily measure	

All variables included in the models follow the assumptions described in chapter 2 (p.78). Correlation coefficients between variables can be found in Appendix A10. For urine and faecal samples, daily data were only included in the GLMM if there were matching data on provisioning. For example, some individuals were not observed feeding on either natural or human food during all hourly scans of a day, and therefore data for these days for these individuals were not included in the GLMM analyses.

Scars, lameness, injuries, disease symptoms and birth success were not included in GLMMs because they are occasional events.

5.3 Results

Hypothesis 1: Provisioning of the Tourist Group has negative impacts on their health.

In order to investigate the impacts of unregulated provisioning on the health of wild Barbary macaques, I first describe the dietary composition for each group, and then test the different predictions associated with the hypothesis that provisioning of the Tourist Group has negative impacts on their health.

5.3.1 Dietary composition in the Tourist Group and the Green Group

On average, TG females spent 16.4 % of scans and males spent 12.8% of scans feeding. TG animals spent a mean of 44.6% of feeding scans eating human food items (females 38.1%, males 51.0%), including on average 32.5% of feeding scans (females 29.8%, males 39.51) eating high energy food such as bread, peanuts, cookies/pastries or chocolate bars/sweets (Figure 5-1). TG Individuals spent 23.5% (females 26.1%, males 20.9%) eating grass, 19.6% (females 21.1%, males 18.9%) eating other natural food (i.e. roots, mushrooms, forage and leaves), 9.7% (females 10.7%, males 8.7%) eating acorns, and 2.7% (females 4.1%, males 1.3%) eating insects.

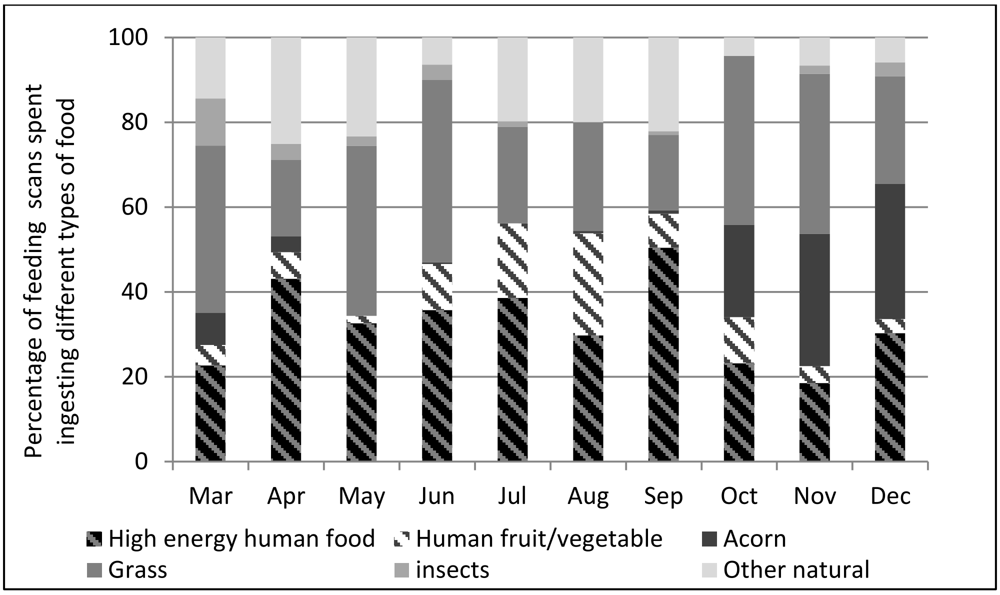


Figure 5-1: Histogram of the percentage of feeding scans spent eating different types of food in TG.

On average, GG females spent 31.7% and males spent 22.2% of scans feeding. GG individuals spent 45.7% of feeding scans (females 46.6%, males 44.8%) eating grass, 24.3% (females 23.7%, males 24.8%) eating insects, 14.7% (females 14.1%, males 15.9%) eating acorns, and 13.8% (females 15.6%, males 14.4%) eating other natural food (i.e. roots, mushrooms, forage and leaves) (Figure 5-2).

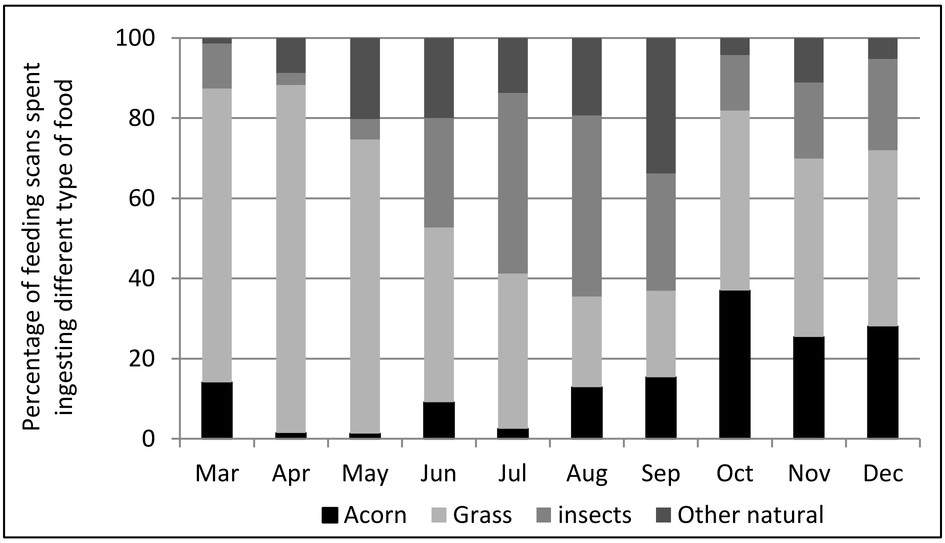


Figure 5-2: Histogram of the percentage of feeding scans spent eating different types of food in GG.

5.3.2 Direct comparison of health measures between the Tourist Group and the Green Group.

Prediction 1i: Females in the Tourist Group have lower birth rates than those in the Green Group.

Wild adult female Barbary macaques generally give birth to one infant every year (Paul and Thommen 1984). The percentage of TG females observed with a new-born infant was lower in 2012 and 2013 than the percentage of GG females giving birth; in 2011 only one female in each group were not observed with a live new-born infant and thus the percentage of females with new-born infant was higher in TG than GG (Table 5-4).

Table 5-4: Summary of births from 2011 until 2013 in TG and GG. Note that in 2012 five females gave birth in the TG, but two of them were sub-adult females, and therefore these females were not included in the data analyses for the other health measures.

Group	Year	Number of reproductive females	Number of live births	% of females observed with live new-born infant
TG	2011	10	9	90.0
GG	2011	7	6	85.7
TG	2012	11	5	45.5
GG	2012	6	6	100.0
TG	2013	12	11	91.7
GG	2013	6	6	100.0

Prediction 1ii: Animals in the Tourist Group have more lameness, scars, injuries and higher mortality than those in the Green Group.

Lameness

In total, five TG individuals (4 males and 1 female) presented lameness with different degrees of disability. Three individuals presented grade 1 lameness, i.e. non-serious lameness, probably due to a healed broken finger or injury on their hand/foot. Two individuals presented grade 2 lameness impairing their walking abilities, and probably due to a severe injury to their hand/foot or leg. Only one GG animal, a male, presented permanent lameness and this was grade 1.

Scars

The majority of individuals from both groups presented some visible scars over their body. There was no significant difference in the number of visible scars between groups for females (Mann-Whitney test: N=15, U=-0.255, P=0.799) or for males (Independent t test: N=13 (8 TG/5 GG), t=2.131, P=0.059), although there was a trend towards TG males having more visible scars than GG males (Figure 5-3).

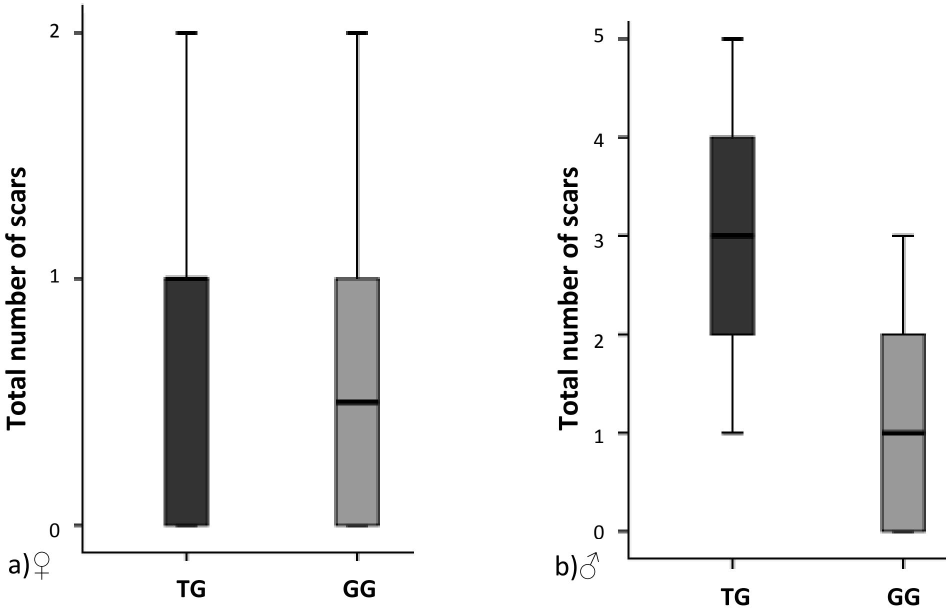


Figure 5-3: Box-plot showing the total number of scars per individual over the 10 month period (from March until December 2012) in TG and GG for (a) females and (b) males. Boxes represent mean values +/- inter-quartile ranges and standard error bars.

Injuries

There was no significant difference between groups in the number of injuries over the 10 month study periods for females (Mann-Whitney test: N=15, U=12.000, P=0.075) or males (Mann-Whitney test: N=13 (8 TG/5 GG), U=13.000, P=0.301).

Deaths

Over the whole study period, in TG there was one miscarriage seen, one adult male died and two other adults disappeared and were presumed dead. One female was witnessed to have a miscarriage in January 2012, but I was not able to determine the cause. One adult male fell from a tree dead, and was autopsied by a vet, Dr. Fouad Elouafi, from Service Vétérinaire ONSSA d'Ifrane. The autopsy revealed the adult male died from a haemorrhage located on its intestinal tract, and it was suggested by the vet that this could potentially be due to food poisoning. However no further examination was conducted. Of the two animals that disappeared, one was a female that was not seen after an attack by a dog present at the tourist site, and the other was a male whose disappearance followed an attack from outsider males during the mating season. In GG, no individuals died, were seen having a miscarriage or disappeared during the whole study period.

Prediction 1iii: Animals in the Tourist Group show more disease symptoms than those in the Green Group.

Coughing and sneezing:

Over the whole study period, individuals from both groups were seen occasionally coughing and sneezing. However, there were three periods when all TG individuals were seen to be heavily coughing and sneezing numerous times per day: from 6th to 24th of March, from 23rd of June to 7th of July, and from 22nd to 29th of December 2012. In the GG, a few individuals were reported heavily coughing and sneezing on the 8TH of August 2012.

Diarrheal symptoms:

Over the whole study period, 32 occurrences of diarrhoea were reported for TG and only one for GG (Figure 5-4). There was a significant difference between groups in the index of diarrheal symptoms (Mann-Whitney test: N=29, U=29.000, P=0.001).

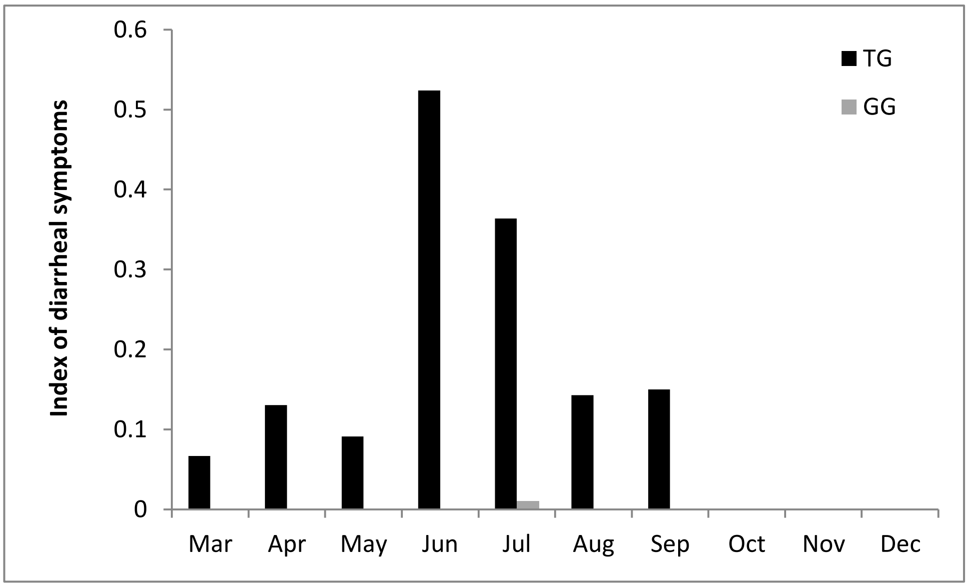


Figure 5-4: Histogram of the index of diarrheal symptoms per months for TG and GG. Index of diarrheal symptoms represents the number of individuals observed with diarrhea relative to the number of individual in the group and the number of days observed per month.

Prediction 1iv: Animals in the Tourist Group have larger body size than those in the Green Group.

Principal component analysis of body measurements

Body measurements assessed by photogrammetry were taken for different body parts: shoulders (back, front side), back, side neck, belly and breast. All measurements were highly correlated with coefficients r > 0.8 and therefore a PCA was run on all measurements. The first principal component, PCA1, accounted for 83.2% of variance and the second PCA 2 accounted for 12.9% of variance. All variables loaded strongly and positively on PCA 1 (Table 5-5). In morphometric measurement studies, PCA 1 generally accounts for body size and PCA 2 for body shape (Jolicoeur and Mosimann 1960); therefore PCA 1 is referred to as body size in the following analyses (Figure 5-5).

Table 5-5: Component matrix showing each variable's loading on PCA 1

	Component PCA 1
Back	0.923
Back shoulders	0.973
Front shoulders	0.918
Side neck	0.948
Breast	0.838
Belly	0.814
Side shoulders	0.959

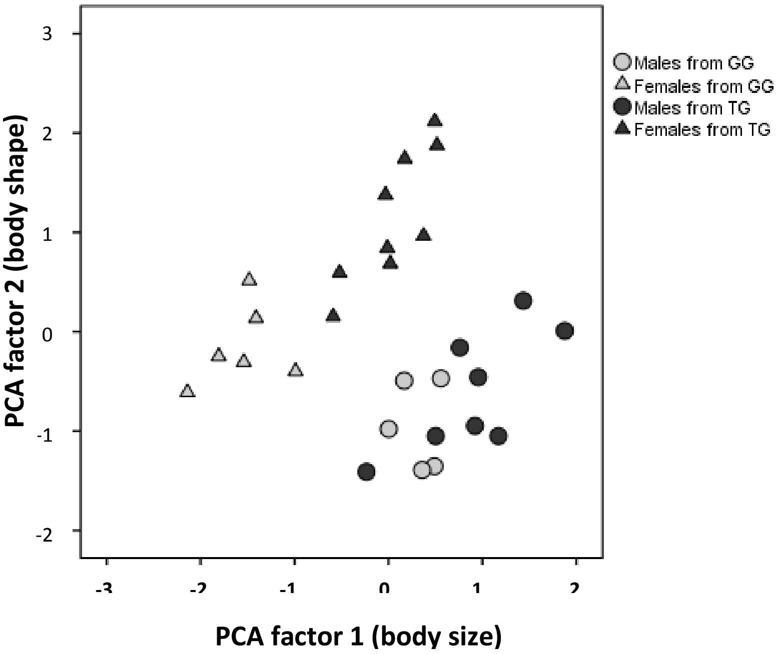


Figure 5-5: Scatterplot showing scores for PCA 1 (body size) and PCA 2 (body shape) for each individual from TG and GG. Each point represents an individual, categorised by group and sex.

Comparison between groups of PCA 1 scores extracted from body size measurements, for data averaged over the 10 months of the study

There was a significant difference between groups in PCA 1 scores for females (Independent t test: TG who gave birth vs. GG: N=9 (3 TG/6 GG), t=7.469, P<0.001; TG who did not give birth vs. GG: N=12 (6 TG/6 GG), t=4.949, P=0.002), indicating that TG females had a significantly larger body size than GG females (Figure 5-6). By contrast, there was no significant difference between groups for males (Independent t test: N=13 (8 TG/5 GG), t=2.082, P=0.062) although there was a trend towards TG males being larger in size. No significant difference was found between TG females who gave birth vs. those who did not give birth (Independent t test: N=9 (3 Birth/6 No birth), t=-0.355, P=0.733).

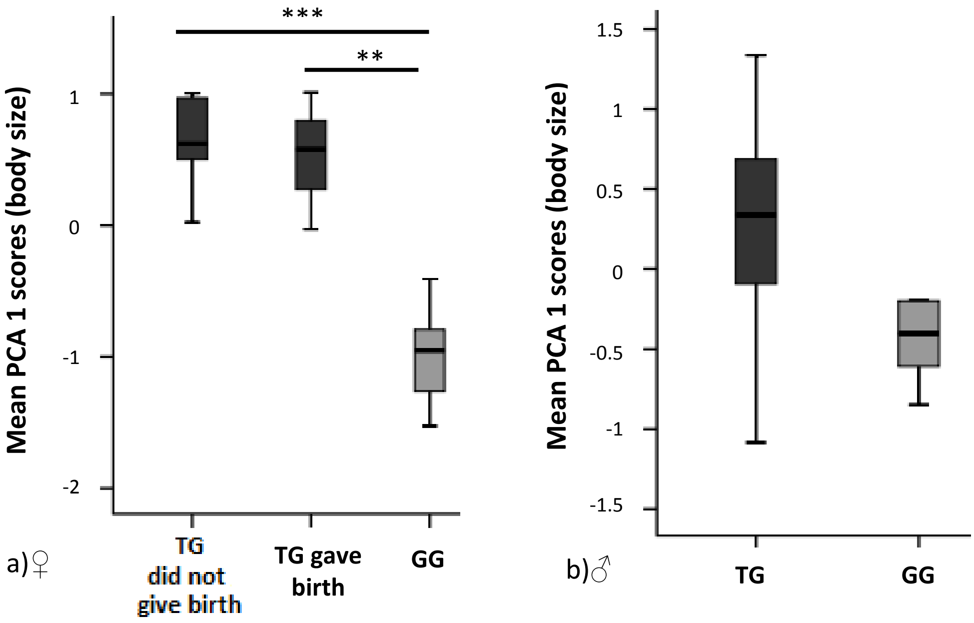


Figure 5-6: Box-plot showing the mean scores derived from a principal component analysis from body measures, PCA 1 scores (body size) over the 10 month period (from March until December 2012) in TG and GG for (a) females and (b) males. P value: *** <0.001; ** <0.01; *<0.05. Boxes represent mean values +/- inter-quartile ranges and standard error bars.

Monthly comparison between groups of PCA 1 scores (body size)

Females

There was a significant difference in PCA 1 scores (body size) between groups for each month (Table 5-6); TG females, both those who gave birth and those that did not had a significantly larger body size every month than GG females (Figure 5-7). The body size of TG females who gave birth was only significantly different from TG females that did not give birth in April, when TG females who gave birth were bigger than females who did not give birth, but this difference was not significant after correction for multiple testing.

Table 5-6: Monthly comparison of PCA 1 scores (body size) between groups for females. t is associated with the independent t-test and U with Mann-Whitney test. Values in red were not significant after sequential Bonferroni corrections.

	March	April	May	June	July	August	September	October	November	December	
t/U	t=3.811	t=7.152	t=3.643	t=2.792	t=3.714	U=0.000	t=4.082	t=5.092	t=3.731	t=5.767	TG gave birth vs. GG
P value	**0.007**	**<0.001**	**0.008**	**0.027**	**0.008**	**0.02**	**0.006**	**0.002**	**0.01**	**0.001**	
t/U	t=3.356	t=5.316	t=3.434	t=3.235	t=8.116	U=0.000	t=6.718	t=6.719	t=6.335	t=7.645	TG did not give birth vs. GG
P value	**0.007**	**<0.001**	**0.006**	**0.009**	**<0.001**	**0.004**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	
t/U	t=1.473	t=3.244	t=0.667	t=0.315	t=-2.181	U=6.000	t=-0.195	t=0.852	t=-0.330	t=-1.243	TG gave birth vs. TG did not give birth
P value	0.184	**0.014**	0.526	0.762	0.066	0.439	0.855	0.423	0.751	0.254	

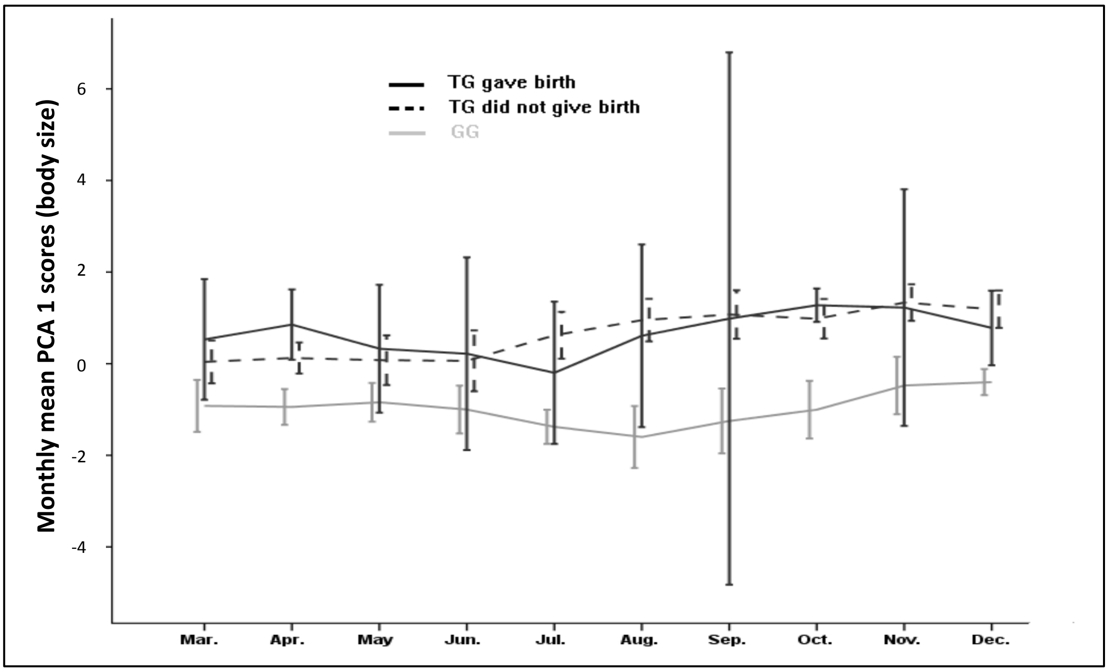


Figure 5-7: Plots of seasonal variation of mean PCA 1 scores (body size) for TG and GG females. Error bars indicate 95% confidence intervals. Please refer to Table 5-6 for results of statistical analyses.

Males

There was a significant difference between groups in male PCA 1 scores from July to October; although for the last of these months the difference was no longer significant after sequential Bonferroni correction (Table 5-7). During this period, TG males had a significantly bigger body size than GG males (Figure 5-8).

Table 5-7: Monthly comparison of PCA 1 scores (body size) between groups for males. Value in red was not significant after sequential Bonferroni correction.

	March	April	May	June	July	August	September	October	November	December
t	0.107	-0.502	0.238	2.122	4.815	5.354	4.200	2.576	1.737	1.013
P value	0.917	0.626	0.816	0.057	**0.001**	**<0.001**	**0.001**	**0.026**	0.113	0.335

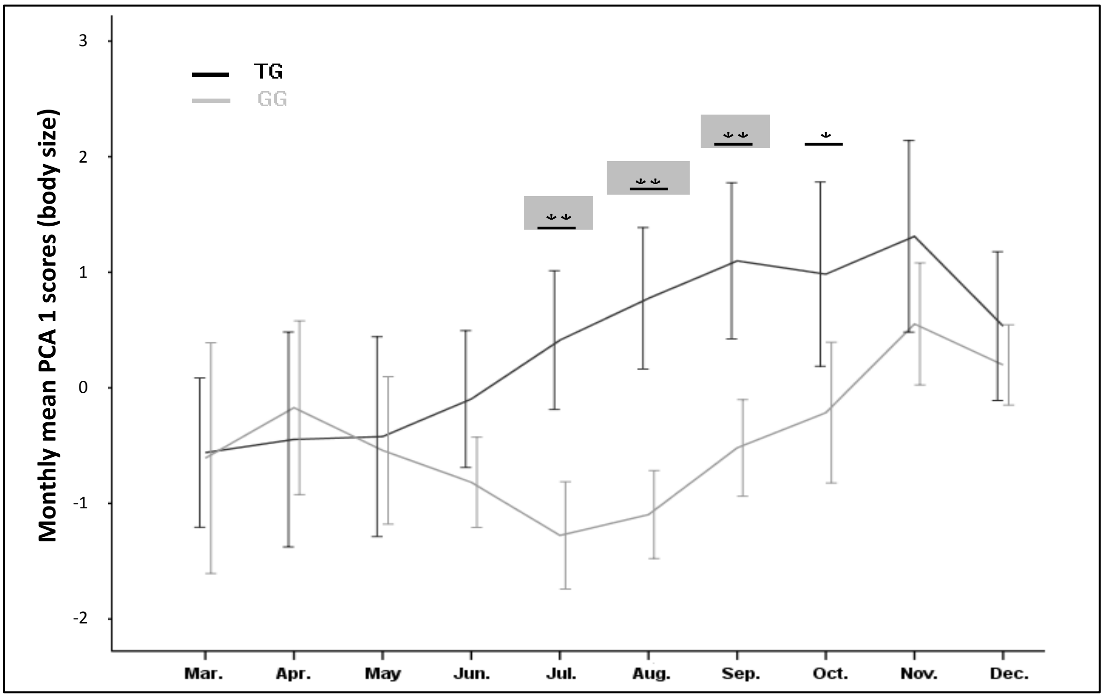


Figure 5-8: Plots of seasonal variation of mean PCA 1 scores (body size) for TG and GG males. Error bars indicate 95% confidence intervals. P value: *** <0.001; ** <0.01; *<0.05. P values highlighted in grey are still significant after sequential Bonferroni correction,

Prediction 1v: Animals in the Tourist Group have worse coat quality than those in the Green Group.

Comparison of coat quality scores between groups, data averaged over the 10 months of the study

There was no significant difference between groups in coat quality for females (Independent t test: TG gave birth vs. GG: N=9 (3 TG/6 GG), t=-1.660, P=0.141; TG did not give birth vs. GG: N=12 (6 TG/6 GG), t=-0.811, P=0.436) or for males (Independent t test: N=13 (8 TG/5 GG), t=0.144, P=0.888, Figure 5-9). There was also no significant difference between TG females who gave birth and TG females who did not give birth (Independent t test: N=9 (3 Birth/6 No birth), t=1.311, P=0.231).

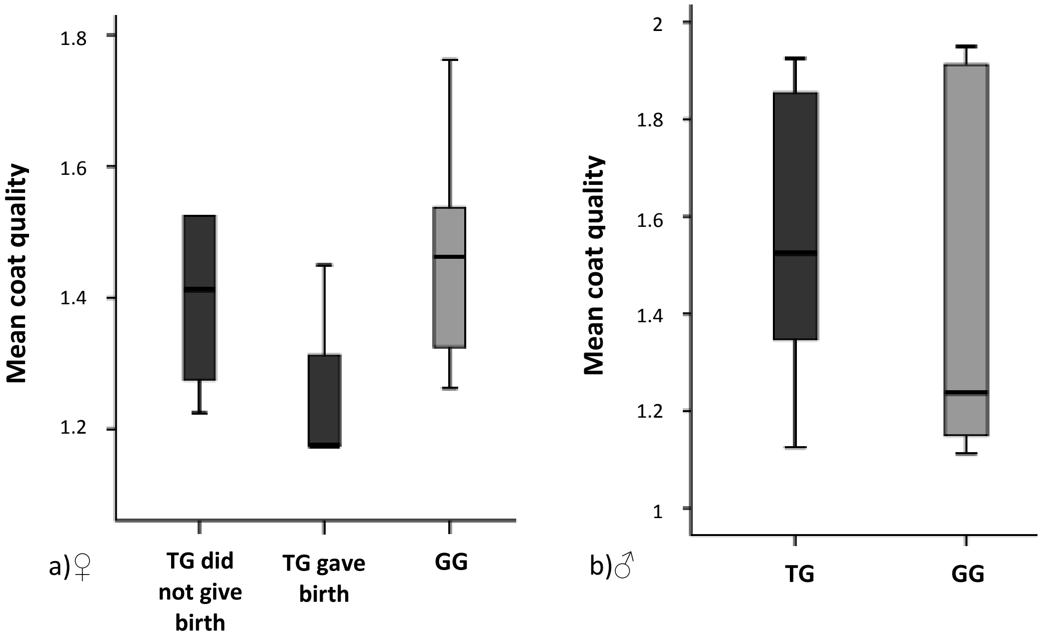


Figure 5-9: Box-plot showing the mean coat quality scores over the 10 month period (from March until December 2012) in TG and GG for (a) females and (b) males. Boxes represent mean values +/- inter-quartile ranges and standard error bars.

Monthly comparison of coat quality scores between groups.

Females

A significant difference in coat quality was found between TG females who gave birth and GG females in July and August, as well as between TG females who did not give birth and GG females in July and August (Table 5-8). During these periods, GG female coat quality was significantly worse than that of TG females (Figure 5-10). In April, TG females who did not give birth had worse coat quality than GG females. In addition, TG females who did not give birth had a coat quality which was significantly worse in March and April than TG females who gave birth. However, none of these differences remained significant after sequential Bonferroni correction.

Table 5-8: Monthly comparison of TG and GG female coat quality scores. t is associated with the independent t-test and U with Mann-Whitney test. Values in red were not significant after sequential Bonferroni corrections.

	March	April	May	June	July	August	September	October	November	December	
t/U	t=-1.594	U=8.000	t=0.333	t=0.509	U=0.000	U=6.500	U=3.000	U=2.000	t=-2.433	U=4.500	TG gave birth vs. GG
P value	0.155	0.783	0.749	0.626	**0.017**	**0.009**	0.248	0.144	0.051	0.584	
t/U	t=1.830	U=3.000	t=-1.296	t=-1.754	U=4.500	U=13.000	U=13.000	U=20.000	t=0.088	U=18.000	TG did not give birth vs. GG
P value	0.097	**0.012**	0.224	0.110	**0.026**	**0.006**	0.159	0.879	0.931	0.619	
t/U	t=-2.667	U=1.000	t=1.468	t=1.528	U=6.000	U=9.000	U=6.000	U=3.000	t=-2.291	U=5.000	TG gave birth vs. TG did not give birth
P value	**0.032**	**0.035**	0.186	0.170	0.289	0.480	0.593	0.195	0.056	0.484	

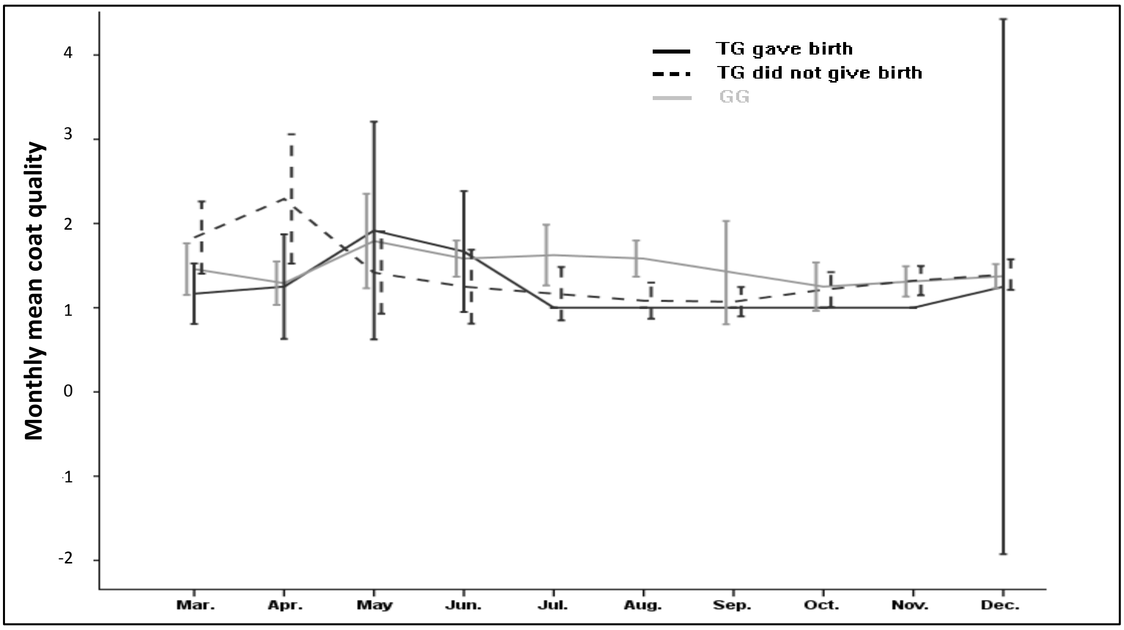


Figure 5-10: Plots of seasonal variation of mean coat quality scores for TG and GG females. Error bars indicate 95% confidence intervals. Please refer to Table 5-8 for results of statistical analyses.

Males

There was no significant difference between groups in male coat quality in any month (Table 5-9, Figure 5-11).

Table 5-9: Monthly comparison of male coat quality between TG and GG groups. t is associated with the independent t-test and U with Mann-Whitney test.

	March	April	May	June	July	August	September	October	November	December
t/U	U=12.500	t=-0.363	U=20.000	U=8.000	t=-1.320	U=19.000	U=17.000	t=0.108	t=0.743	t=0.611
P value	0.263	0.724	1.000	0.062	0.214	0.876	0.627	0.916	0.474	0.555

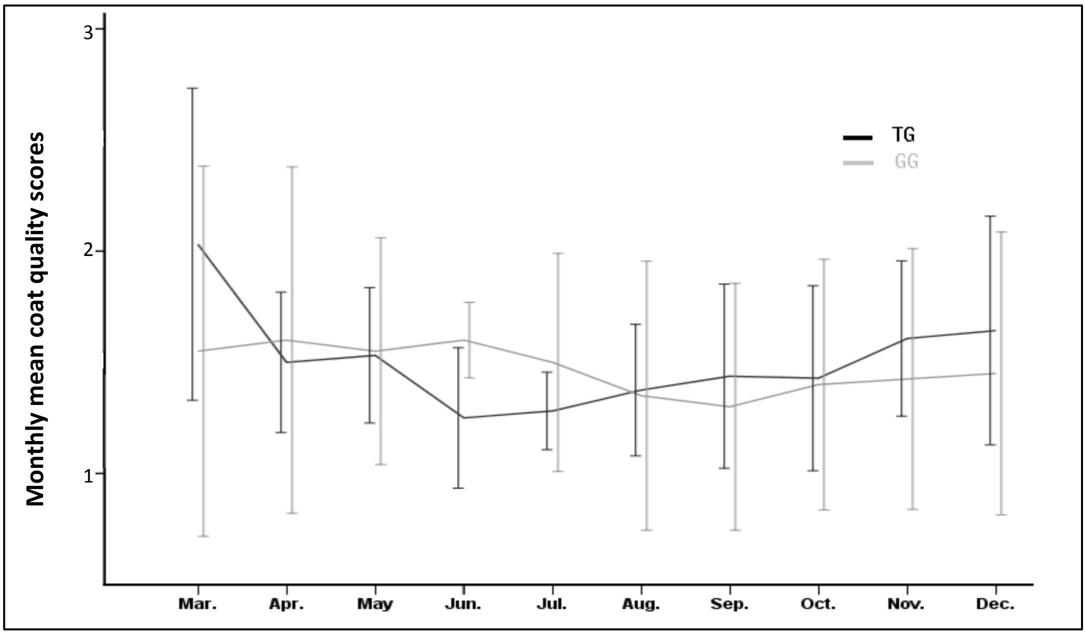


Figure 5-11: Plots of seasonal variation of mean coat quality for TG and GG males. Error bars indicate 95% confidence intervals.

Prediction 1vi: Animals in the Tourist Group have more alopecia than those in the Green Group.

Comparison of alopecia scores between groups, data averaged over the 10 months of the study.

There was no significant difference between groups in female alopecia scores (Independent t test: TG gave birth vs. GG: N=9 (3 TG/6 GG), t=0.036, P=0.973; TG did not give birth vs. GG: N=12 (6 TG/6 GG), t=-0.155, P=0.880); In addition, no significant difference in alopecia was found between TG females who gave birth and TG females who did not give birth (Independent t test: N=9 (3 Birth/6 No birth), t=-0.166, P=0.873). However, there was a significant difference between groups for males (Independent t test: N=13 (8 TG/5 GG), t=2.304, P=0.042, Figure 5-12), with TG males having more alopecia than GG males.

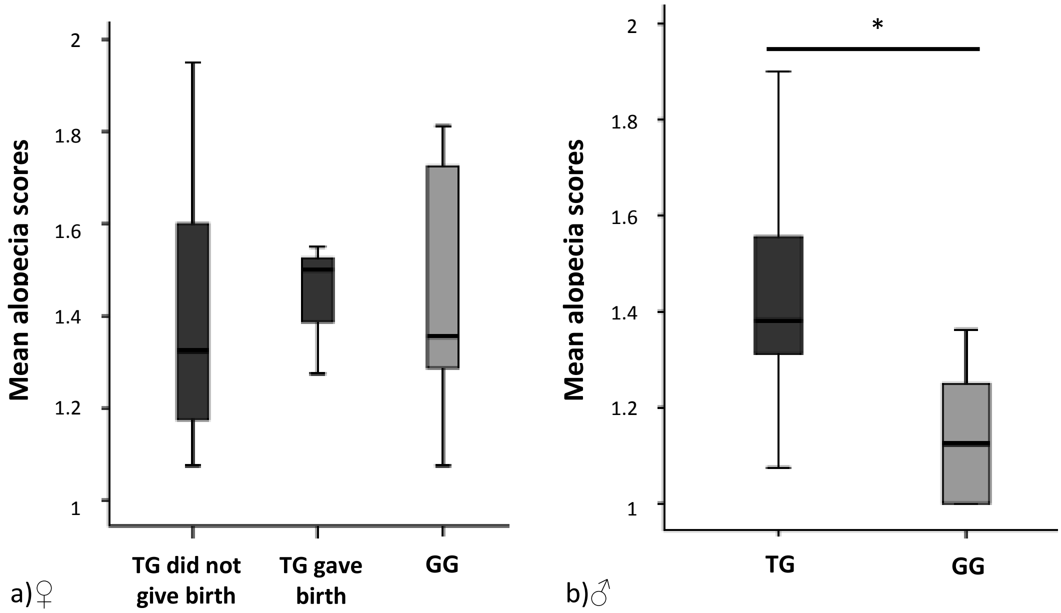


Figure 5-12: Box-plot showing the mean alopecia scores over the 10 month period (from March until December 2012) in TG and GG for (a) females and (b) males. P value: *** <0.001; ** <0.01; *<0.05. Boxes represent mean values +/- inter-quartile ranges and standard error bars.

Monthly comparison of alopecia scores between groups.

Females

TG females who gave birth had significantly more alopecia than GG females in May; however in July, GG female alopecia covered a significantly larger part of the body than that of TG females that did not give birth (Table 5-10, Figure 5-13), but this was not significant after sequential Bonferroni correction. In addition, TG females who gave birth had more alopecia than TG females who did not give birth in May but this difference was reversed in June, and the latter was not significant after sequential Bonferroni corrections.

Table 5-10: Monthly comparison of female alopecia scores between groups. t is associated with the independent t-test and U with Mann-Whitney test. Values in red were not significant after sequential Bonferroni corrections.

	March	April	May	June	July	August	September	October	November	December	
t/U	t=0.189	U=8.000	t=3.311	U=6.000	U=5.000	U=6.500	U=3.500	t=-0.463	t=0.829	t=0.000	TG gave birth vs. GG
P value	0.855	0.785	**0.013**	0.394	0.283	0.496	0.378	0.660	0.439	1.000	
t/U	t=1.771	U=15.500	t=-0.591	U=12.000	U=6.500	U=13.000	U=15.000	t=0.221	t=-0.217	t=-0.066	TG did not give birth vs. GG
P value	0.107	0.666	0.568	0.140	**0.047**	0.388	0.361	0.829	0.833	0.948	
t/U	t=-1.239	U=8.500	t=4.277	U=3.000	U=7.500	U=9.000	U=7.000	t=-0.367	t=0.497	t=0.038	TG gave birth vs. TG did not give birth
P value	0.255	0.891	**0.004**	**0.033**	0.593	1.000	1.000	0.725	0.634	0.971	

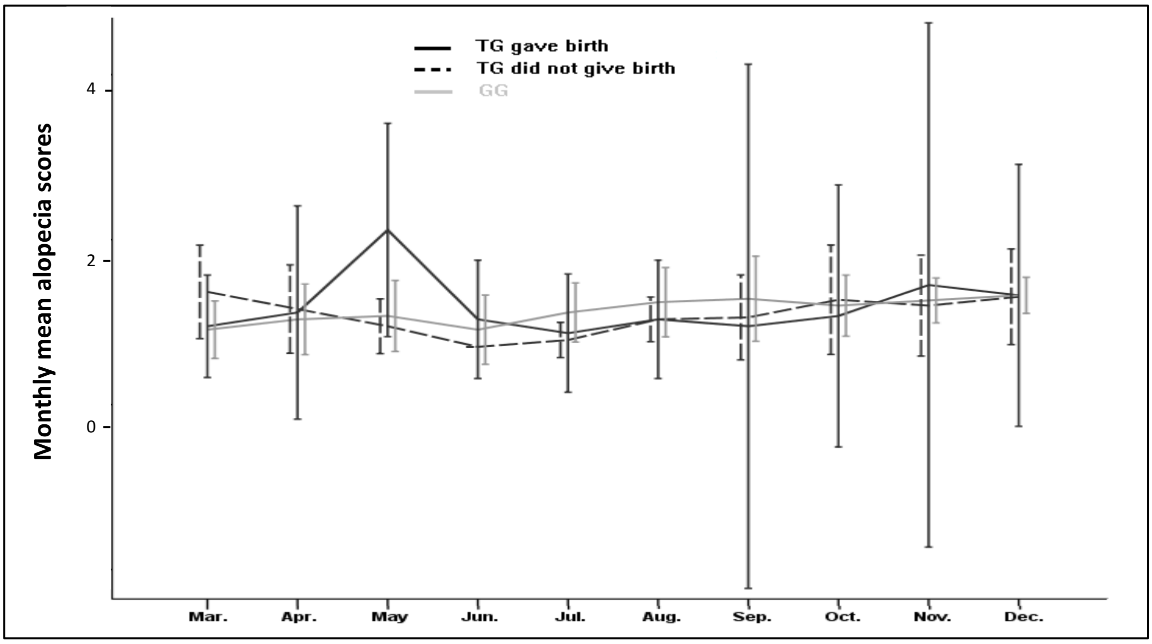


Figure 5-13: Plots of seasonal variation of mean alopecia scores for TG and GG females. Error bars indicate 95% confidence intervals. Please refer to Table 5-10 for results of statistical analyses.

Males

There was a significant difference between groups in male alopecia scores in March and April (Table 5-11), when TG male alopecia covered significantly a larger part of the body than GG male alopecia (Figure 5-14). The differences were not significant after sequential Bonferroni correction.

Table 5-11: Monthly comparison of male alopecia scores between groups. t is associated with the independent t-test and U with Mann-Whitney test. Values in red were not significant after sequential Bonferroni corrections.

	March	April	May	June	July	August	September	October	November	December
t/U	U=2.500	U=7.500	U=10.000	U=11.000	U=19.000	U=10.000	U=18.000	U=13.500	t=0.438	t=2.083
P value	**0.007**	**0.036**	0.109	0.139	0.816	0.073	0.747	0.300	0.670	0.064

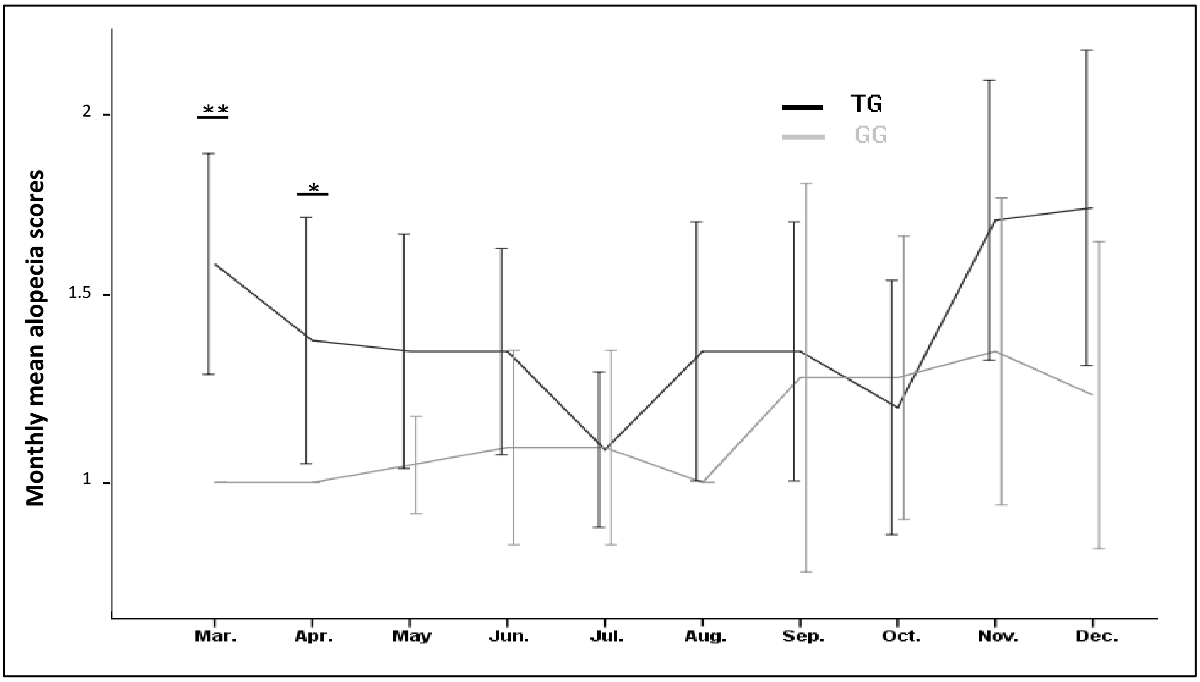


Figure 5-14: Plots of seasonal variation of mean alopecia scores for TG and GG males. Error bars indicate 95% confidence intervals. P value: *** <0.001; ** <0.01; *<0.05.

Prediction 1vii: Animals in the Tourist Group have higher UCP levels than those in the Green Group.

Comparison of UCP levels between groups, data averaged over the 10 months of the study.

There was no significant difference between groups in UCP levels for females (Independent t test: TG gave birth vs. GG: N=9 (3 TG/6 GG), t=1.164, P=0.283; TG did not give birth vs. GG: N=12 (6 TG/6 GG), t=-0.617, P=0.551) or for males (Mann-Whitney test: N=13 (8 TG/5 GG), U=14.000, P=0.380, Figure 5-15). There was also no significant difference between TG females who gave birth and TG females who did not give birth (Independent t test: N=9 (3 Birth/6 No birth), t=-1.584, P=0.157).

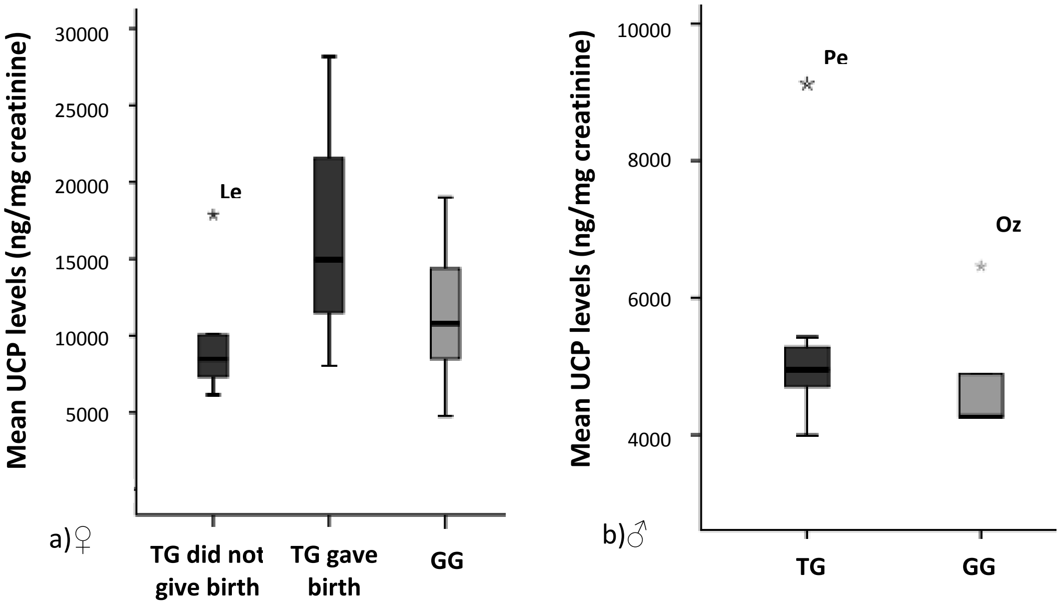


Figure 5-15: Box-plot showing the mean UCP levels over the 10 month period (from March until December 2012) in TG and GG for (a) females and (b) males. The outliers Pe and Oz are presumed to be the oldest males in each group, while the outlier Le corresponds to the largest female,that did not give birth in 2012. Boxes represent mean values +/- inter-quartile ranges and standard error bars.

Monthly comparison of UCP levels between groups.

Females

There was a significant difference in UCP levels only in March between TG females who gave birth and both GG and TG females who did not give birth, with GG females and TG females that did not give birth having lower UCP levels than TG females who gave birth (Table 5-12, Figure 5-16). However, these differences were not significant after correction for multiple testing.

Table 5-12: Monthly comparison of female UCP levels (ng/mg creatinine) between groups. t is associated with the independent t-test and U with Mann-Whitney test. Values in red were not significant after sequential Bonferroni corrections.

	March	April	May	June	July	August	September	October	November	December	
t/U	U=0.000	U=8.000	t=-0.201	t=-0.488	U=7.000	t=0.738	U=4.000	t=-0.364	t=1.659	U=5.000	TG gave birth vs. GG
P value	0.050	0.796	0.846	0.641	0.606	0.485	0.505	0.728	0.148	0.739	
t/U	U=4.000	U=16.000	t=0.216	t=-0.764	U=15.000	t=1.028	U=14.000	t=-1.293	t=0.443	U=17.000	TG did not give birth vs. GG
P value	0.197	0.749	0.833	0.462	0.631	0.328	0.317	0.222	0.666	0.568	
t/U	U=1.000	U=8.000	t=-0.663	t=0.188	U=5.000	t=-0.277	U=5.000	t=0.62	t=1.583	U=5.000	TG gave birth vs. TG did not give birth
P value	0.039	0.796	0.529	0.856	0.302	0.790	0.558	0.555	0.157	0.558	

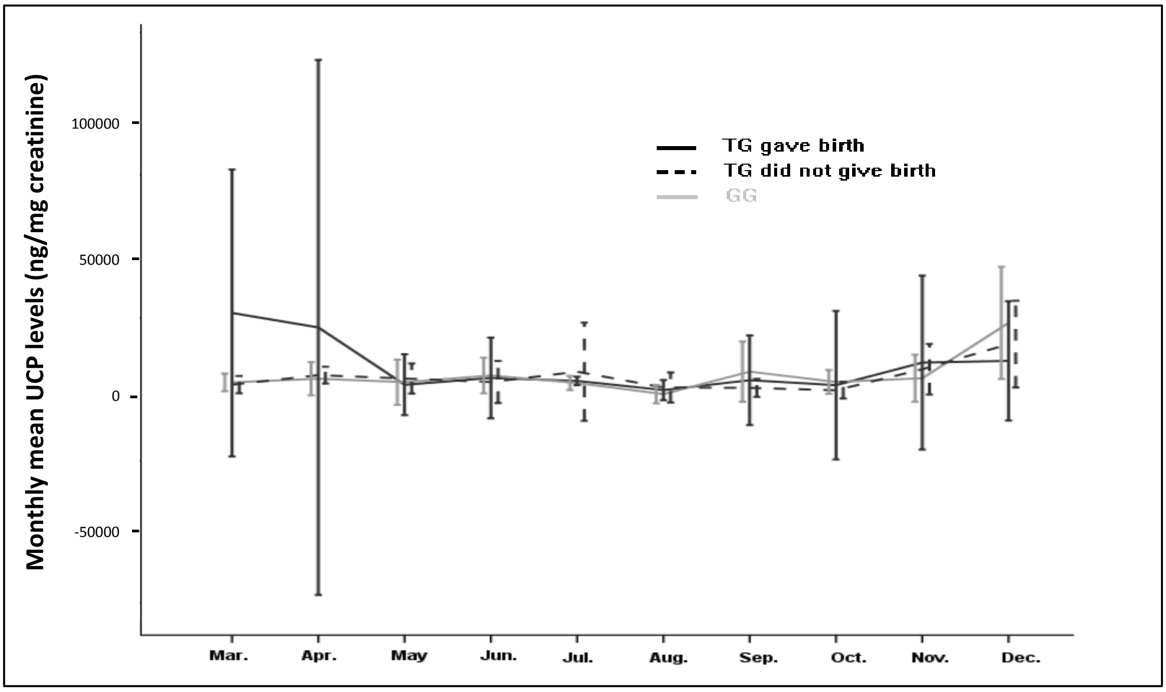


Figure 5-16: Plots of seasonal variation of mean UCP levels for TG and GG females. Error bars indicate 95% confidence intervals. Please refer to Table 5-12 for results of statistical analyses.

Males

There was a significant difference between groups in male UCP levels in April and May, when TG male UCP levels were significantly higher than GG males (Figure 5-17), but neither was significant after sequential Bonferroni correction (Table 5-13).

Table 5-13: Monthly comparison of male UCP levels (ng/mg creatinine) between groups. t is associated with the independent t-test and U with Mann-Whitney test. Values in red were not significant after sequential Bonferroni corrections.

	March	April	May	June	July	August	September	October	November	December
t/U	t=0.04	t=3.592	U=3.000	t=0.109	t=0.896	t=1.23	U=9.000	t=-0.458	t=-2.037	t=1.544
P value	0.969	**0.006**	**0.027**	0.915	0.389	0.254	0.234	0.657	0.072	0.157

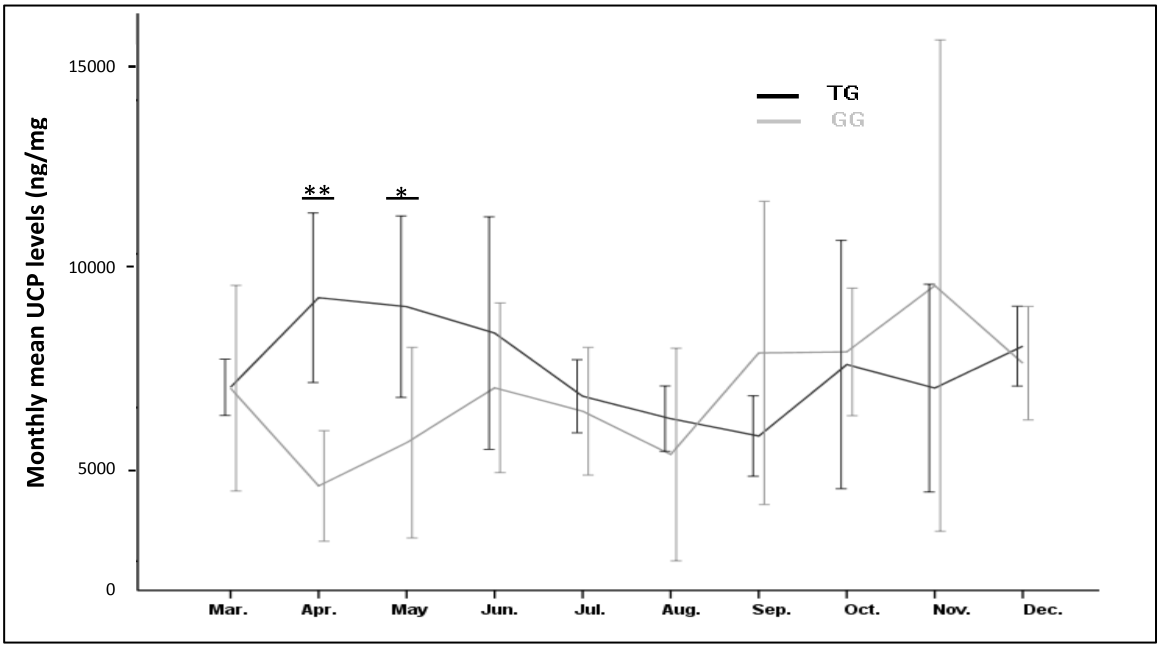


Figure 5-17: Plots of seasonal variation of mean TG and GG male UCP levels. Error bars indicate 95% confidence intervals. P value: *** <0.001; ** <0.01; *<0.05.

Prediction 1viii: Animals in the Tourist Group have higher FGC levels than those in the Green Group.

Comparison of FGC levels between groups, data averaged over the 10 months of the study.

TG females who gave birth had higher FGC levels than GG females but there was no significant difference between TG females that did not give birth and GG females (Independent t test: TG females who gave birth vs. GG: N=9 (3 TG/6 GG), t=3.943, P=0.006; TG females that did not give birth vs. GG: N=12 (6 TG/6 GG), t=0.966, P=0.357). There was no significant difference between TG females who gave birth and TG females that did not (Independent t test: N=9 (3 Birth/6 No birth), t=-2.016, P=0.084).TG males had significantly higher FGC levels than GG males (Independent t test: N=13 (8 TG/5 GG), t=2.701, P=0.021, Figure 5-18).

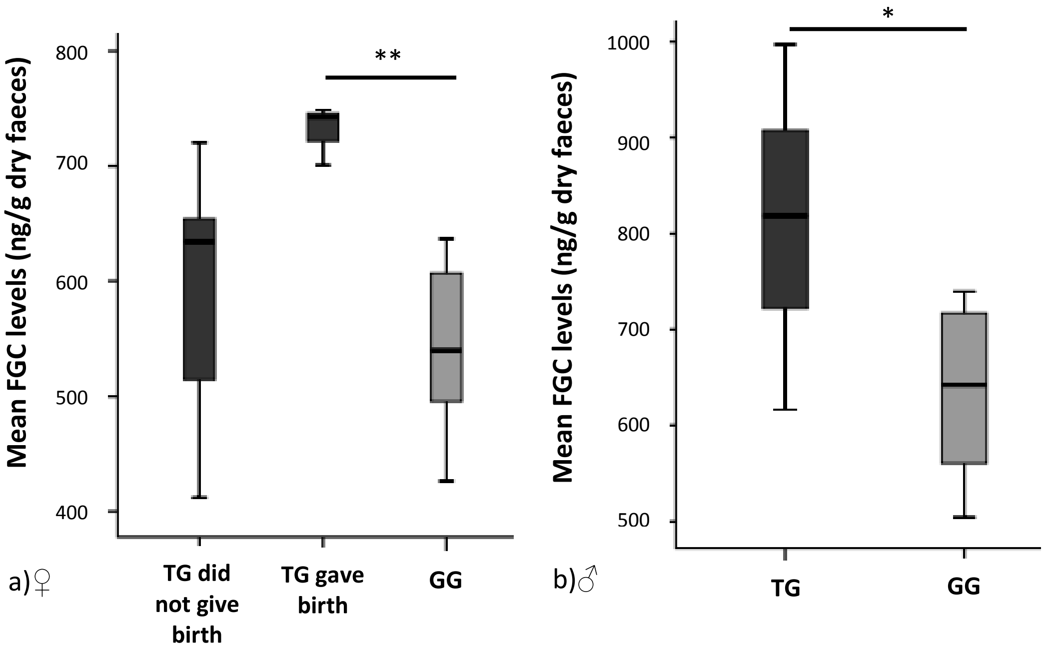


Figure 5-18: Box-plot showing the mean FGC levels over the 10 month period (from March until December 2012) in TG and GG for (a) females and (b) males. P value: *** <0.001; ** <0.01; *<0.05. Boxes represent mean values +/- inter-quartile ranges and standard error bars.

Monthly comparison of FGC levels between groups.

Females

A significant difference was found in FGC levels between TG females who gave birth and GG females from March to July, although for April and May the results were not significant after sequential Bonferroni correction (Table 5-14), and between TG females who did not give birth and GG females in June and July, and finally between TG females who gave birth vs. TG females that did not give birth in March, May and July, although in May this was not significant after correction for multiple testing. During these periods, FGC levels of TG females who gave birth were significantly higher than those of TG females who did not give birth and GG females. In addition, FGC levels of TG females that did not give birth were higher than those of GG females (Figure 5-19).

Table 5-14: Monthly comparison of female FGC levels (ng/g dry faeces) between groups. t is associated with the independent t-test and U with Mann-Whitney test. Values in red were not significant after sequential Bonferroni corrections.

	March	April	May	June	July	August	September	October	November	December	
t/U	t=4.116	t=2.8	t=2.973	t=4.806	t=5.966	t=0.811	t=0.321	t=1.833	U=2.000	t=-0.367	TG gave birth vs. GG
P value	**0.004**	**0.027**	**0.021**	**0.002**	**0.001**	0.444	0.759	0.116	0.182	0.727	
t/U	t=-1.624	t=0.891	t=1.346	t=4.455	t=3.716	t=0.108	t=0.312	t=1.346	U=16.000	t=-0.888	TG did not give birth vs. GG
P value	0.135	0.394	0.208	**0.001**	**0.004**	0.916	0.761	0.205	0.475	0.394	
t/U	t=4.362	t=2.247	t=2.414	t=-0.485	t=4.587	t=0.567	t=0.044	t=1.167	U=2.000	t=0.164	TG gave birth vs. TG did not give birth
P value	**0.003**	0.059	**0.046**	0.642	**0.003**	0.588	0.966	0.281	0.143	0.874	

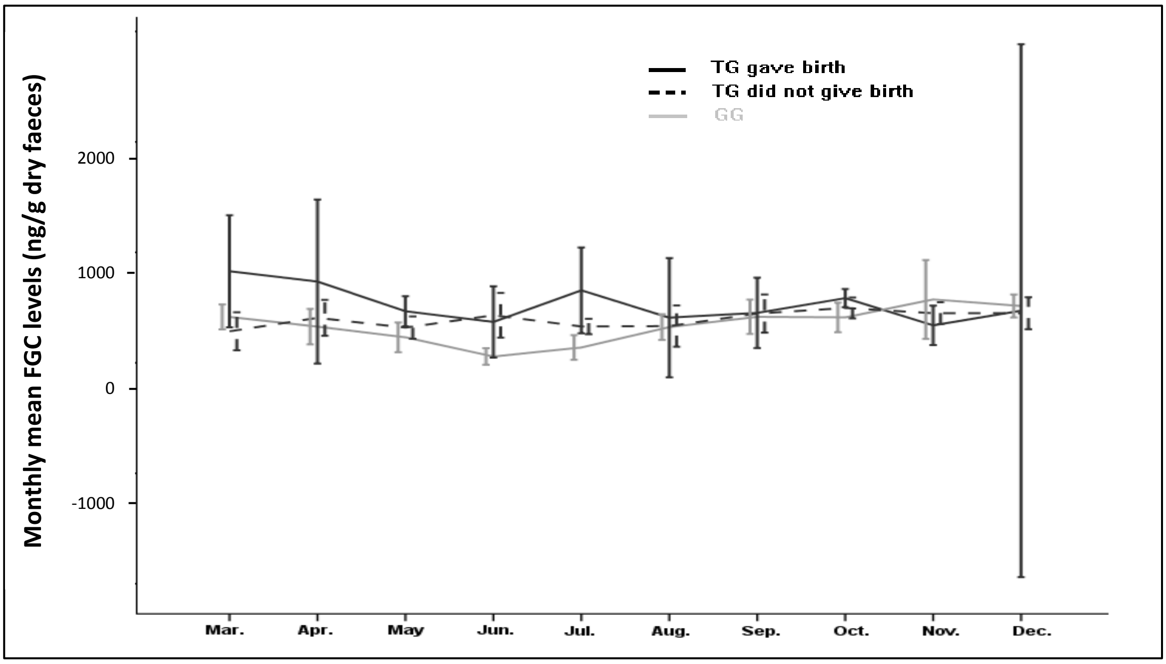


Figure 5-19: Plots of seasonal variation of mean FGC levels for TG and GG females. Error bars indicate 95% confidence intervals. Please refer to Table 5-14 for results of statistical analyses.

Males

There was a significant difference between groups in male FGC levels from April to July and December, although in May, July and December these were not significant after sequential Bonferroni correction (Table 5-15). TG male FGC levels were significantly higher than GG male FGC levels from April to July but lower in December (Figure 5-20).

Table 5-15: Monthly comparison of male FGC levels (ng/g dry faeces) between groups. t is associated with the independent t-test and U with Mann-Whitney test. Values in red were not significant after sequential Bonferroni corrections.

	March	April	May	June	July	August	September	October	November	December
t/U	t=1.699	t=4.264	U=4.000	t=4.651	t=2.885	t=1.410	t=0.857	t=0.883	t=-0.655	t=-2.288
P value	0.117	**0.001**	**0.019**	**0.001**	**0.015**	0.186	0.410	0.396	0.527	**0.045**

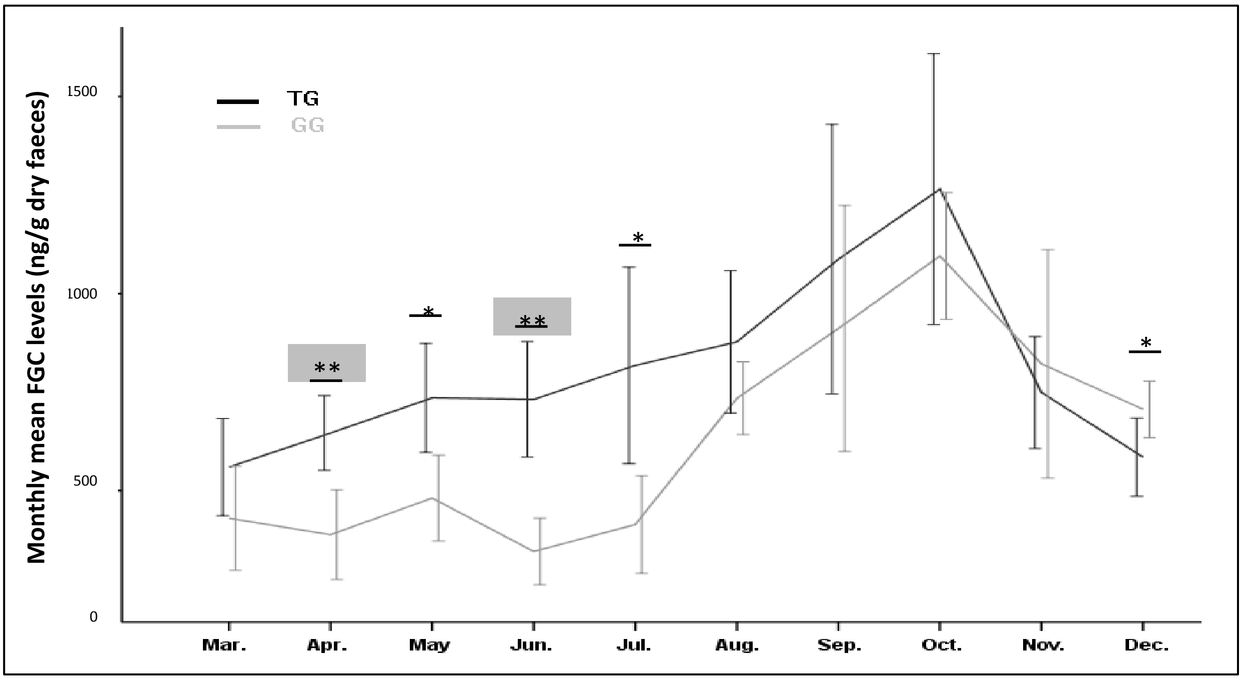


Figure 5-20: Plots of seasonal variation of mean TG and GG male FGC levels. Error bars indicate 95% confidence intervals. P value: *** <0.001; ** <0.01; *<0.05. P values highlighted in grey are still significant after sequential Bonferroni correction,

5.3.3 The relationships between health measures and provisioning in TG

Prediction 2i: Body size in the Tourist Group is positively related to amount of provisioning.

Females

TG females were bigger when the percentage of provisioned feeding was higher and during months when rainfall was higher (Table 5-16, Figure A15-1). However, rainfall did not predict GG female body size.

Table 5-16: Results of GLMM testing the relationships between female body size and provisioning in TG, and related GLMM run for females in GG. x indicates that the variable was not included in the model.

	Model **TG** female body size				Model **GG** female body size			
Null vs.	N	df	χ2	P	N	df	χ2	P
full model	99	7	59.892	**<0.001**	60	5	25.569	**<0.001**
	Estimate	±SE	t	P	Estimate	±SE	t	P
Intercept	-1.11	0.413	-2.691	**0.01**	-0.89	0.205	-4.337	**<0.001**
Gave birth vs. did not give birth	0.215	0.198	1.089	0.345	x	x	x	x
Provisioning	0.01	0.003	3.183	**0.004**	x	x	x	x
Environment								
rainfall	0.08	0.013	5.95	**<0.001**	-0.001	0.023	-0.037	0.983
Social								
Rank	0.007	0.119	0.06	0.928	-0.056	0.143	-0.392	0.67
Season								
Birth vs Mating	0.83	0.165	5.034	**<0.001**	0.272	0.211	1.287	0.244
Birth vs. PostBirth	0.646	0.193	3.343	**0.003**	-0.418	0.167	-2.495	**0.025**
Birth vs. PreBirth	0.749	0.255	2.933	**0.009**	-0.032	0.218	-0.145	0.901
Mating vs. PostBirth	-0.184	0.131	-1.409	0.197	-0.689	0.276	-2.494	**0.02**
Mating vs. PreBirth	-0.082	0.19	-0.429	0.7	-0.303	0.312	-0.974	0.363
PostBirth vs. PreBirth	0.103	0.181	0.568	0.605	0.386	0.178	2.171	0.052

Males

TG males were bigger when the percentage of provisioned feeding was higher and during months when rainfall was higher (Table 5-17, Figure A15-3). GG males were also larger during months when rainfall was higher.

Table 5-17: Results of GLMM testing the relationships between male body size and provisioning in TG, and related GLMM run for males in GG. x indicates that the variable was not included in the model.

	Model **TG** male body size				Model **GG** male body size			
Null vs. full model	N	df	χ2	P	N	df	χ2	P
	86	6	52.126	**<0.001**	50	5	48.389	**<0.001**
	Estimate	±SE	t	P	Estimate	±SE	t	P
Intercept	-2.063	0.518	-3.986	**<0.001**	-0.715	0.184	-3.894	**0.004**
Provisioning	0.012	0.004	2.588	**0.013**	x	x	x	x
Environment								
rainfall	0.098	0.022	4.404	**<0.001**	0.076	0.027	2.818	**0.01**
Social								
Rank	-0.354	0.155	-2.29	**0.023**	-0.216	0.06	-3.623	**0.047**
Season								
Birth vs Mating	1.353	0.262	5.165	**<0.001**	0.026	0.248	0.106	0.922
Birth vs. PostBirth	1.496	0.331	4.521	**<0.001**	-0.258	0.196	-1.312	0.226
Birth vs. PreBirth	0.921	0.389	2.369	**0.026**	0.075	0.256	0.292	0.782
Mating vs. PostBirth	0.143	0.208	0.687	0.529	-0.284	0.324	-0.875	0.412
Mating vs. PreBirth	-0.432	0.288	-1.501	0.174	0.049	0.365	0.133	0.907
PostBirth vs. PreBirth	-0.574	0.252	-2.283	**0.038**	0.332	0.209	1.593	0.135

Prediction 2ii: Coat quality in the Tourist Group is positively related to amount of provisioning.

Females

There was a significant negative association between TG female coat quality and the percentage of provisioning (Table 5-18, Figure A15-2). Coat quality scores of GG females, but not TG females, were worse during drier months.

Table 5-18: Results of GLMM testing the relationships between female coat quality and provisioning in TG, and related GLMM run for females in GG. x indicates that the variable was not included in the model.

	Model **TG** female coat quality scores				Model **GG** female coat quality scores			
Null vs.	N	df	χ2	P	N	df	χ2	P
full model	99	7	36.384	**<0.001**	60	5	17.677	**0.003**
	Estimate	±SE	t	P	Estimate	±SE	t	P
Intercept	2.615	0.245	10.679	**<0.001**	1.011	0.046	21.761	**<0.001**
Gave birth vs. Did not give birth	-0.178	0.085	-2.104	0.085	x	x	x	x
Provisioning	-0.007	0.003	-2.504	**0.016**	x	x	x	x
Environment								
rainfall	-0.013	0.012	-1.156	0.261	-0.02	0.006	-3.156	**0.003**
Social								
Rank	0.013	0.04	0.325	0.796	0.036	0.023	1.548	0.191
Season								
Birth vs Mating	-0.809	0.143	-5.649	**<0.001**	0.049	0.057	0.852	0.421
Birth vs. PostBirth	-0.748	0.17	-4.398	**<0.001**	-0.071	0.046	-1.565	0.145
Birth vs. PreBirth	-0.604	0.222	-2.725	**0.01**	-0.109	0.059	-1.832	0.087
Mating vs. PostBirth	0.061	0.115	0.533	0.606	-0.12	0.075	-1.599	0.136
Mating vs. PreBirth	0.206	0.167	1.234	0.242	-0.158	0.085	-1.861	0.079
PostBirth vs. PreBirth	0.144	0.157	0.917	0.387	-0.038	0.048	-0.78	0.467

Males

There was no significant link between TG male coat quality and percentage of provisioning, and in both groups there was no relationship between rainfall and male coat quality (Table 5-19).

Table 5-19: Results of GLMM testing the relationships between male coat quality and provisioning in TG, and related GLMM run for males in GG. x indicates that the variable was not included in the model.

	Model **TG** male coat quality scores				Model **GG** male coat quality scores			
Null vs. full model	N	df	χ2	P	N	df	χ2	P
	86	6	47.532	**<0.001**	50	5	3.914	0.562
	Estimate	±SE	t	P	Estimate	±SE	t	P
Intercept	1.565	0.193	8.108	**<0.001**	1.589	0.188	8.45	**<0.001**
Provisioning	0	0.003	-0.159	0.887	x	x	x	x
Environment rainfall	-0.017	0.009	-1.816	0.088	-0.003	0.015	-0.194	0.872
Social Rank	0.409	0.052	7.923	**<0.001**	0.114	0.162	0.704	0.316
Season								
Birth vs Mating	0.327	0.164	1.997	0.059	-0.13	0.139	-0.94	0.424
Birth vs. PostBirth	-0.175	0.159	-1.101	0.298	-0.15	0.11	-1.36	0.261
Birth vs. PreBirth	0.286	0.177	1.611	0.121	-0.038	0.144	-0.262	0.837
Mating vs. PostBirth	-0.502	0.119	-4.215	**<0.001**	-0.019	0.182	-0.105	0.928
Mating vs. PreBirth	-0.041	0.124	-0.335	0.742	0.093	0.205	0.454	0.697
PostBirth vs. PreBirth	0.461	0.129	3.57	**0.002**	0.112	0.117	0.959	0.424

Prediction 2iii: Alopecia scores in the Tourist Group are positively related to amount of provisioning.

Females

In both groups, female alopecia levels were unrelated to provisioning or rainfall (Table 5-20).

Table 5-20: Results of GLMM testing the relationships between female alopecia and provisioning in TG, and related GLMM run for females in GG. x indicates that the variable was not included in the model.

	Model **TG** female alopecia scores				Model **GG** female alopecia scores			
Null vs.	N	df	χ2	P	N	df	χ2	P
full model	99	7	5.759	0.568	60	5	9.769	0.082
	Estimate	±SE	t	P	Estimate	±SE	t	P
Intercept	1.42	0.335	4.243	**<0.001**	1.343	0.141	9.495	**<0.001**
Gave birth vs. Did not give birth	0	0.003	-0.107	0.903	x	x	x	x
Provisioning	-0.059	0.137	-0.43	0.632	x	x	x	x
Environment								
rainfall	0.014	0.014	0.973	0.361	0.002	0.015	0.158	0.891
Social								
Rank	-0.029	0.068	-0.427	0.715	0.028	0.104	0.265	0.766
Season								
Birth vs Mating	0.055	0.172	0.32	0.773	0.193	0.137	1.404	0.208
Birth vs. PostBirth	-0.026	0.203	-0.13	0.9	0.093	0.109	0.856	0.436
Birth vs. PreBirth	0.189	0.266	0.71	0.511	-0.136	0.142	-0.956	0.381
Mating vs. PostBirth	-0.081	0.138	-0.593	0.59	-0.099	0.18	-0.553	0.609
Mating vs. PreBirth	0.134	0.2	0.672	0.52	-0.328	0.203	-1.621	0.136
PostBirth vs. PreBirth	0.216	0.189	1.14	0.289	-0.229	0.116	-1.98	0.075

Males

There was no significant association between TG male alopecia and percentage of provisioning, nor between alopecia scores and rainfall in either group (Table 5-21).

Table 5-21: Results of GLMM testing the relationships between male alopecia and provisioning in TG, and related GLMM run for males in GG. x indicates that the variable was not included in the model.

	Model TG male alopecia scores				Model **GG** male alopecia scores			
Null vs.	N	df	χ2	P	N	df	χ2	P
full model	86	6	14.939	**0.02**	50	5	14.253	**0.014**
	Estimate	±SE	t	P	Estimate	±SE	t	P
Intercept	1.167	0.204	5.734	**<0.001**	0.98	0.105	9.365	**<0.001**
Provisioning	0.002	0.003	0.753	0.435	X	X	X	X
Environment								
rainfall	-0.004	0.011	-0.369	0.691	0.009	0.013	0.704	0.525
Social								
Rank	0.061	0.047	1.288	0.392	0.052	0.06	0.866	0.463
Season								
Birth vs Mating	0.46	0.132	3.482	**0.002**	0.221	0.123	1.795	0.104
Birth vs. PostBirth	0.102	0.177	0.575	0.566	0.139	0.097	1.426	0.187
Birth vs. PreBirth	0.236	0.144	1.646	0.103	0.015	0.127	0.121	0.904
Mating vs. PostBirth	-0.359	0.183	-1.965	0.059	-0.082	0.161	-0.507	0.654
Mating vs. PreBirth	-0.224	0.137	-1.633	0.116	-0.205	0.181	-1.131	0.303
PostBirth vs. PreBirth	0.135	0.198	0.681	0.515	-0.124	0.104	-1.194	0.276

Prediction 2iv: UCP levels in the Tourist Group are positively related to amount of provisioning.

Females

UCP levels of TG females were not significantly associated with percentage of provisioning. GG and TG female UCP levels were significantly higher during months when rainfall was lower (Table 5-22).

Table 5-22: Results of GLMM testing the relationships between female UCP levels and provisioning in TG, and related GLMM run for females in GG. x indicates that the variable was not included in the model.

	Model **TG** female UCP levels				Model **GG** female UCP levels			
Null vs.	N	df	χ2	P	N	df	χ2	P
full model	214	7	17.419	**0.015**	112	5	18.169	**0.003**
	Estimate	±SE	t	P	Estimate	±SE	t	P
Intercept	9.515	0.734	12.956	**<0.001**	9409.8	2276.8	4.133	**0.008**
Gave birth vs. Did not give birth	0.266	0.287	0.925	0.537	x	x	x	x
Provisioning	0.004	0.003	1.249	0.184	x	x	x	x
Environment								
rainfall	-0.1	0.047	-2.115	**0.042**	-419.7	171.6	-2.446	**0.028**
Social								
Rank	0.067	0.129	0.522	0.662	2427.3	1203.4	2.017	0.196
Season								
Birth vs Mating	-0.193	0.502	-0.384	0.776	10070.9	3146.9	3.2	**0.002**
Birth vs. PostBirth	-2.045	0.626	-3.27	**0.002**	-714.9	3059	-0.234	0.82
Birth vs. PreBirth	-1.561	0.646	-2.417	**0.027**	5237.2	7577.9	0.691	0.502
Mating vs. PostBirth	-1.853	0.548	-3.38	**0.001**	-10785.9	3003.3	-3.591	**0.001**
Mating vs. PreBirth	-1.368	0.557	-2.455	**0.016**	-4833.7	7610.2	-0.635	0.505
PostBirth vs. PreBirth	0.485	0.392	1.237	0.211	5952.1	7528.5	0.791	0.45

Males

UCP levels of TG males were not significantly associated with provisioning nor were UCP levels of males in either group related to rainfall (Table 5-23).

Table 5-23: Results of GLMM testing the relationships between male UCP levels and provisioning in TG, and related GLMM run for males in GG. x indicates that the variable was not included in the model.

	Model **TG** male UCP levels				Model **GG** male UCP levels			
Null vs.	N	df	χ2	P	N	df	χ2	P
full model	164	6	5.632	0.466	88	5	13.672	**0.018**
	Estimate	±SE	t	P	Estimate	±SE	t	P
Intercept	6037.319	1173.124	5.146	**<0.001**	2789.46	1006.39	2.772	**0.03**
Provisioning	2.997	7.215	0.415	0.686	x	x	x	x
Environment								
rainfall	32.864	33.315	0.986	0.346	91.85	139.87	0.657	0.61
Social								
Rank	288.797	400.64	0.721	0.539	-216.17	409.18	-0.528	0.732
Season								
Birth vs Mating	-638.204	1154.028	-0.553	0.582	3067.85	1416.49	2.166	**0.034**
Birth vs. PostBirth	-1222.241	1075.214	-1.137	0.267	1463.75	1138.05	1.286	0.27
Birth vs. PreBirth	-2019.888	1305.914	-1.547	0.129	1446.64	2399.22	0.603	0.493
Mating vs. PostBirth	-584.037	769.349	-0.759	0.458	-1604.1	1688.93	-0.95	0.276
Mating vs. PreBirth	-1381.684	1036.996	-1.332	0.195	-1621.21	2750.36	-0.589	0.592
PostBirth vs. PreBirth	-797.647	949.602	-0.84	0.423	-17.12	2304.06	-0.007	0.857

Prediction 2v: FGC levels in the Tourist Group are positively related to amount of provisioning.

Females

TG female FGC levels were not linked with percentage of provisioning (Table 5-24). FGC levels for GG females, but not for TG females, were significantly higher during months when rainfall was higher.

Table 5-24: Results of GLMM testing the relationships between female FGC levels and provisioning in TG, and related GLMM run for females in GG. x indicates that the variable was not included in the model.

	Model **TG** female FGC levels				Model **GG** female FGC levels			
Null vs.	N	df	χ2	P	N	df	χ2	P
full model	262	7	27.131	**<0.001**	192	5	53.54	**<0.001**
	Estimate	±SE	t	P	Estimate	±SE	t	P
Intercept	6.112	0.156	39.22	**<0.001**	438.486	45.484	9.64	**<0.001**
Gave birth vs. did not give birth	0.196	0.069	2.86	**0.025**	x	x	x	x
Provisioning	0.001	0.001	1.82	0.081	x	x	x	x
Environment								
rainfall	-0.006	0.009	-0.71	0.488	4.316	1.789	2.413	**0.022**
Social								
Rank	0.098	0.033	2.96	**0.032**	3.108	29.394	0.106	0.946
Season								
Birth vs Mating	0.154	0.088	1.75	0.089	260.322	49.999	5.207	**<0.001**
Birth vs. PostBirth	-0.124	0.115	-1.08	0.29	-3.815	45.485	-0.084	0.951
Birth vs. PreBirth	-0.033	0.124	-0.27	0.798	165.26	73.05	2.262	**0.023**
Mating vs. PostBirth	-0.279	0.1	-2.79	**0.007**	-264.137	43.298	-6.1	**<0.001**
Mating vs. PreBirth	-0.187	0.109	-1.72	0.089	-95.062	71.616	-1.327	0.194
PostBirth vs. PreBirth	0.091	0.076	1.2	0.226	169.075	66.582	2.539	**0.012**

Males

TG male FGC levels were higher when the percentage of provisioning was higher (Table 5-25, Figure A15-4). In both groups, male FGC levels were significantly higher during months when rainfall was higher.

Table 5-25: Results of GLMM testing the relationships between male FGC levels and provisioning in TG, and related GLMM run for males in GG. x indicates that the variable was not included in the model.

	Model **TG** male FGC levels				Model **GG** male FGC levels			
Null vs. full model	N	df	χ2	P	N	df	χ2	P
	309	6	32.716	**<0.001**	149	5	50.968	**<0.001**
	Estimate	±SE	t	P	Estimate	±SE	t	P
Intercept	6.029	0.117	51.71	**<0.001**	5.863	0.092	63.61	**<0.001**
Provisioning	0.001	0.001	2.33	**0.021**	x	x	x	x
Environment								
rainfall	0.031	0.008	3.84	**<0.001**	0.038	0.012	3.21	**0.002**
Social								
Rank	-0.022	0.039	-0.57	0.612	0.034	0.057	0.61	0.663
Season								
Birth vs Mating	0.165	0.091	1.8	0.069	0.397	0.131	3.02	**0.004**
Birth vs. PostBirth	0.436	0.106	4.11	**<0.001**	0.409	0.089	4.6	**<0.001**
Birth vs. PreBirth	0.165	0.116	1.43	0.167	0.248	0.146	1.7	0.107
Mating vs. PostBirth	0.272	0.085	3.19	**0.002**	0.012	0.147	0.08	0.953
Mating vs. PreBirth	0.001	0.096	0.01	0.996	-0.15	0.19	-0.79	0.411
PostBirth vs. PreBirth	-0.271	0.077	-3.53	**<0.001**	-0.161	0.132	-1.22	0.219

5.3.4 Result summary

Overall summaries of the results of direct comparison between groups according to predictions 1i to 1 iii provide evidence that TG individuals had worse general health than those in GG, such as more lameness, higher death rate, more disease symptoms, and lower birth success in 2 out of 3 years of data (Table 5-26).

However, there was no significant difference between groups for the number of scar and injuries per individuals.

Table 5-26: Summary of the results of direct comparisons between groups for general health measures, including scars, injuries, death, disease symptoms and birth rates, predictions 1i to 1iii. Ns=not significant, – not included, A>B indicates the direction of difference where statistical analyses were not done. The cases highlighted in light grey indicate that the results that do not meet the predictions.

	TG Females vs. **GG** Females	**TG** males vs. **GG** males	**TG** individuals vs. **GG** individuals
			Overall 10 months
<u>Hypothesis 1:</u> Provisioning of the Tourist Group has negative impacts on their health.	1.Direct comparison of health measures between the Tourist Group and the Green Group.		
Prediction 1i: Females in the Tourist Group have lower birth rates than those in Green Group	2011 (TG > GG) 2012 (TG < GG) 2013 (TG < GG)	-	-
Prediction 1ii: Animals in the Tourist Group have more lameness, scars, injuries and higher mortality than those in Green Group.	Scars (Ns) Injuries (Ns)	Scars (trend) Injuries (Ns)	Lameness (TG > GG) Death (TG > GG)
Prediction 1iii: Animals in the Tourist Group show more disease symptoms than those in Green Group.	-	-	Coughing/sneezing period (TG > GG) diarrhoea (TG > GG)

A summary of results in relation to predictions 1iv to 1 viii is presented in Table 5-27; evidence was found to support the prediction that TG females had a larger body size across the year than those in GG whereas TG males had a significantly larger body size than GG males only from July to September. Also, TG individuals had higher FGC levels than those in GG. Furthermore, TG males had more alopecia then GG males. By contrast, no evidence was found supporting the idea that the provisioned group had worse coat condition, or higher UCP levels compared to the non-provisioned group.

Table 5-27: Summary of the results of direct comparison between groups over the whole study period (10 months) and by months, (predictions 1iv to 1viii). P value: *** <0.001; ** <0.01; *<0.05; NS=not significant. The cases highlighted in light grey indicate that the results are opposite to predicted.

	TG Females (gave birth) vs. **GG** Females		**TG** Females (did not give birth) vs. **GG** Females		**GG** Males vs. **TG** Males	
	Overall 10 months	**Between months**	**Overall 10 months**	**Between months**	**Overall 10 months**	**Between months**
Hypothesis 1: Provisioning of the Tourist Group has negative impacts on their health.	1.Direct comparison of health measures between the Tourist Group and the Green Group.					
Prediction 1iv: Animals in the Tourist Group have larger body size than those in Green Group.	**	Mar **, Apr ***, May**, Jun*, Jul**, Aug*, Sep**, Oct**, Nov**, Dec**	***	Mar **, Apr ***, May**, Jun**, Jul***, Aug**, Sep***, Oct***, Nov***, Dec***	NS	Jul**, Aug***, Sep**, Oct*
Prediction 1v: Animals in the Tourist Group have worse coat quality than those in Green Group.	NS	Jul*, Aug**	NS	Apr*, Jul*, Aug**	NS	NS
Prediction 1vi: Animals in the Tourist Group have more alopecia than those in Green Group.	NS	May*	NS	Jul*	*	Mar**, Apr*
Prediction 1vii: Animals in the Tourist Group have higher UCP levels than those in Green Group.	NS	Mar*	NS	NS	NS	Apr**, May*
Prediction 1viii: Animals in the Tourist Group have higher FGC levels than those in Green Group.	**	Mar**, Apr*, May*, Jun**, Jul**	NS	Jun**, Jul**	*	Apr**, May*, Jun**, Jul*, Dec*

Table 5-28 provides an overall summary of the results of the models organised according to the predictions 2i to 2v. Some evidence was found in support of the idea that provisioning was positively associated with body size in both sexes, and with FGC levels only in males. Provisioning was also negatively related with coat quality in females.

Table 5-28: Summary of the results of the GLMMs testing the relationships between health measures and provisioning (predictions 2i to 2v). P value: *** <0.001; ** <0.01; *<0.05; NS=not significant; Cases highlighted in light grey indicate that the results are opposite to predicted. ↗ positive relationship, and ↘ negative relationship. Figures Appendices A12-A13.

	GG Females	**TG** Females		**GG** Males	**TG** Males	
	Rainfall	**Rainfall**	**Provisioning**	**Rainfall**	**Rainfall**	**Provisioning**
Hypothesis 1: Provisioning of the Tourist Group has negative impacts on their health.	2. Relationships between health measures and provisioning in TG.					
Prediction 2i: Provisioning would positively be related to body size.	NS	↗ ***	↗ **	↗ **	↗ **	↗ *
Prediction 2ii: Provisioning would positively be related to coat quality score.	↘ **	NS	↘ *	NS	NS	NS
Prediction 2iii: Provisioning would positively be related alopecia score.	NS	NS	NS	NS	NS	NS
Prediction 2iv: Provisioning would positively be related to UCP levels.	↘ *	↘ *	NS	NS	NS	NS
Prediction 2v: Provisioning would positively be related to FGC levels.	↗ *	NS	NS	↗ **	↗ **	↗ *

5.4 Discussion

Food availability has an important impact on the health of wild animals, and provisioning can therefore have important consequences for these animals. Supplementing natural resources with provisioned food might be beneficial for animals during periods of food deprivation (Brittingham and Temple 1988, Persson 2005); however, uncontrolled and unbalanced provisioning, as is often associated with wildlife tourism, might potentially be harmful for animals' health. In the present study I investigated the impacts of tourist provisioning on the health of wild Barbary macaques. For this, I explored several non-invasive indicators of health, while taking into account ecological and social factors that might also influence animals' health.

Overall, evidence was found that Barbary macaques from the Tourist Group (TG) had worse health than those in the Green Group (GG), and that provisioning in the Tourist Group had negative effects on these animals' health. These findings need to be interpreted cautiously as the optimum (or optimal range) for each health measure is not known in this species. In this discussion, I first explore in depth the results associated with the different health measures, under the predictions that underpin this part of my study. Finally, I discuss the interpretation of the results.

5.4.1 Prediction 1i: Females in the Tourist Group have lower birth rates than those in the Green Group.

It was predicted that provisioned females would produce fewer offspring than non-provisioned females. Although in 2012, TG females had a lower total number of births than GG females, in the two other years there was not a marked difference between groups in the number of births. These findings do not allow a clear conclusion to be drawn about the impacts of provisioning on birth rates.

It is difficult to determine the causes for a decrease in the number of births among TG females in 2012, because a number of factors in addition to provisioning might influence the production of offspring, such as age, stress or environmental factors. Fa (1984) suggested that stress related to intraspecific competition during provisioning might have been a cause of reduced fertility in female Barbary macaques in Gibraltar and that provisioning also improved survival of old female Barbary macaques with low fertility (Fa 1984), both factors leading to a decrease in number of offspring produced per female per year. An increase in interbirth intervals was also reported to be a factor in the decreased number of births associated with provisioning in yellow baboons (*Papio cynocephalus:* Altmann et al. 1978). More recent studies have similarly suggested that an excessive amount of food given to wildlife, as well as an unbalanced diet, might reduce breeding productivity. For example, a study of wild birds found that winter food supplementation resulted in decreased breeding success the following spring, which was suggested to be related to an unbalanced diet especially rich in fats (Plummer et al. 2013a). The present results indicate that over 30% of the food consumed by animals from the TG was high energy content human food, generally consisting of bread, peanuts, or other highly fat and sweet food. Therefore, it is possible that this rich diet, potentially in combination with stress related to high intraspecific competition during provisioning (see chapter 4), may explain the low number of births in TG in 2012. However, longer term data are needed to confirm the idea that provisioning negatively affects birth rates.

Provisioning has been suggested to increase breeding productivity in a number of species (wolverines: Persson 2005; plaice: Kennedy et al. 2008), especially in periods of food shortage. The present findings do not show any apparent increase in productivity in TG compared with GG. Barbary macaques are seasonal breeders (Deag 1984), and produce a maximum of one offspring per year (Paul and Thommen 1984), meaning that if the natural food availability is sufficient to cover the energy costs of reproduction, females might be able to give birth every year (Garcia et al. 2011). The fact that of 19 possible births in GG across the 3 years considered, 18 births occurred, suggests that GG females might be able to cope with seasonal food shortage (i.e. fewer grass and acorns) by consuming other sources of food to reach their energy needs for reproduction. Previous studies found that Barbary macaques have a highly flexible diet, and were able to cope with seasonal fluctuation of food availability by feeding on a variety of foods ranging from underground plants, tree leaves and fruits to insects and small animals (Drucker 1984, Ménard 2002, Young et al. 2012). Therefore any possible increase in birth rates linked to tourist provisioning may be hard to detect in this population.

5.4.2 Prediction 1ii: Animals in the Tourist Group present more lameness, scars, injuries and higher mortality than those in the Green Group.

It was predicted that provisioned individuals would present more evidence of physical harm such as scars, lameness, injuries or even higher mortality rates. Provisioning is generally expected to increase the risk of intraspecific competition to gain access to the limited food resource, and thus agonistic interactions between animals, increasing the risk of injuries (Orams 2002). In addition to this potential risk linked to intraspecific competition, animals may receive aggression from tourists, which could also lead to injuries (Maréchal et al. 2011). In the present study, no evidence was found that TG animals had more visible scars or injuries than those in GG. However, more TG individuals presented lameness and more died over the study period compared to GG individuals, although a statistical analysis was not feasible for these comparisons.

Although previous studies indicate that animals show higher rates of aggression towards conspecifics during provisioning (Hill 1999, Ram et al. 2003, Semeniuk and Rothley 2008, Hsu et al. 2009, chapter 4), animals might display non-physical aggression, generally classified as mild aggression, rather than physical aggression, generally defined as severe aggression that can lead to injury. Rhesus macaques, for example, displayed higher rates of mild rather than severe aggression during provisioning (Southwick 1967). In the present study, Barbary macaques in TG showed higher rates of aggression during provisioning compared to periods with no provisioning occurring (see chapter 4); however Barbary macaques have an ‘egalitarian’ dominance style, and display more non-physical aggression rather than physical forms (de Waal and Luttrell 1989), which may explain why there was no significant difference between provisioned and non-provisioned groups in the numbers of scars or injuries per individual.

In contrast to the results in relation to visible scars and injuries, five individuals from TG presented non-serious or severe lameness, whereas only one GG individual presented lameness and this was not serious. Since provisioning might generate an increase in intraspecific competition and/or human-animal conflicts, the higher number of individuals presenting lameness in TG might be due to such agonistic interactions. Additionally, harmful garbage (e.g. opened metal cans, broken bottle glass, or sharp plastic bottles) is very common on the ground at the tourist site (Personal observation), and may pose a high risk of injury to body parts in contact with the ground, i.e. hands and feet.

Finally, one confirmed death, two disappearances of adult monkeys and one miscarriage occurred in TG, but no deaths occurred in GG over the same period. The one animal found dead in TG was suggested to have died from food poisoning, possibly linked with provisioning. Only a few studies have suggested that the death of an animal may directly result from provisioning in wild settings (Burger 1997, Alves et al. 2013). However, little is generally known about the direct or indirect causes of these deaths (Orams 2002), highlighting the difficulty in interpreting such results. Autopsying animals might shed light on how they died when no apparent cause can be determined directly, but this is rarely an option in remote field sites and may also be very costly. In addition, animals often simply disappear and are presumed to have died (Neil and Breize 1998, Ménard and Vallet 1993), which makes the determination of the cause of potential death impossible. Furthermore, mortality rates in wild populations vary over time due to stochastic events (Lacy 1993), and thus long term data, over many years for long lived animals such as primates, may be required to fully understand how mortality rates are affected by provisioning.

5.4.3 Prediction 1iii: Animals in the Tourist Group show more disease symptoms than those in the Green Group.

It was hypothesised that provisioned individuals would show more disease symptoms than non-provisioned animals, and the present results provided evidence supporting this idea. Although no statistical comparison was possible, the data indicate that TG individuals more often presented disease symptoms associated with respiratory infections and diet-related disease or disorders than GG animals. Since the risk of disease transmission between human and non-human primates is high (Muehlenbein and Wallis 2014), the high frequency of disease symptoms in the provisioned group may be due to the interactions between tourists and macaques, facilitated by provisioning. In fact, provisioning is particularly concerning in relation to disease transmission because it reduces the distance between humans and wildlife, as well as increasing the chances of the direct transmission of disease via food (Honess et al. 2006). For example, in Morocco, I often observed tourists cracking peanut shells in their mouth, and giving them to the monkeys, or drinking water from a bottle, and then handing it to the monkeys to drink from, greatly increasing the risks of disease transmission by fluid exchange.

However, it is often very difficult to determine the actual origin of a disease in animal populations. A number of diseases in wild primates were suspected to have resulted from transmission from humans to primates (Goodall 1986, Nizeyi et al. 2001, Hill et al. 2001, Graczyk et al. 2002), and it is only recently that such transmission events have been confirmed (Salzer et al. 2007, Goldberg et al. 2007, Rwego et al. 2008). The difficulty in identifying the source of a pathogen is even greater in the context of potential tourist-wildlife transmission, because the time of incubation of a pathogen after infection may be from a few hours to several days or weeks. This is a key reason why no study has yet been able to confirm disease transmission between tourists and wildlife (Muehlenbein and Wallis 2014).

In addition to disease transmission, tourist provisioning may present a risk of diet-related disorders such as food poisoning, which may explain the higher frequency of diarrhoea observed in the provisioned TG compared to the non-provisioned GG. I observed that the type of food given by tourists to the monkeys depends on the season, with large quantities of fruits such as watermelon given in summer, which can provoke digestive problems resulting in diarrheal symptoms (Blaser 1986). Also, food that is well past the recommended date of consumption by humans was observed being given to the macaques, including out of date yoghurts and mouldy bread, presenting a risk of food poisoning (Zinedine and Mañes 2008). A potential example of the outcome of consumption of such food is provided by Fa (1984) who described how in 1968 Barbary macaques from Gibraltar had increased mortality as a result of the spread of ringworm, which was suggested to have been caused by unsuitable food given by tourists. Such issues regarding the quality of food given by tourists to wildlife have rarely been investigated, and therefore the impacts are poorly understood.

Tourist interactions with animals, and the quantity and quality of food they give to them, are among the main concerns in relation to the impacts of wildlife tourism. Overall, the present study provides evidence that tourists and tourist provisioning may negatively affect the welfare of animals, i.e. more disease symptoms recorded in the TG than in GG; however, no causal relationships can be determined due to the difficulty of identifying the origin of an infection or disorder. Nevertheless, since tourists may present a serious risk of disease transmission (Muehlenbein and Wallis 2014), it may be useful and beneficial to implement rules and regulations in relation to monkey tourism, similar to those in place for great apes. Recently, guidelines have been published by Macfie and Williamson (2010) for great ape tourism, to reduce the potentially negative impacts of tourism on the welfare of animals involved. Measures proposed include wearing masks and gloves and keeping a minimum distance between tourists and animals of 7m, to reduce the risk of respiratory disease transmission (Macfie and Williamson 2010).

5.4.4 Prediction 1iv: Animals in the Tourist Group have larger body size than those in the Green Group, and Prediction 2i: Body size in the Tourist Group is positively related to amount of provisioning.

It was predicted that TG individuals would have a larger body size than those in GG, and that body size would be positively related to quantity of provisioning in TG. Evidence was found supporting these predictions, although only a trend was found in the comparison between groups for males. TG females, both those that gave birth and those that did not, had a significant larger body size than GG females; in addition, variation in body size was positively related to amount of provisioning in TG individuals.

Provisioning wildlife generally leads to an increase in animal body size, which is often thought to reflect a better body condition, helping animals to cope better with environmental stochasticity, and thus increasing their chance of survival (Mori 1979, Crout at al. 2002, Cabrera-Guzmán et al. 2013). On the other hand, larger body size might also reflect poor health when animals are ranging from overweight to obese, and this may lead to an increased risk of diet-related disease and disorders, such as diabetes or cardiovascular disease (Mokdad et al. 2001, Sapolsky 2014). Previous studies have suggested that some tourist-exposed animals might suffer from obesity, which was suspected to be the case in Barbary macaques in Gibraltar (Honess et al. 2006), and long-tailed macaques in Bali (Lane et al. 2010), but no further research was conducted to determine if these animals were actually suffering from obesity and whether provisioning was related to this condition.

Using only body size as a non-invasive measure, it is not possible to determine whether larger body size reflects animals reaching the level of overweight or obese by simply comparing a provisioned group and non-provisioned group. The large body size of provisioned animals might be considered as normal or overweight, while the non-provisioned individuals might be underweight or normal (Borg et al. 2014). Although it cannot be confirmed, considering the body size of TG animals with additional observations gives indications that some TG females might be potentially overweight/obese. First, during pregnancy, animals generally gain weight, have an increase in fat deposition, and thus an increase in body size (Hytten and Leitch 1971). In the present study, there was no significant difference in body size between TG females who did not give birth and those who did, even in late pregnancy. Second, most of the TG females presented an anogenital swelling all year round; this was present only during the mating season in GG females. An anogenital swelling present outside of the mating period might be related to a period of high body weight (Mori et al. 1997). Nevertheless, as optimum body size is unknown for Barbary macaques, it is not possible to confirm the actual body condition of TG individuals, or whether such body condition negatively affects their health.

Overall, although provisioning was linked here with a larger body size in Barbary macaques, it was not possible in such a short term study to determine if this larger body size had any positive or negative impacts on health. However, if tourist provisioning continues to increase animals' body size, this might increase the risk of diet-related disease and disorders, and thus regulating provisioning may be beneficial in prevention of these issues.

5.4.5 Prediction 1v: Animals in the Tourist Group have worse coat quality than those in the Green Group, and Prediction 2ii: Coat quality in the Tourist Group is positively related to amount of provisioning.

No evidence was found in the present study to support the prediction that provisioning negatively affects coat quality. There was no difference between groups in coat quality for either sex. Furthermore, a greater amount of provisioning was associated with better (not worse) coat quality for TG females, but no such effect was seen for TG males.

A number of studies have suggested that because tourist-exposed animals are often provided with poor nutritional food, this might affect their body condition (Burger 1997, Perez and Bensusan 2005). Poor diet is associated with poor coat quality in a number of species, such as dogs (March 1999) and sheep (Khan et al. 2012). By constrast, provisioning wildlife may improve body condition by increasing energy intake, and therefore be reflected by a good coat quality. Evidence was found in the present study supporting the idea that high levels of provisioning were related to better coat quality for TG females but not for TG males. However, results also indicate that there is no overall difference in coat quality between provisioned and non-provisioned individuals. Barbary macaques have a flexible diet, and may be able to cope with seasonal variations in food availability and nutritional requirements by diversifying their diet (Ménard 2002), which may explain the lack of difference in coat quality between groups.

The present results stand in contrast to the findings by Borg et al. (2014), who compared the same two groups of wild Barbary macaques in 2011 and found evidence for worse coat condition in TG than GG adult males but no difference between groups for adult females. As pointed out by Berg et al. (2009), assessing coat quality may be difficult because the difference between the categories used for scoring can be blurred. In addition, the visual scoring used in the present study did not include alopecia, which might explain the difference in results between this and the study of Borg et al. (2014). An individual with good coat quality but with alopecia would have been classified as ‘ragged’, meaning low coat condition, by Borg et al. (2014), whereas in the present study the coat quality of the same individual would have been classified as good. In addition, since coat quality might be influenced by a number of factors such as pregnancy, age and environmental conditions, the difference in results between the two studies might also reflect a difference in such factors. Nevertheless, it is difficult to determine precisely what factors might affect coat quality because of the long time scale between an event and its apparent effect on the coat (Berg et al. 2009, Jolly 2009).

5.4.6 Prediction 1vi: Animals in the Tourist Group have more alopecia than those in the Green Group and Prediction 2iii: Alopecia in the Tourist Group is positively related to amount of provisioning.

Hair loss is a serious issue because it compromises the efficient protection provided by an animal’s fur (Tregear 1965). It was predicted that provisioned animals would have more alopecia than those that are non-provisioned, and that the extent of alopecia would be positively related to the amount of provisioning. No evidence was found in the present study to support the idea that amount of provisioning has an overall impact on alopecia in TG; however TG males had significantly more alopecia than GG males, though no such difference was found for females. The present results are in line with previous findings in the same groups of Barbary macaques, which showed that TG males, but not TG females, had worse coat condition compared to GG animals (Borg et al. 2014). Furthermore, in ring-tailed lemurs and Japanese macaques, individuals from provisioned groups had more alopecia than those from non-provisioned groups (Jolly 2009, Zhang 2011).

Stress is one of the main factors that might influence alopecia, and a number of studies have found positive relationships between stress levels and levels of alopecia (Steinmetz et al. 2006, Novak and Meyer 2009). Since provisioning might cause stress due to the increased risk of aggression received from conspecifics and/or tourists (Maréchal et al. 2011, Majolo et al. 2013, chapter 4), feeding by tourists might indirectly influence the amount of alopecia via increased stress in wild animals. This might explain why there is a difference between groups in alopecia for males, but not females because they might use different coping mechanisms (Chapter 4). In addition, TG males had higher physiological stress levels than those in GG, providing additional support for this idea that alopecia might be related to stress. Females appear to use different behavioural mechanisms to cope with such stressful situations (Chapter 4) or experience less stress in such environments, and therefore stress might not affect their levels of alopecia. Nevertheless, it is very difficult to determine which factors influence coat condition, and the results need to be interpreted with caution (Jolly 2009, Borg et al. 2014). The time scale over which the effects of a short or long term stressor might be revealed is highly variable, making it very difficult to determine the primary causes of alopecia (Berg et al. 2009, Jolly 2009). This limits the application of such a health measure in wild animals to that of a general and complementary tool for assessing animals' health.

5.4.7 Prediction 1vii: Animals in the Tourist Group have higher UCP levels than those in the Green Group, and Prediction 2iv: UCP levels in the Tourist Group are positively related to amount of provisioning.

Urinary C-peptide (UCP) levels have been used as an indicator of nutritional status in a number of primate species (Kruszynska 1987, Sherry and Ellison 2007, Girard-Buttoz et al. 2011), and there is evidence confirming that they vary depending on the amount of food consumed relative to energy expenditure (Wolden-Hanson et al. 1993, Deschner et al. 2008). Therefore, it was predicted that UCP levels in TG would be positively related to provisioning, and that TG animals would have higher UCP levels than GG animals, both as a result of high energy intake and potentially lower energy expenditure because of the ease of food availability. No evidence was found to support these predictions. A number of factors might explain these results.

First, the number of individuals in this study may not be sufficient to find a significant difference between groups, particularly given the large variation both individual and temporal that is typically seen in UCP levels. In addition, individuals from the TG might expend more energy in physical activity than do those from the Green Group. For example, overweight and obese individuals use more energy on average than lean individuals for similar activities (Johannsen et al. 2008, DeLany et al. 2014). TG individuals might also expend more energy due to being involved in low level activities such as restlessness, associated with interacting with tourists (chapter 4). Similar low level activities were found to be highly energy costly in overfed humans (Levine et al. 1999, 2000).

The lack of difference in UCP levels between TG and GG implies a similar energy balance in the two groups. TG may have high energy intake from provisioning and high energy expenditure linked to increased activity levels and high physiological stress levels; GG may have lower energy intake from their natural foraging but also lower energy expenditure. However, this hypothesis does not seem consistent with the fact that body size is positively related to provisioning, which suggests that TG individuals might have an increased energy intake and lower energy expenditure when provisioning increased leading to an increase in body size.

The section above highlights the difficulty in interpreting such findings, which may result from a combination of factors such as individual state (e.g. age, pregnancy, and fat mass) and other environmental factors. In fact, little is known about the different factors influencing UCP levels, and a recent study in humans suggested that UCP was not in fact an accurate bioindicator of energy balance (Bergouignan et al. 2012). No relationships were found in that study between UCP and body mass either at baseline or after experimental bed-rest (Bergouignan et al. 2012). This suggests that the relationships between UCP levels and energy balance should be considered with caution, in particular under field conditions where factors influencing UCP levels are difficult to control for.

Three individuals (one female in TG and two males, one from each group) presented markedly higher UCP levels compared to the other animals in their respective groups. One TG female who did not give birth presented higher UCP levels than the other females who did not give birth. This young adult female was also the female with the largest body size. The combination of high UCP levels and large body size suggest that this female might suffer from type II diabetes (Mokdad et al. 2001). However, further clinical tests would need to be conducted to confirm this potential diagnosis. Regarding the two males presenting higher UCP levels compared to the rest of the males in their respective groups, their levels may potentially be associated with their age rather than diet-related disorder because they were the slimmest individuals from their groups but estimated to be among the oldest. In fact, it has been found in humans that older individuals have higher C-peptide levels than younger ones (French et al. 1992), and the present results might reflect the same effect in the study animals.

Overall, provisioning does not seem to be related to elevated UCP levels in wild Barbary macaques, but the present results also highlighted the difficulty of interpreting this measure of energy balance, due to the different factors that can influence it. However, measuring UCP levels might still be a useful tool to assess the health of animals, especially for identifying individuals with particularly high levels, as in the present study. Nevertheless, the results need to be interpreted with caution, and a diagnosis can only be confirmed when corroborated with additional measures, such as cholesterol levels, body mass or fat mass. In fact, it was suggested by Sapolsky (2014) that for animals presenting obesity, high levels of insulin and cholesterol, constitute the profile of ‘metabolic syndrome’, which increases the risk for both diabetes and cardiovascular diseases.

5.4.8 Prediction 1viii: Animals in the Tourist Group have higher FGC levels than those in the Green Group, and Prediction 2v: FGC levels in the Tourist Group are positively related to amount of provisioning.

It was predicted that faecal glucocorticoid (FGC) levels in TG would be positively related to provisioning, and that TG animals would have significantly higher FGC levels than those in GG. The present results provide evidence to support both predictions, although the relationship between provisioning and FGC levels was only a trend for females. Furthermore, there was no significant difference in FGC levels between TG females who did not give birth and GG females.

Stress responses enable animals to cope with challenges in their environment (Sapolsky et al. 2000). For example, agonistic interactions with conspecifics have been associated with higher physiological stress levels (Honess and Marin 2006). In captive bonnet macaques, when clumped provisioning was presented, there was an increase in aggression between conspecifics and an increase in physiological stress levels (Boccia et al. 1995). Therefore, tourist provisioning might affect physiological stress levels through increasing social tension among animals. In addition to causing increased social tension between conspecifics, interactions with tourists such as agonistic interactions during provisioning might also lead to elevations in physiological stress levels (Maréchal et al. 2011). Evidence was found in the present study to support the idea that provisioned animals have higher physiological stress levels than non-provisioned individuals, and social tension associated with clumped food resources and/or interactions with tourists might explain this difference. However, the possibility cannot be excluded that the elevated FGC levels in TG individuals may also be related to the death of several individuals from this group. In baboons, it was found that females who lost a close relative to predation had a significant increase in FGC levels following their relative’s death, although this increase only lasted a short time and only affected them, not other females unrelated to the victim (Engh et al. 2006a).

Since prolonged high FGC levels might increase the risk of stress-related disease such as cardiovascular disease, and can impair the immune system and reproduction (Sapolsky 1992), higher FGC levels found in provisioned Barbary macaques might indicate a threat to their long-term health. However, the threshold over which high FGC levels might be detrimental for the health and welfare of an animal is unknown, making it impossible to confirm whether the FGC levels found in the present study are likely to have a negative impact on the health of TG individuals. For instance in the present study, GG animals had smaller body sizes and quite a skeletal appearance during summer, when food availability was very low, and their FGC levels at this time were at the lowest levels for the year. Laboratory experiments on fasting animals and humans found that they did not activate their HPA axes, and hence they showed no increase or decrease in cortisol levels (Gonzalez-Bono et al. 2002), or in concentrations of plasma adrenocorticotropic hormone (Hanson et al. 1994), suggesting that here a lack of activation of the HPA axis was related to nutritional stress. In the present study, low FGC levels in GG individuals could be an indicator of poor health, complicating the interpretation of the comparison between groups. The higher FGC levels found in TG might not reflect the poor health of TG individuals, but rather their good condition.

Overall, although provisioned animals had higher FGC levels than those in non-provisioned condition, and provisioning appears to be related to FGC levels, it cannot be confirmed that the higher FGC levels have negative impacts on the health of the animals involved.

5.4.9 Interpreting the results of health measures

There are two main types of wildlife provisioning: by tourists and by conservation biologists. Both are controversial because of the difficulty of determining whether their effects are beneficial or detrimental to the health of animals involved. Conservation biologists generally provide food supplementation to improve the body condition and potentially the fitness of animals they aim to conserve. Tourist provisioning may also improve animal fitness, and it may additionally be beneficial in terms of its economic support for conservation, by attracting tourists who pay fees to feed wildlife (Japan: Knight 2011, Gibraltar: Perez and Bensusan 2005). However, it might also be detrimental in terms of quantity and quality of food provided. Since clear detrimental effects of tourist provisioning are often difficult to determine, and the financial benefits for the local communities and other tourist business are generally high, wildlife feeding has become a very popular tourist activity, in particular for endangered species, making the need to understand its impacts on wildlife particularly pressing.

Previous studies suggested that provisioning may have beneficial effects (Persson 2005, Harrison et al. 2010), no impact (Clout et al. 2002), or detrimental effects (Burger 1997, Kemnitz et al. 2002, Blanco et al. 2011, Plummer et al. 2013). A number of studies could not provide evidence of the full impacts of provisioning on health, but rather often suggested that these effects may be seen only in the long term. For example, Knapp et al. (2013) were able to determine that levels of glucose, potassium, and uric acid were higher in a provisioned group of Northern Bahamian rock iguanas compared to a non-provisioned one. However, they concluded that the effects of altered biochemical concentrations may not be revealed over a short time period, but might have deleterious impacts on long-term fitness and population stability (Knapp et al. 2013). In such conditions, it appears difficult to advise those involved in tourism and conservation management on how to regulate provisioning in order for this to be beneficial – or at least not detrimental – for the animals involved.

Similar difficulties are evident in the present study, due to the lack of clear negative and immediate impacts of tourist provisioning on the health of wild Barbary macaques. Nevertheless, when considering the results of the different health measures, it could be suggested that some regulations of tourist provisioning might be beneficial. By regulating food supplementation, it may be possible to reduce the potential risk for disease transmission, animals' physiological stress levels, the number of individuals with lameness, and the number of deaths, which overall might improve the health of the animals involved and the long term viability of the population. However, long term data are necessary to test robustly for these potential effects.

The main difficulty in interpreting the results of studies of health impacts in wild animals is the lack of an optimum index or range for the health measures employed, and a lack of knowledge of the threshold levels, under or over which the health of an animal might be affected. Knowing such parameters would allow informed decisions on the occurrence and nature of provisioning to be made. In Figure 5-21, I provide a schematic tool for helping to visualise the potential costs and benefits of provisioning. More data on health and fitness impacts (positive and negative) of provisioning in wild populations are now needed to parameterise this schematic.

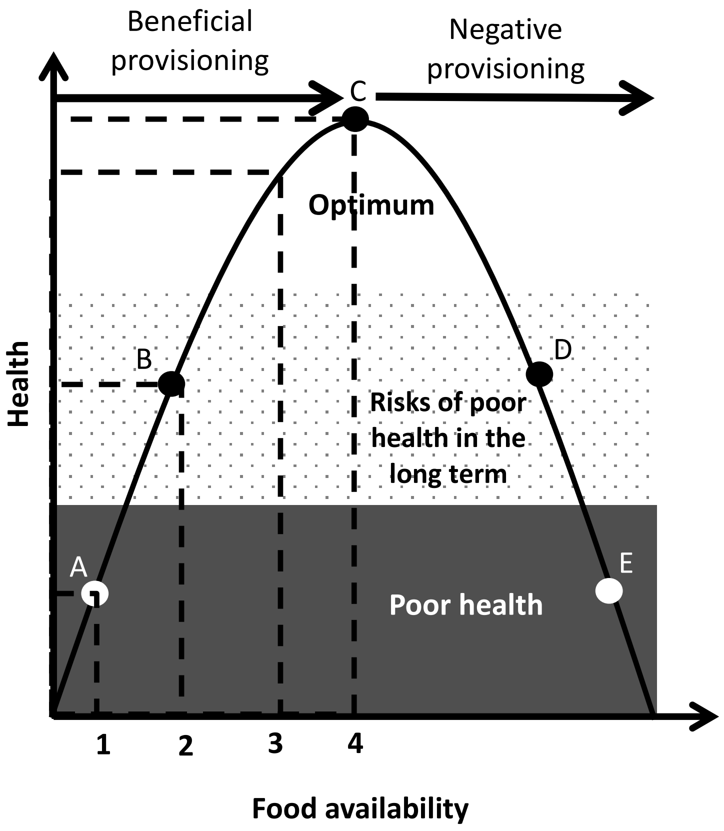


Figure 5-21: Diagram of the effects of food availability, including both natural food and provisioning, on the health of wild animals. A: Animal in poor health which threatens its immediate survival, and for which provisioning might improve its chance of survival. **B:** Animal in relatively poor health condition which decreases its chance of survival in the long term, but can be improved by provisioning. **C:** Optimal health. **D:** Animal in relatively poor health condition, due to excessive food intake with lower chance of survival in long term, but can be improved by reducing provisioning. **E:** Animal in poor health which threatens its immediate survival, but its chance of survival might be improved by drastically reducing provisioning. The numbers (1-4) represent the different levels of natural food availability.

To illustrate this point, I describe in detail the different levels of natural food availability and the potential consequences of provisioning on the health of wild animals, as shown in figure 5-21. The difference in natural food availability may be due to seasonal or annual variations. Therefore this schematic may help to compare the different situations over time, or different settings, and also facilitate management decisions on whether provisioning may be acceptable or not, according to its impacts on the health of wild animals. The schematic also highlights the importance of assessing natural food availability as well as optimal health requirements for the animal (e.g. energy intake/energy expenditure) in order to estimate whether provisioning may be an acceptable practice.

Provisioning may be beneficial if the natural food availability is too low (Figure 5-21, numbers 1, 2 and 3), which may compromise the health of wild animals, and ultimately their chance of survival. In these cases, provisioning may be acceptable or indeed desirable. In scenario number 1, natural food availability is so low that animals are in imminent threat for their survival, and provisioning in this case may be recommended. In scenario number 2, natural food availability is low, increasing the risks of long term health problems or premature death, and provisioning may be beneficial. In scenario number 3, natural food availability is in the range required for good health, and provisioning may have only limited beneficial impacts or no impact. Nevertheless, in each case, although provisioning may be beneficial, increasing such provisioning over an optimal level has a down side, which may ultimately have negative impacts on health. Finally, when natural food availability is optimal (Figure 5-22, scenario number 4), provisioning may have negative impacts on health ranging from no to limited negative effects, being costly or in extreme cases highly detrimental for the health of the animals.

5.4.10 Conclusion

My study has explored impacts of provisioning on the health of tourist-exposed animals using a range of non-invasive measures, and more broadly provides a basis for better understanding wildlife health. The findings highlight the importance of considering fitness outcomes and body condition when assessing health, and the importance of understanding both short and long term effects on health. The present results also highlight the difficulty in interpreting the full impacts of provisioning on health measures, suggesting that further research should be conducted to assess what represents optimum health. Finally the schematic on the effects of provisioning on the health of animals proposed may also provide a useful tool to assess and manage provisioning for both wildlife tourism and conservation purposes.

Chapter 6

General Discussion

Wildlife tourism is a growing industry, and one that has the potential to significantly benefit conservation. Such benefits may be achieved if this tourism is sustainable, meaning that the potential negative impacts on the animals are eliminated, or at least reduced and outweighed by the positive impacts on animal population size, the benefits to the local community, and the quality of the tourist experience (Reynolds and Braithwaite 2001, Russon and Wallis 2014). Tourists and the animals they come to see are the two principal components of wildlife tourism, and it is important to understand this phenomenon from their respective standpoints. This is particularly true when provisioning occurs as part of this activity; feeding wildlife is a common practice, but one which may have impacts on both the tourist experience and on the welfare of the animals involved. The aim of the present study was to investigate primate tourism at a tourist site in the Middle Atlas Mountains of Morocco, using a multidisciplinary approach which considered both the attitudes and expectations of tourists, and the responses of, and impacts on, the Barbary macaques they visit there.

In this general discussion I first summarise the key findings of the thesis, and then discuss the implications of these results for wildlife tourism and conservation. I also discuss the value of using a multidisciplinary approach to understand human-animal relationships, both within the context of wildlife tourism, and more broadly. Finally, I present the overall conclusions of the entire thesis.

6.1 Summary of the key findings: understanding primate tourism at a site in Morocco

It has previously been stated that provisioning creates a connection between tourists and the animals involved, based on tourists' attraction for the animals as well as animals' attraction for food they may receive from tourists (Orams 2002). In the present study, I used a multidisciplinary approach to investigate this particular relationship from both tourist (Chapter 3) and macaque standpoints (Chapter 4 and 5).

Barbary macaques were found to be very attractive to tourists (Chapter 3), as was expected because they present particular features suggested to be appealing, such as a similarity to humans (like other primates), aesthetic appeal (e.g. cute, fluffy, playful), or being rare or endangered (Newsome et al. 2005); these features may enhance tourists' willingness to interact closely with them. Feeding the macaques appeared to be one of the principal tourist-macaque interactions at the study site (Chapter 4). Tourists seemed to have a number of motivations - not mutually exclusive - for feeding Barbary macaques, and these could be classified into three main groups: the reward from sharing food, the creation of a relationship, and taking control over the animal (Chapter 3). These findings can be related to the different motivations of wildlife tourism participants described by Kellert (1989), Reynolds and Braithwaite (2001), and Newsome et al. (2005). According to these authors, individuals may associate animals with different values and thus view wildlife differently – holding, for example, naturalistic, moralistic, dominionistic, aesthetic, or humanistic views (Reynolds and Braithwaite 2001, Newsome et al. 2005); these views in turn were suggested to shape tourists' motivations to interact with wild animals. Based on these provisioning interactions with Barbary macaques, I suggested that a particular tourist experience may be shaped, taking away the notions of wilderness and the independence of wildlife, and replacing them with a sense of control over the encounters with wild animals. Similar reflections were suggested regarding Japanese macaque tourism (Knight 2011), and more broadly in wildlife tourism (Newsome et al. 2005). Finally, as stated by Curtin (2009), tourist feeding may lead to some degree of disappointment about the wildlife experience, as it can take away the authenticity and uniqueness thought to be sought by wildlife tourists.

From the animals' standpoint, tourist encounters and interactions may be perceived as stressful (Maréchal et al. 2011), and it was suggested that animals might respond in various ways to tourists, with responses ranging from avoidance, to habituation, to attraction (Whittaker and Knight 1998). In the context of tourist provisioning, I suggested that behavioural mechanisms might be used to cope with potentially conflicting motivational situations associated with the risks of interacting with tourists and the attraction of potential food. The present study (Chapter 4) provides evidence that animals use a range of behavioural coping mechanisms to cope with different aspects of exposure to tourists, such as adjusting their spatial positioning or using displacement behaviours, and that their use of such mechanisms may depend on a trade-off between perceived risks and benefits. Previous studies have found, for example, that animals avoid tourists by moving higher into the trees (e.g. howler monkeys: Treves and Brandon 2005, marmosets: de la Torres et al. 2000), or simply by avoiding some locations frequented by humans (e.g. brown bears: Martin et al. 2010; forest-dwelling caribou: Leblond et al. 2013). Other studies have found that animals express significantly more displacement behaviour in the presence of tourists (e.g. royal penguins: Holmes et al. 2005; mountain gorillas: Muyambi 2005), or when in close proximity to such people (e.g. male Barbary macaques: Maréchal et al. 2011; Tibetan macaques: Berman et al. 2014).

In the present study, a range of coping mechanisms was explored which enabled the development of a framework for exploring the balance of these factors (Chapter 4), and better understanding of how animals respond to such conflicting motivational situations. For example, using this framework might facilitate comparison of the impacts of different kinds of tourism disturbance on animals' behavioural responses, and the differences in behavioural responses between species experiencing similar tourism pressure. A wealth of studies have attempted to investigate how tourism affects wildlife, but because research often focuses on one or a few different behavioural responses (e.g. aggression in Tibetan macaques: McCarthy et al. 2009, Berman et al. 2014; self-scratching in male Barbary macaques: Maréchal et al. 2011), often in different tourist behaviours and contexts, there is limited potential for comparison of findings between studies. The framework developed in this thesis may therefore provide a comprehensive method to better understand the impacts of human disturbance on wildlife more broadly.

This study also highlighted the importance of taking into consideration the social context in which animals interact with tourists (Chapter 4). Results indicated that social context might help animals to cope with stress associated with tourists by providing support or stress buffering, but also the findings suggested that the presence of conspecifics might itself be stressful. Therefore, evidence was found that animals make a trade-off between the risks and the benefits of interacting with tourists, whilst also balancing the risks and benefits of having a conspecific present in close proximity. To date, social context has rarely been taken into account when investigating the impacts of tourists on animals' behavioural responses; however, it may greatly influence the way coping mechanisms are used to deal with tourist-related stress.

Tourists may also have a range of impacts on the health of wild animals in terms of elevated risks of injuries, mortality or disease transmission, elevated stress levels or consequences of poor nutrition (Russon and Wallis 2014); notably, the results in this thesis suggest that tourist provisioning may significantly affect all these aspects of animals' health. While the results of Chapter 5 generally indicate that tourist provisioning has a potential negative impact on the health of wild Barbary macaques (e.g. physiological stress levels, occurrence of alopecia, body size), a number of health measures did not appear to be affected by provisioning, suggesting that the relationship between provisioning and health is complex, and may be influenced by a number of individual and environmental factors. The results also highlighted the key issue of not knowing what is optimum - or even good - health, making the interpretation of the findings difficult.

Several individuals disappeared or died in the Tourist Group during the study period, whereas none disappeared or died in the Green Group. Animals experiencing high tourist presence and numbers, close to an easily accessible road that they frequently cross, may face greater and more frequent risks than non-habituated individuals, as suggested by Macfie and Williamson (2010); this may explain the higher mortality rate in the Tourist Group compared to the Green Group. However, the possibility cannot be excluded that the daily presence of local fossil sellers and horse riders at the site may actually help reduce potential poaching or injuries from tourists, which could therefore have been higher if local people were absent. Assessing the roles and effects of the local community with respect to risks for the animals visited will help contribute to the understanding of their potential effectiveness in mediating the negative impacts of tourists on Barbary macaques.

Disease transmission between people and animals is a serious concern when humans interact with wildlife, particularly during provisioning when physical contact between people and animals is often observed (Fuentes 2006b). The present study provides further evidence of the validity of such concerns in the context of primate tourism, especially as tourists at the study site do not appear to be aware of this potential issue, displaying a number of high-risk behaviours such as sharing food with the macaques. These issues raise fears both for human and non-human primate health, and therefore have implications both for wildlife conservation (Lonsdorf et al. 2006, Fuentes 2006b, Muehlenbein and Wallis 2014), and for human health (Becker and Hall 2014). Although there was a higher number of individuals with disease symptoms in the Tourist Group than in the Green Group, it was not possible to determine whether such diseases were actually transmitted from tourists or whether they had an effect on animals' long term survival. Indeed, to date, no study has been able to confirm disease transmission between tourists and wild animals (Muehlenbein and Wallis 2014). Therefore, in order to better assess the likelihood of disease outbreaks and potentially better understand the real risks of disease transmission by tourists, standardised and regular assessments of disease symptoms, injuries and behaviours should be conducted for both wild animals and tourists, as suggested by Lonsdorf et al. (2006), Leendertz et al. (2006) and Muehlenbein et al. (2010).

Stress might have negative impacts on the fitness of animals, through decreases in survival and reproduction (Romero and Wikelski 2001, Pride 2005). Measuring stress is an important part of assessing the welfare of animals, and this may be achieved non-invasively, for example by quantifying alopecia (Honess et al. 2005) or assessing physiological stress levels from faecal samples (Heistermann 2010). The present study provides further evidence that tourist provisioning is stressful for the animals involved, with provisioned animals found to have higher physiological stress levels than non-provisioned ones. Also, for males, provisioned individuals had more alopecia than non-provisioned animals, and in the Tourist Group the level of provisioning of individuals was positively related to physiological stress levels. Since physiological stress levels have been found to be negatively related to body condition (Romero and Wikelski 2001, Cabezas et al. 2007), and to the chances of survival (Romero and Wikelski 2001, Pride 2005), the evidence presented here suggests that tourist provisioning may have a negative impact on the welfare and fitness of Barbary macaques. It may be that higher physiological stress levels are due to an increase in the intensity of intraspecific competition due to the clumped nature of food resources received from tourists (Majolo et al. 2013, Berman et al. 2014), or because of the potential agonistic interactions with tourists (Maréchal et al. 2011). Regulating provisioning may therefore help to reduce such stress. For example, intraspecific competition may be reduced by spreading food resources and prohibiting the giving of food by hand (such provisioning was often observed at the site), and these changes have been implemented in a number of primate tourism settings, such as with Tibetan macaques (Usui et al. 2014), and Japanese macaques (Knight 2011). Nevertheless, the present results must be interpreted with caution as the optimum is not known for physiological stress levels; a long term study would be needed to confirm whether such higher levels of FGC have negative impacts on survival and reproduction.

Provisioning may have important effects on the energy balance of an animal, by increasing energy intake and decreasing energy expenditure (Kemnitz et al. 2002), which may affect general health. In the present study, tourist provisioning seemed to have no negative effects on the nutritional status of female Barbary macaques, with a significantly better coat quality in provisioned females compared to those that were non-provisioned. Provisioned females also had larger body size than non-provisioned females, but it was not possible to determine if this difference had a positive or negative impact on their health. For males, there was no significant difference in coat quality and only a trend for a difference in body size between provisioned and non-provisioned animals. For neither sex was there a difference in C-peptide levels, a measure of enegy balance, between animals receiving and not receiving provisioning.

The interpretation of such results is again hampered by the lack of understanding of what represents an optimal range for this species for measures such as body size or C-peptide levels; without this, it is not possible to determine if the values seen in the current study - and differences linked to provisioning - may lead to costs in terms of fitness or survival. In addition, despite the number of studies that provide evidence that urinary C-peptide levels may provide a reliable indicator of primates' nutritional health (Sherry and Ellison 2007, Deschner et al. 2008, Emery Thompson et al. 2009, Girard-Buttoz et al. 2011), no study has explored the relationships between UCP levels and survival rates in wild animals.

Overall, the results presented in Chapter 5 provide evidence that tourist provisioning may affect the health of Barbary macaques; however these impacts might affect differently the various aspects of health. These findings therefore highlighted the importance of taking into consideration a range of health measures, which encompass the different aspects of health described in this thesis. In addition, this study highlighted the difficulty of interpreting such results because of the lack of understanding of what is optimum health and how to measure it. Long term surveys using a range of health measures would help to assess such optima, by enabling the determination of the relationships between health and survival and reproduction, which ultimately would be invaluable for informing conservation of endangered species.

6.2 Implications for wildlife tourism and conservation

Feeding interactions were found to be the one of the principal tourist-macaque interactions at the site (Chapter 4), and seemed to influence the tourist experience, animals' behavioural responses and their physical health. Since feeding monkeys seems to be an important part of the tourist activity at this and many other sites (Orams 2002, Newsome et al. 2005), it is crucial to explore whether such interactions are compatible with conservation actions. This requires consideration of whether provisioning has the potential to be beneficial to all parties involved in wildlife tourism. Dubois and Fraser (2013) created a wildlife feeding acceptability framework based on three factors: the ability to control the activity, the effects of provisioning on conservation goals, and the effects on the long-term welfare of the animals. According to this framework, feeding primates for tourism purposes should generally not be acceptable, and therefore be prohibited, because of the poor control over such activity, and the potential negative impacts on the welfare of animals as well as the low benefits for conservation (Dubois and Fraser 2013). As reviewed recently by Russon and Wallis (2014) and Newsome and Rodger (2013), it is true that feeding primates might generally present more negative impacts than positive ones for all three criteria cited by Dubois and Fraser (2013), although the negative impacts on the welfare of the animals involved and for conservation are still poorly understood. However, feeding wildlife, and in particular primates, still occurs in many locations where it is tolerated or where prohibition has failed (e.g. Gibraltar: Perez and Bensusan 2005, Morocco: Maréchal et al. 2011, Majolo et al. 2013, Bali: Fuentes 2010), and the desire to feed wildlife has created an important demand for such tourism, which therefore might provide important economic benefits for the local population.

When attempting to propose solutions to facilitate sustainable wildlife tourism that could benefit all parties, it is important to point out that there is a difference in the currencies of the different costs and benefits associated with wildlife tourism. For instance, how can we assess what is more important between financial or animal welfare benefits, when economy and welfare are measured in two different currencies? It is therefore very difficult to integrate within the same framework the different values and currencies of the different parties involved in wildlife tourism.

As stated by Russon and Wallis (2014) in their book “Primate Tourism: A Tool for Conservation?”, primate tourism - and wildlife tourism more broadly - often presents different strengths and weaknesses that should be carefully assessed and balanced to determine the potential benefits for conservation. Different examples of wildlife tourism clearly show that although such activity has potential as a conservation tool, it has often not proven to be without negative impacts on both wildlife and the local community (Newsome et al. 2005, Russon and Wallis 2014). In this context, the costs and benefits of a particular tourist interaction with wildlife, such as provisioning, need to be carefully assessed in order to evaluate if feeding wildlife may be acceptable.

In addition, it is important to take into consideration the difference in time scale for outcomes of the different costs and benefits of such activity, which may have an impact on management decisions. For example, a long term study on mountain gorilla tourism suggested that benefits for the conservation for mountain gorilla population may have changed over time, and may now be outweighed by the risks for their welfare (Goldsmith 2014). The impacts of tourist provisioning on the health of Barbary macaques (Chapter 5) also suggested that such effects may only be seen fully in the long term, suggesting that long term surveys should be implemented and also that management decisions should be re-evaluated regularly.

Finally, another important point to consider is management in the long term, as it may need to go through phases of progressive change, and sudden major changes may not be a satisfactory strategy because they can have unexpected associated costs. For example, provisioning of Japanese macaques, which quickly became a popular tourist attraction, was also thought to be the solution to eliminate crop raiding by these monkeys, thus solving the conflicts with local communities (Knight 2011). However, provisioning induced an increase in the population size of Japanese macaques, which had negative impacts on their natural habitats by increasing its degradation, as well as increasing conflicts with local people because of crop raiding (Kurita 2014). In 1972, provisioning was severely restricted at Takasakiyama Park, reducing macaques' reproduction and therefore numbers, but also increasing in some locations the occurrence of crop raiding (Kurita 2014). Kurita (2014) suggested therefore that provisioning must be carefully managed and regulated in order to control the population size, but when macaques have been habituated to receive food a sudden cessation of provisioning should not be recommended, rather a progressive reduction of provisioning is needed. The example of Japanese macaques may hold lessons that are also relevant for other macaque species, including Barbary macaques.

Overall, the different issues raised above are important to take into consideration before any management decisions are made regarding wildlife tourism, and in particular tourist provisioning. I propose that wildlife feeding may be assessed, and ultimately improved, by using a concept I call optimal provisioning. This aims to take into consideration the different costs and benefits of provisioning wildlife, and to facilitate the assessment of the most beneficial feeding situation. This does not exclude the prohibition of wildlife feeding if the risks exceed the benefits.

What is the concept of optimal provisioning?

Optimal provisioning is a concept that allows the visualisation of the relationships between provisioning and the benefit:cost ratios for each party involved in wildlife tourism (e.g. animals, tourists, local communities, local and national business, conservationists, government). Different levels of provisioning will potentially have a different benefit:cost ratio for different parties; optimal provisioning is a pragmatic approach that allows assessment of the impacts of provisioning on the different actors in the face of such differences. The key logic underpinning this concept is that the shape and nature of the relationship between costs/benefits and provisioning differ for each party. This is demonstrated in the schematics of

Figure 6-1, in which I develop two examples applying this concept. In order to keep the description simple, I describe the concept using only two parties, wild animals and tourists. The vertical axis represents benefits gained for either animals or tourists (or costs incurred, where values are below 0), and the horizontal axis represents intensity of provisioning. The curves in the most of figure 6-1 indicate the relationships between provisioning and potential benefits or costs to the different parties involved. In these examples, the curve for the animals is based on an assessment of health measures such as nutritional health, whereas the tourist curve is based on tourist experience, assessed for example via a satisfaction survey and qualitative ethnography.

The schematic in Figure 6-1a is based on a scenario of animals living in a degraded habitat, where natural food availability is low. In this case, the benefits for the animals would initially increase when levels of provisioning increase and optimal benefits of provisioning reached at point B (Figure 6-1a). However, if levels of provisioning increase after reaching this point, the benefits would decrease until the levels of provisioning become detrimental to (costly for) the animals.

For tourists, tourist satisfaction would increase as the levels of authorised provisioning increase because of their strong motivations to feed wildlife (Orams 2002, Newsome et al. 2005, Chapter 3). Therefore the tourist curve will be positively related to levels of provisioning until it reaches a point of optimal benefits at point C, after which benefits decline; if provisioning is too intensive, there becomes a point where it is actually detrimental to the tourist experience (Chapter 3) and thus benefits decline and ultimately turn into costs.

In the scenario of Figure 6.1a, the points of optimal benefits for both animals and tourists are not reached at the same levels of provisioning. However, there is a range of provisioning that may be beneficial for both parties (range A), suggesting that the intensity of provisioning may be considered acceptable within this range and still be of benefit to both parties. However, the ideal situation may be to reach a level of provisioning that optimises the overall benefits for both parties in combination (point D, Figure 6-1a).

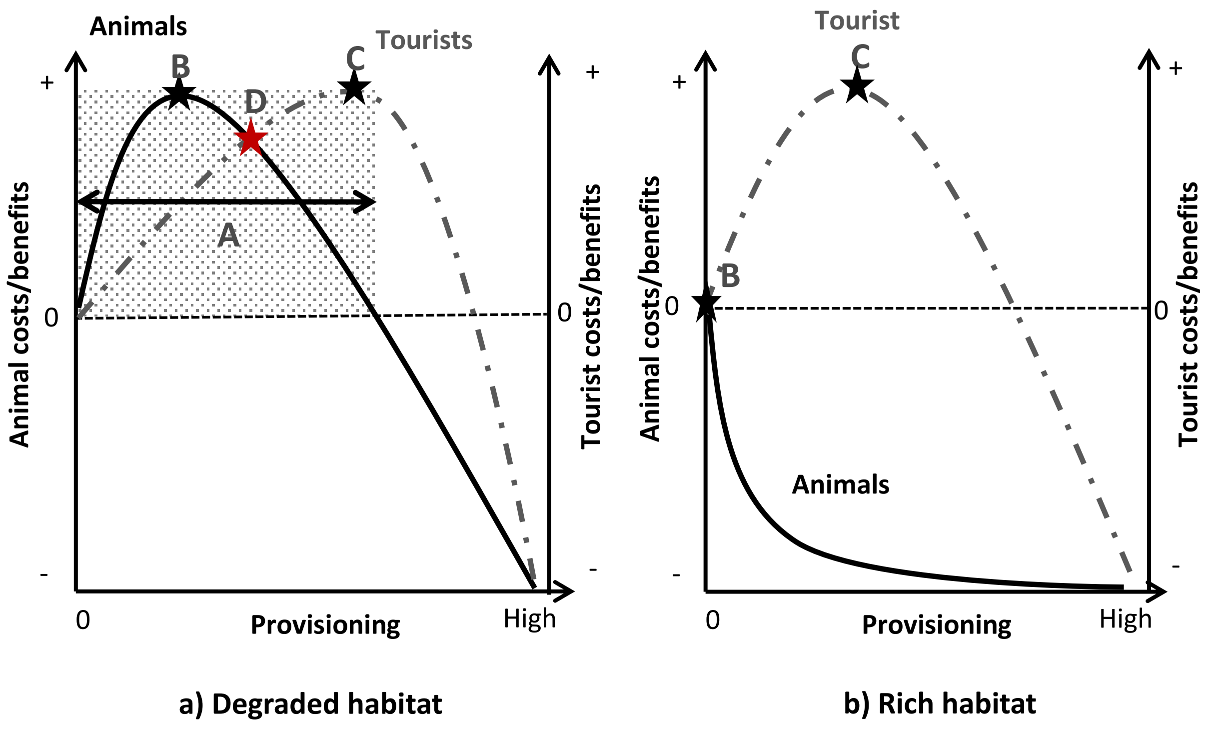
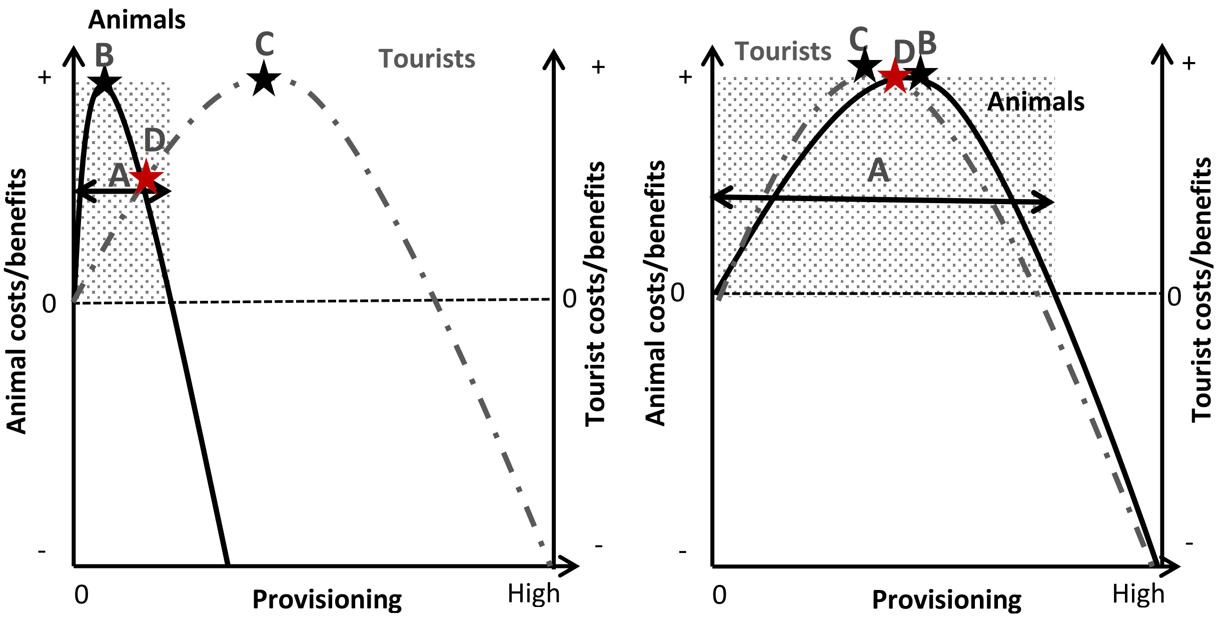


Figure 6-1: Schematic of the logic underpinning the optimal provisioning concept for a species living (a) in a degraded habitat or (b) in a rich habitat. The costs and benefits of provisioning are relative to the non-provisioning situation. **A:** represents the range within which provisioning may be beneficial for all parties. **B:** represents the optimal provisioning for animals. **C:** represents the point of optimal provisioning for tourists. **D:** represents the point of provisioning which would provide the optimal overall possible benefits for both parties combined.

In the second scenario (Figure 6-1b), animals live in a rich habitat, where natural food availability is high, and any provisioning has a negative effect on the health of the animals, and therefore the curve lies below the 0 line, with costs becoming higher when levels of provisioning increase. The tourist curve would have a similar pattern that in Figure 6-1a; however the tourist curve would reach its optimal at lower levels of provisioning compared to Figure 6-1a, and would be followed by a decline in benefits because increasing levels of provisioning would have negative impacts on the health of animals, and therefore may decrease tourist interest in feeding wildlife. In this scenario, there is no level of provisioning that may be beneficial for both parties. Therefore, those involved in tourist management would have to decide which party to prioritise.

Figure 6.2 extends the logic of this approach to look at different types (as well as levels) of provisioning; specifically, this figure compares benefit:cost ratios between clumped (Figure 6.2a) and widely spread (Figure 6.2b) provisioning.



a) Clumped **b) Spread**

Figure 6-2: Schematic of the logic underpinning the optimal provisioning concept for different distribution of provisioning - clumped (a) and spread (b). The costs and benefits of provisioning are relative to the non-provisioning situation. **A:** represents the range within which provisioning may be beneficial for all parties. **B:** represent the optimal provisioning for animals. **C:** represents the point of optimal provisioning for tourists. **D:** represent the point of provisioning which would provide the optimal overall benefits for both parties combined.

In the scenario Figure 6-2a, there is an initial increase in benefits to the animals when levels of provisioning increase, which is rapidly followed by the point of optimal benefits for animals (point B). After this point, when levels of provisioning increase, the benefits for the animals decrease, due to the elevated levels of aggression and competition known to result from large amounts or highly clumped food in macaques for example (Hill 1999, Majolo et al. 2013), so further provisioning becomes costly for the animals. The tourist curve in figure 6-2a follows the same pattern as in Figure 6-1a. Tourist experience satisfaction would increase because tourists would be able to see a number of monkeys feeding at the same location, giving them the experience of viewing the ‘whole group’ and seeing interactions between animals (Knight 2011). However, after this optimal benefit point, tourist satisfaction may decrease due to elevated levels of aggression between conspecifics, as well as potential redirection of aggression towards tourists themselves (Wheatley and Putra 1994, Matheson et al. 2006). In this scenario, the range within which levels of provisioning may be beneficial for both parties is narrow, and the point of optimal benefits for tourists is outside this range, suggesting that if the levels of provisioning are managed by taking into account only the tourist standpoint, this would be costly for the health of the animals involved.

In scenario Figure 6-2b with food spread widely, the curves for both the animals and the tourists follow a similar pattern, increasing when levels of provisioning increase, reaching optimal benefits and becoming costly for both parties at similar levels of provisioning. In a situation where provisioned food is widely spread, animals would benefit from a supplement to natural food availability, which is easily accessible and predictable, and which also should not increase levels of intraspecific aggression as is the case for clumped food resources. However, when the intensity of provisioning is too high, such provisioning may have negative impacts on health, and therefore become costly for the animals. The tourist experience may benefit from wide spread provisioning because it ensures the presence of animals at specific locations, making the encounter more predictable (Knight 2011). However, such provisioning would not allow tourists to get close to the animals, reducing their chance to create an intimate relationship with the animals and loosing a sense of control over the animals, which may decrease overall tourist satisfaction (Chapter 3). In this scenario, there is a large range of provisioning intensity that may be beneficial for both parties, and optimal benefits for both animals and tourists may be reached at a similar level of provisioning. Hence, those involved in management decisions should aim for a level of provisioning that benefits both parties (point D).

Overall, the two schematics help to visualise the different impacts of provisioning in different tourist settings according to the habitat or the different types of provisioning distribution, and have the potential to facilitate management decisions about whether provisioning – or what level/type of provisioning – may be acceptable. This concept also highlights the fact that although in some conditions certain levels of provisioning might be beneficial for all parties, in certain scenarios it may be impossible to manage provisioning to benefit all. In the latter situation, those involved in tourism management must take a decision about which party they are aiming to prioritise, and how to mitigate the potential costs for the other party. The optimal provisioning concept may help to assess and visualise the impacts of such decisions. In addition, this schematic suggests that even if different currencies are applied for different parties and the effects are not measured on the same scale, since both parties vary on the same x axis, it is still possible to visualise the interconnection between them. However, the main challenge highlighted by the concept is the need for appropriate data related to different levels of provisioning, in order to determine the shapes and positioning of curves.

Assessing the different costs and benefits for the different parties

In order to use the optimal provisioning concept, the different costs and benefits must be assessed for all parties. Using the findings of this thesis as well as those from other studies, I assess and discuss the potential different benefits and costs of provisioning for the two parties I consider in the schematics above, i.e. macaques and tourists, at the tourist site in Morocco. I then discuss how the different values and currencies associated with this tourism might be brought together to create the schematic on which the concept of optimal provisioning is based. Finally, I discuss the different challenges, limitations and other considerations for applying the concept.

Macaques

The following costs and benefits of provisioning for the welfare of Barbary macaques are based on the findings of chapter 5. The results showed that, overall, provisioning may be costly for the health of animals. However, provisioning may affect differently different measures of health and for some measures a certain level of provisioning may be beneficial. For example, the welfare of Barbary macaques was assessed in terms of nutritional health and stress in the present thesis, and therefore in order to produce a line representing overall macaque welfare, both health measures, i.e. currencies, should be taken into consideration. How this maybe done is shown in figure 6-3.

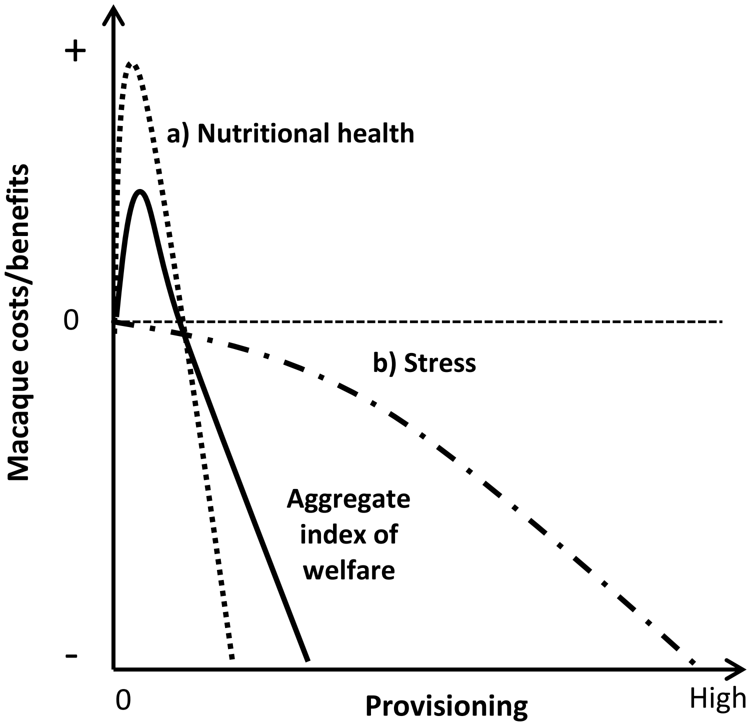


Figure 6-3: Schematic of the logic underpinning the optimal provisioning concept for assessing the welfare of Barbary macaques at the tourist site in Morocco. The dashed curves represent the different cost:benefit ratios for each health measure – nutritional health and stress – and the solid line represents the overall aggregated cost:benefit ratio.

Provisioning may be beneficial for the nutritional health of Barbary macaques (curve a, Figure 6-3) when natural food availability is limited, which was suggested for both groups especially in summer. However, after reaching the optimum benefits of provisioning for health, for example if natural food availability is enough to meet fully nutritional requirements, increasing provisioning could have a down side, potentially leading to negative impacts for the health of the Barbary macaques, and therefore costs for their welfare. Therefore, assessing natural food availability and the nutritional requirement of these animals in different seasons may help inform potential management decisions about provisioning. In addition, the present results suggested that tourist provisioning may also have negative impacts on stress (curve b, Figure 6-3), and therefore provisioning may not be beneficial but costly for the animals.

Tourists

Provisioning at the site represents 50% of the interactions between tourists and macaques (Chapter 4), and may greatly affect the tourist experience (Chapter 3). Provisioning appeared to be perceived positively by tourists, as an act of generosity towards the animals but also in order to establish a connection with them. At the same time, tourists find provisioning entertaining, allowing them to gain some control over a wild animal. Despite the risks associated with provisioning, tourists seemed to have a strong desire to feed monkeys, and therefore there is an increase in benefits for the tourist experience when certain levels of provisioning are allowed. However, if provisioning is too prevalent this may lead to a different experience of wildlife than expected, changing the perception of these wild animals to being more like zoo animals (Knight 2010), such that the 'wild experience' is diminished, and provisioning becomes costly for the tourist experience. For example, when provisioning reaches the point of negatively affecting the health of animals, some physical features such as obesity or alopecia may appear, potentially reducing the number of tourists interested in feeding monkeys or their experiential benefit from doing so.

Overall, the schematic considering both macaques and tourists could represented as shown in Figure 6.4.

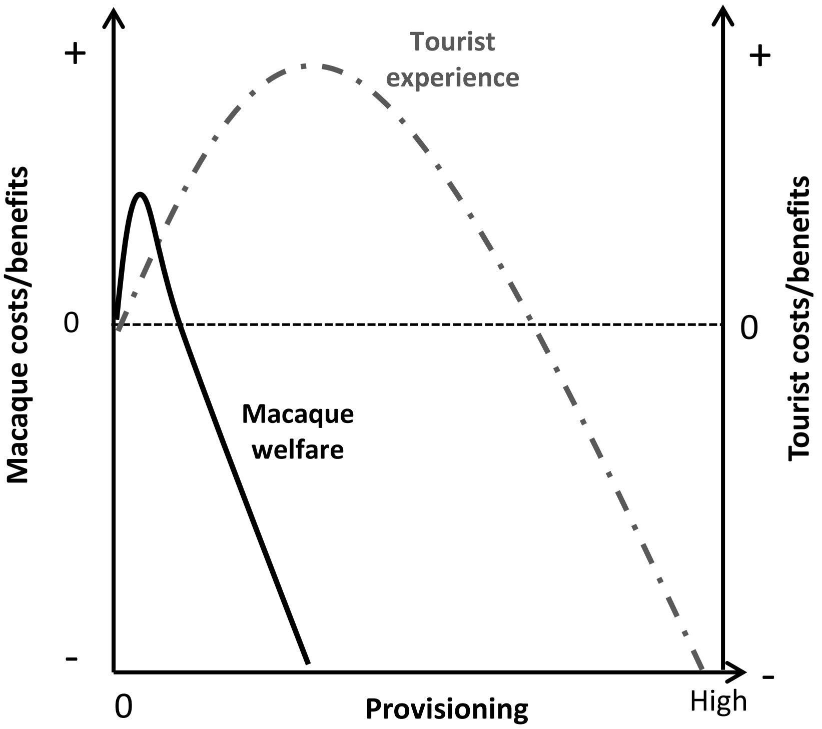


Figure 6-4: Schematic and simple representation of the logic underpinning the optimal provisioning concept for the tourist site in Morocco. The curves represent the different cost:benefit ratios for each party.

Challenges, limitations and other considerations for applying the concept

In this example, the benefits/costs for Barbary macaques may be assessed using different measures or currencies – e.g. nutritional health and stress. Therefore there are two main points to consider for bringing together such different currencies, and assessing the impacts of provisioning on the overall welfare of Barbary macaques. First, further research is needed to assess the range within which the fitness of an animal would be optimal. Long term surveys and comparisons between groups with different levels of provisioning may help to determine the relationships between provisioning and the different health measures. Secondly, research is needed to determine the relationships between the different health measures and fitness in order to evaluate the *relative* importance of each. For example, nutritional health and stress measures may not reflect similar impacts on animals' fitness, with impacts on nutritional health perhaps more costly in terms of animal fitness than those on stress. This information would help to draw more accurately the curve related to the different health measures.

Other factors that may influence the welfare and the conservation of Barbary macaques were not included in the present thesis, but are also important to take into consideration. For example, since tourists at the site are currently unregulated and may travel further inside the forest to encounter other wild Barbary macaque groups, control over tourist provisioning at the site and its impacts on other surrounding animals appear to be important factors to assess before making any management decision (Dubois and Fraser 2013). Suddenly prohibiting tourists from feeding macaques at the site is likely to shift these interactions onto other nearby macaque groups, consequently increasing the number of groups habituated to humans and therefore increasing the associated risks. Therefore, in order to create the schematic of the optimal provisioning concept, additional information is needed on other factors potentially affected by provisioning.

Although no eco-tourists were identified at the site during the study period (and hence no curve for such tourists is shown in Figure 6.3), this category of tourists may be interested to see wild Barbary macaques in their natural environment, and therefore be a potential component of primate tourism in Morocco. The curve for eco-tourists is likely to be different from the one related to other tourists, because they are likely to avoid feeding wildlife as such behaviour would change their experience from that of a pristine wildlife, untouched by humans (Russell 1995), to wildlife controlled by humans. In addition, provisioning wildlife would mean that tourists have an impact on the natural environment they came to visit, contradicting the basis of eco-tourism (Boo 1990). In this scenario, the curve would never pass above the zero line, leading to very different conclusions about the optimal level of provisioning.

Other party: Local community

For simplicity, and because it was not studied as part of the present thesis, the local community was not represented in the schematics of figures 6-3 and 6-4. However, tourist provisioning may directly or indirectly affect the local economy and have other impacts. The local economy can be affected through production of a market for the sale of monkey food to tourists or by ensuring the presence of monkeys at the tourist site (Chapter 3, Knight 2011). At the study site in Morocco, feeding monkeys mostly ensures their presence rather than providing a significant source of income to local people; there is in fact only one person daily selling peanuts to tourists (Chapter 3). In this context, increased tourist provisioning may be beneficial for the local economy as long as tourists have a strong desire to feed monkeys. In addition, tourist provisioning may influence the local perception of wild animals, either positively (Chapter 3) or negatively (Kurita 2014). Provisioned Barbary macaques seem to enjoy a more positive reputation than non-provisioned animals, being seen as cute and nice, with even their misbehaviour, such as stealing food from tourists, often perceived as amusing (Chapter 3). However, such positive perceptions may quickly reach a maximum, after which increasing provisioning may have negative impacts on the local population, increasing potential conflicts such as crop raiding (Kurita 2014). Therefore, it would be useful to assess the relationships between provisioning and local economy, welfare and perceptions, in order to incorporate the local community into the optimal provisioning schematic.

Overall, the optimal provisioning concept may be used for any wildlife tourism setting, as long as the different parties involved in this activity are identified, and the different currencies assessed. The concept may be a useful tool for facilitating tourism management, and visualising the impacts of management decisions on all parties. In addition, this concept may be used for different practices other than provisioning such as other types of interactions, or it could be applied to wildlife tourism activity more broadly.

6.3 An evaluation of the multidisciplinary approach to studying primate tourism

Wildlife tourism is based on the relationships between humans and wild animals, and both anthropocentric and ecocentric standpoints need to be considered for understanding such activity. In the present study, I attempted to use approaches from both social and biological anthropology to investigate primate tourism at a tourist site in Morocco, and in particular to understand the different standpoints of tourists and animals in this specific human-animal relationship. Below, I discuss the issues and challenges involved in adopting such an approach, and explore its importance for understanding wildlife tourism, conservation, and human-animal relationships more broadly.

Considering and bringing together different approaches to investigate a multidimensional topic such as wildlife tourism, where biological and social aspects are interconnected, is difficult. A number of authors working in the field of ethnoprimatology pointed out these issues, which include the difficulty of integrating two approaches with such different methodologies and standpoints (Riley 2006). In her paper, *Ethnoprimatology: toward reconciliation of both biological and cultural anthropology*, Riley (2006) assesses whether these two sub-fields of anthropology may be used together to help understand the multifaceted nature of human-animal relationships. She argues that these disciplines are based on similar goals, namely to understand human and non-human primate behaviour in their natural or cultural environment, and therefore this common basis might help to link the two (Riley 2006). In addition, MacClancy and Fuentes (2011) highlighted some common practices of fieldwork in both biological and social anthropology (e.g. long term studies, observation, participation), and the importance for primatologists to also understand and consider local people as part of their animals’ environment.

Although I would agree with these ideas, the difference in methodologies – the predominant use of quantitative methods in biological anthropology and qualitative methods in social anthropology - makes their integration challenging. Biological anthropology currently mostly aims for objectivity, reducing observer biases to facilitate comparisons with other animal species, including primates (Strier 2003). On the other hand, cultural or social anthropology relates to the differences in human behaviour in relation to individualist experience and perception to understand human societies and cultures, in which subjectivity is accounted for in the interpretation of the different views of the world experienced by people (Hendry 1999). In my opinion, both the difference in points of view (objectivity and subjectivity) and methodology (quantitative and qualitative) make the use of both approaches complex from the planning to the writing up of the study. For instance, in biological anthropology, the study is generally based on testing a hypothesis, while in social anthropology, the themes developed in the study often come as, or after, the material and information are gathered.

The day to day organisation of the fieldwork is also different. For example, in my study the data collection on macaques used standardised quantitative methods, and therefore was constrained to a daily routine; by contrast, the collection of useful ethnographic material was much more irregular. Although I used semi-structured interviews, most of my material was collected via informal conversations with tourists, which required reacting quickly to their answers or thoughts in order to ask appropriate questions for gathering the most useful information. Coming from a biological background, where a study is generally well structured and carefully prepared beforehand, I found the spontaneity and unstructured methods I needed to use for gathering the ethnographic material unsettling. Another issue I encountered with the ethnographic methods is the lack of certainty in the value of my material. It is very difficult to assess if people tell you what they really think or rather what they think you would like to hear. This was particularly so in the present study because tourists were very fleeting, and I could not spend much time with them to ask similar questions in different ways to assess more fully their thoughts and behaviour. Finally, writing differs markedly between the fields, in terms of style and setting, making it challenging to integrate both approaches and potentially reducing the depth of the results. In the present thesis, I attempted to overcome these issues by using a multidisciplinary rather than an interdisciplinary approach. Therefore each results chapter of this thesis is based on either biological or social methods; only in this discussion chapter do I bring together findings from both approaches to consider both human and animal standpoints simultaneously and in depth.

Conducting a multidisciplinary study on both humans and animals is extremely time consuming, and may be difficult to do for one person alone. In the present study, I led the data collection, which was also conducted by a team of research assistants. When I started the study, I envisioned that both social and biological data and material would be collected by each member of the team. While the biological data collection was easily divided between researchers in different repetitive tasks from 8 am to 5 pm daily (i.e. behaviour, faecal and urine collection), I quickly realised that collecting ethnographic material would need a different work organisation, more individualistic and more flexible. Therefore I generally spent half of my time collecting data on macaques and the rest with local fossil sellers, horse riders, tourists and local authorities, while the rest of the team was mostly collecting data on macaques.

Although I opportunistically collected some ethnographic material, understanding tourists' and local people's behaviours and perspectives regarding this touristic activity necessitated spending a lot of time 'hanging out' with people, disconnected from the animal standpoints. In fact, I realised that when I observed or interacted with tourists while I was collecting data on macaques, I had a negative perception of tourists. I perceived tourists as a nuisance, and certainly felt psychologically tired and upset to see tourists often interacting badly with monkeys. Involuntarily, I felt empathic for what monkeys experienced daily; to an extent, I projected my own perceptions of what monkeys may feel when interacting with tourists, which made it difficult to keep a neutral view about these tourists. After a few weeks spent working with animals, most of the researchers, myself included, expressed their dislike of tourists and their behaviour towards the macaques.

However, I noticed that when I spent my time only interacting with tourists and not collecting data on macaques at the same time, my views and perceptions of tourists were different, more positive, and I had a better understanding of their behaviour towards the animals. Often, tourists do not realise their behaviour may negatively affect the animals (Chapter 3). Therefore, using a multidisciplinary approach allowed me to have a better perception of the whole situation from different perspectives, taking into considering my own subjective perception of the different standpoints. By doing this, I believe that I was able to have a broader understanding of the relationships between the macaques and the tourists. Using a multidisciplinary approach may therefore be useful for deciding and implementing regulations and management based on a broader understanding of the different parties.

Considering both human and animal standpoints by using a multidisciplinary approach may help us to have a greater understanding of wildlife tourism and human-animal relationships, and may provide a powerful tool for conservation action (Fuentes and Hockings 2010). Until recently, conservation approaches were mainly (or only) interested in either human or animal standpoints, ignoring the full context in which both humans and animals are interconnected. Ethnoprimatology aims to consider both human and primate standpoints, in order to understand their relationships within a shared ecosystem (Sponsel 1997, Wheatley 1999, Fuentes and Wolfe 2002, Fuentes 2010). To do this, often a team of researchers from different disciplines (e.g. primatology, ecology, social anthropology) are brought together to investigate such complex interconnections (Fuentes 2010). As stated above, having experts in their own discipline may help to investigate a question in more depth, and therefore the overall research become more multidisciplinary. However, this also arguably necessitates having a principal investigator who is able to understand and bring together all these findings in a coherent manner. Hence, as in my present study, using a multidisciplinary approach and myself collecting both data on macaques and tourists, and ethnographic material, allowed me to consider the different standpoints from my own perspective and this helped me to have a greater understanding of the context. For example, using a multidisciplinary approach allowed the creation of the optimal provisioning concept, which has the potential to facilitate the development of a more sustainable wildlife tourism, which may provide benefits to both tourists and local community, while reducing or eliminating the costs for the welfare of animals involved, and ultimately be potentially beneficial for the conservation of endangered species.

6.4 General Conclusion

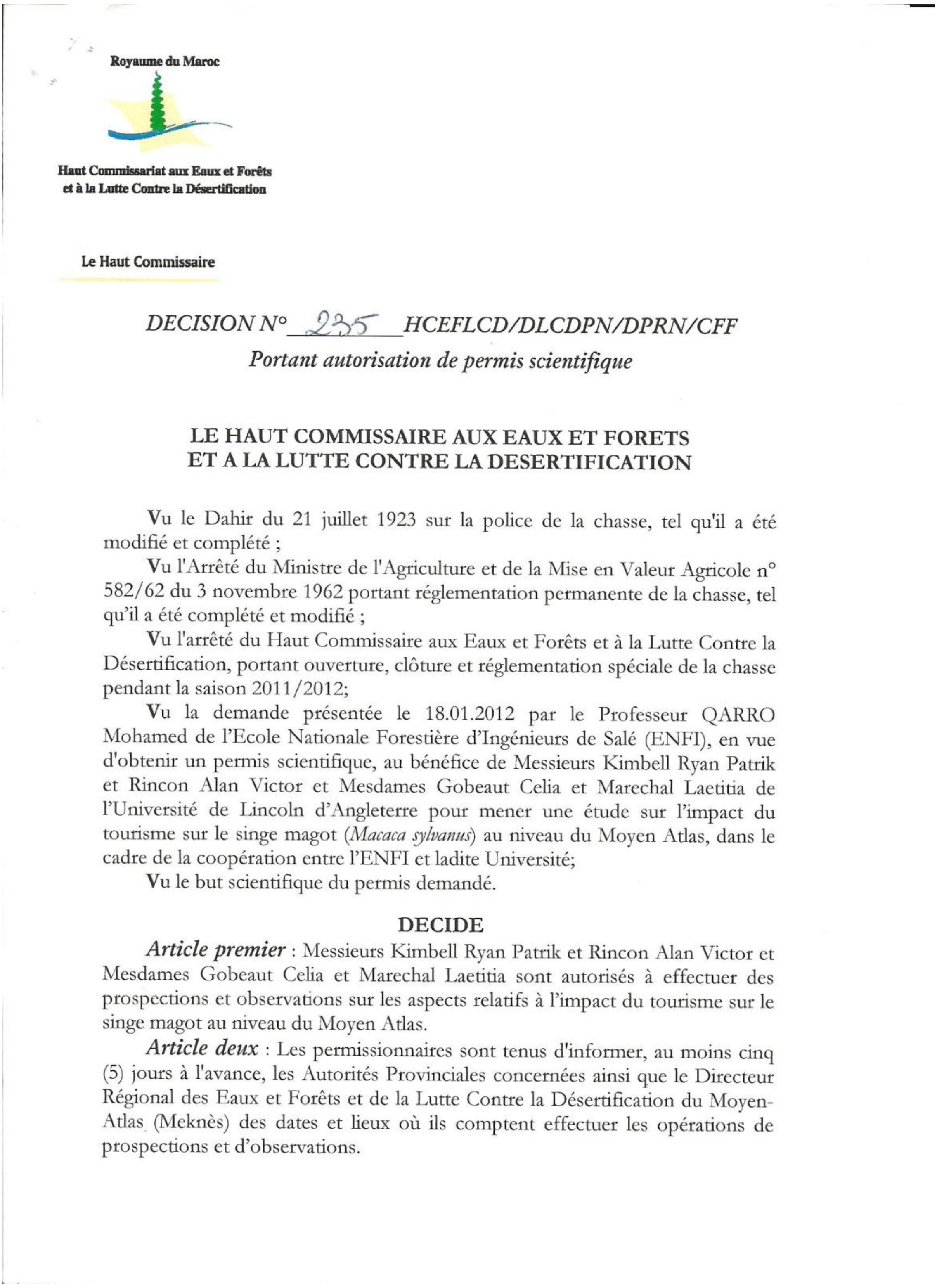
The present study has provided additional insights into wildlife tourism, and highlighted the importance of using a multidisciplinary approach to explore human-animal relationships in this context. Frameworks developed in this thesis, based on the findings at the site in Morocco - to explore coping strategies and to assess the impacts of provisioning - may be used more broadly across different wildlife tourism settings. These frameworks may aid better understanding of tourist-animal relationships, making comparisons possible between wildlife tourism settings; these comparisons have been to date limited, due to the difficulty of having only a basic understanding of the relationships between tourists and wild animals. Finally, the optimal provisioning concept may provide a useful tool for integration of the different standpoints of the parties involved in such activity, and ultimately may facilitate the development of more sustainable wildlife tourism, beneficial to both humans and animals.

Appendices

Appendix A1: Ethics approval: University of Roehampton

The research for this project was submitted for ethics consideration under the reference LSC 15/ 124 in the Department of Life Sciences and was approved under the procedures of the University of Roehampton's Ethics Committee on the 19.02.2015.

Appendix A2: Research permit provided by the Haut-commissariat aux eaux et forêts et à la lutte contre la désertification, Royaume du Maroc.



Royaume du Maroc

Haut Commissariat aux Eaux et Forêts
et à la Lutte Contre la Désertification

Le Haut Commissaire

DECISION N° 235 *HCEFLCD/DLCDPN/DPRN/CFF*
Portant autorisation de permis scientifique

LE HAUT COMMISSAIRE AUX EAUX ET FORETS
ET A LA LUTTE CONTRE LA DESERTIFICATION

Vu le Dahir du 21 juillet 1923 sur la police de la chasse, tel qu'il a été modifié et complété ;

Vu l'Arrêté du Ministre de l'Agriculture et de la Mise en Valeur Agricole n° 582/62 du 3 novembre 1962 portant réglementation permanente de la chasse, tel qu'il a été complété et modifié ;

Vu l'arrêté du Haut Commissaire aux Eaux et Forêts et à la Lutte Contre la Désertification, portant ouverture, clôture et réglementation spéciale de la chasse pendant la saison 2011/2012;

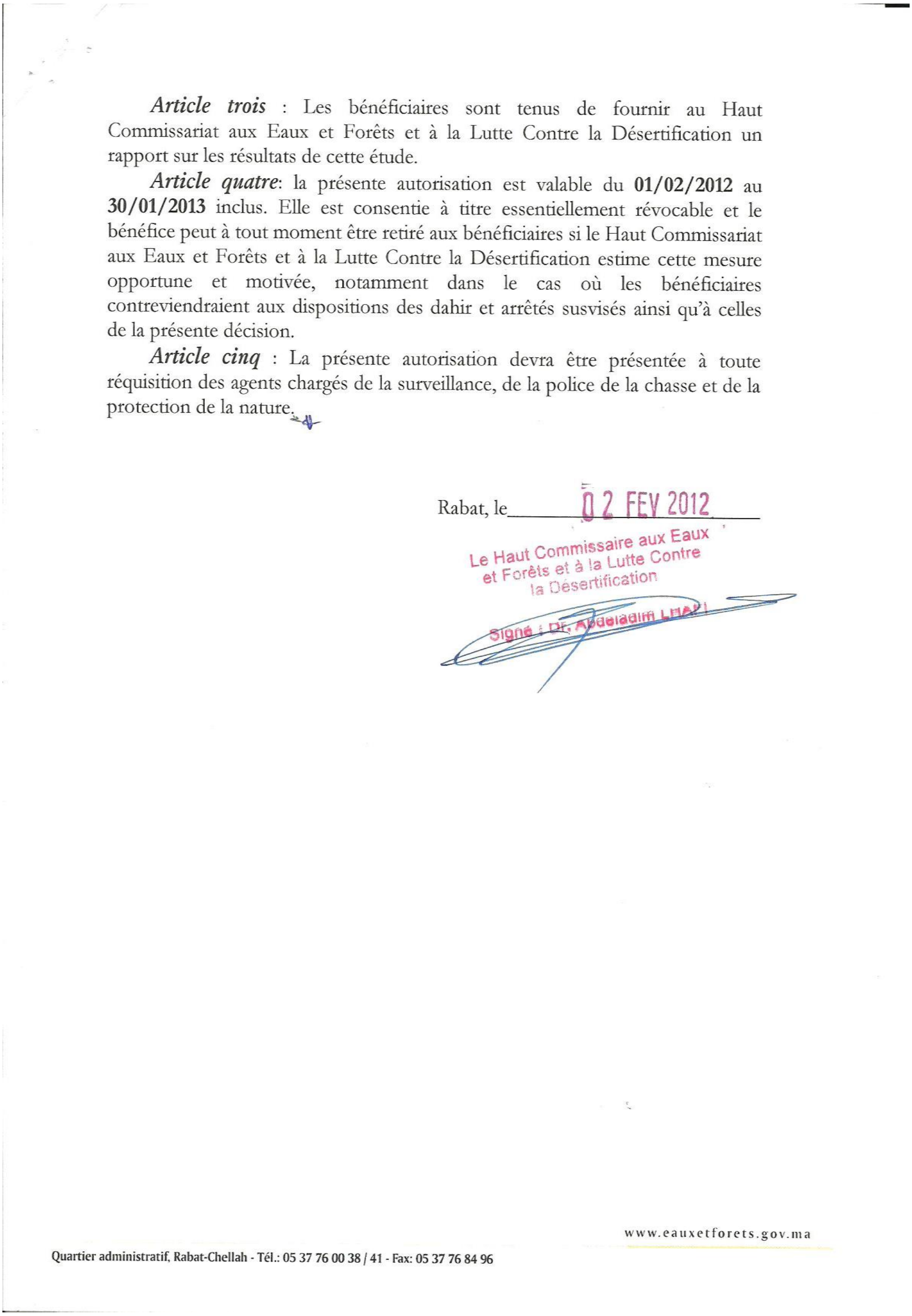
Vu la demande présentée le 18.01.2012 par le Professeur QARRO Mohamed de l'Ecole Nationale Forestière d'Ingénieurs de Salé (ENFI), en vue d'obtenir un permis scientifique, au bénéfice de Messieurs Kimbell Ryan Patrik et Rincon Alan Victor et Mesdames Gobeaut Celia et Marechal Laetitia de l'Université de Lincoln d'Angleterre pour mener une étude sur l'impact du tourisme sur le singe magot (*Macaca sylvanus*) au niveau du Moyen Atlas, dans le cadre de la coopération entre l'ENFI et ladite Université;

Vu le but scientifique du permis demandé.

DECIDE

Article premier : Messieurs Kimbell Ryan Patrik et Rincon Alan Victor et Mesdames Gobeaut Celia et Marechal Laetitia sont autorisés à effectuer des prospections et observations sur les aspects relatifs à l'impact du tourisme sur le singe magot au niveau du Moyen Atlas.

Article deux : Les permissionnaires sont tenus d'informer, au moins cinq (5) jours à l'avance, les Autorités Provinciales concernées ainsi que le Directeur Régional des Eaux et Forêts et de la Lutte Contre la Désertification du Moyen-Atlas (Meknès) des dates et lieux où ils comptent effectuer les opérations de prospections et d'observations.



Article trois : Les bénéficiaires sont tenus de fournir au Haut Commissariat aux Eaux et Forêts et à la Lutte Contre la Désertification un rapport sur les résultats de cette étude.

Article quatre: la présente autorisation est valable du **01/02/2012** au **30/01/2013** inclus. Elle est consentie à titre essentiellement révocable et le bénéfice peut à tout moment être retiré aux bénéficiaires si le Haut Commissariat aux Eaux et Forêts et à la Lutte Contre la Désertification estime cette mesure opportune et motivée, notamment dans le cas où les bénéficiaires contreviendraient aux dispositions des dahir et arrêtés susvisés ainsi qu'à celles de la présente décision.

Article cinq : La présente autorisation devra être présentée à toute réquisition des agents chargés de la surveillance, de la police de la chasse et de la protection de la nature.

Rabat, le 02 FEV 2012

Le Haut Commissaire aux Eaux
et Forêts et à la Lutte Contre
la Désertification

Signé : Dr. Abdeladim LHAFI

www.eauxetforets.gov.ma

Quartier administratif, Rabat-Chellah - Tél.: 05 37 76 00 38 / 41 - Fax: 05 37 76 84 96

Appendix A3a: Sample consent form in English

Roehampton University
London

ETHICS BOARD

PARTICIPANT CONSENT FORM PRO FORMA

Title of Research Project: "Primate tourism" as a tool for the conservation of Barbary macaques in Morocco: an interdisciplinary approach

Brief Description of Research Project:

The study aims to determine the relationships between humans and primates involved in primate tourism. This is to promote the conservation of the Barbary macaque facilitating the development of responsible tourism with low impact on animals while generating financial benefits for the local population.

Investigator Contact Details:

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Phone: + 44 (0) 208 392 3473
Fax: + 44 (0) 280 3923529
E-mail: marechal11@roehampton.ac.uk

Consent Statement:

I agree to take part in this research, and am aware that I am free to withdraw at any point. I understand that the information I provide will be treated in confidence by the investigator and that my identity will be protected in the publication of any findings.

Name ………………………………….

Signature ……………………………….

Date …………………………………….

Please note: if you have a concern about any aspect of your participation or any other queries please raise this with the investigator. However if you would like to contact an independent party please contact the Head of Department (or if the researcher is a student you can also contact the Director of Studies.)

Director of Studies Contact Details:

Dr. Stuart Semple

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Head of Department Contact Details:

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Appendix A3b: Sample consent form in French

Comité d'éthique
Formulaire de consentement du participant

Titre du projet de recherche :

Etude anthropologique interdisciplinaire sur le tourisme en relation avec les primates

Bref description du projet de recherche :

L'étude a pour objectif de déterminer les relations entre les hommes et les primates impliqués le tourisme des primates. Ceci dans le but de promouvoir la conservation du macaque de Barbarie en facilitant le développement d'un tourisme responsable ayant un faible impact sur les animaux tout en générant des bénéfices financiers pour la population locale.

Contact détails du chercheur:

Laetitia Marechal
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Déclaration de consentement :

Je consens à participer à cette recherche et je suis conscient que je suis libre de me rétracter à tout moment. Je suis au courant que les informations fournies seront traitées confidentiellement par le chercher et que mon identité sera protégée dans toutes publications des résultats.

Nom ………………………………….

Signature ………………………………

Date ……………………………………

Notez s'il vous plaît : si vous avez quelques concernes à propos de votre participation ou que vous avez des questions, n'hésitez pas à en informer le chercheur. Cependant, si vous souhaitez contactez une tierce personne, contactez le chef du département (ou si le chercheur est un étudiant, vous pouvez aussi contacter son superviseur).

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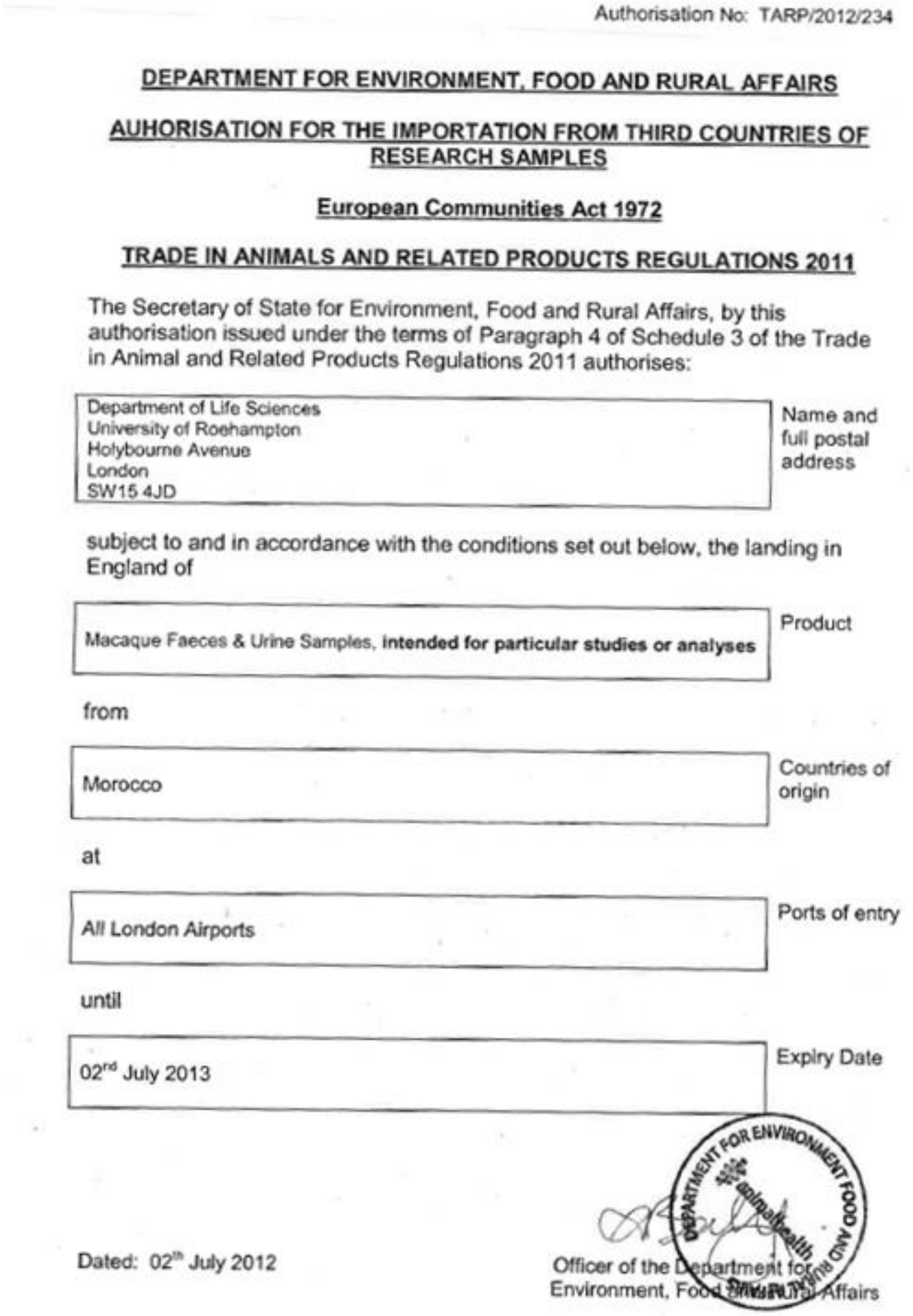
Appendix A4: DEFRA licence for the importation of biological samples



Authorisation No: TARP/2012/234

DEPARTMENT FOR ENVIRONMENT, FOOD AND RURAL AFFAIRS

AUHORISATION FOR THE IMPORTATION FROM THIRD COUNTRIES OF RESEARCH SAMPLES

European Communities Act 1972

TRADE IN ANIMALS AND RELATED PRODUCTS REGULATIONS 2011

The Secretary of State for Environment, Food and Rural Affairs, by this authorisation issued under the terms of Paragraph 4 of Schedule 3 of the Trade in Animal and Related Products Regulations 2011 authorises:

Department of Life Sciences University of Roehampton Holybourne Avenue London SW15 4JD	Name and full postal address

subject to and in accordance with the conditions set out below, the landing in England of

Macaque Faeces & Urine Samples, **intended for particular studies or analyses**	Product

from

Morocco	Countries of origin

at

All London Airports	Ports of entry

until

02rd July 2013	Expiry Date

Dated: 02th July 2012

Officer of the Department for Environment, Food and Rural Affairs

Appendix A5: Assay procedures described by Heistermann et al. (2004)

The enzyme immunoassay method was run over two days. The first day was dedicated to mixing together the reagents, namely the sample to be analysed, labelled antigen hormone, antibody and antigen. After incubation overnight, the results were revealed by colorant reaction. The protocol for the assay is described below:

All reagents that were to be used during the day were removed from the fridge/freezer in order to equilibrate them at room temperature.

Day 1:

1: Preparation of the standard curve solutions from 12500 pg/ 50 µl 'stock' diluted in 0.1% B.S.A/Buffer assay for a concentration range to 0.6 to 156 pg/50 µl.

2: Dispense 50 µl of each standard, controls and samples in appropriate wells. (100 µl of 0.1% B.S.A/Buffer assay in Blank well).

3: Preparation of biotin labelled steroid and steroid specific antibody by adding 0.1% B.S.A/Buffer assay to, respectively, 25 µl of Biotin labelled steroid and 30 µl of steroid specific antibody.

4: Dispense 50 µl of biotin labelled steroid in each well.

5: Dispense 50 µl of steroid specific antibody in each well (expected Blank).

6: Incubate the plate overnight at + 4°C.

Day 2:

1: Wash the plate 4 times.

2: Preparation of Streptavidin peroxidase (2500ng/25 µl) by adding 21 µl of streptavidin peroxidase to 17 ml of 0.1% B.S.A/Buffer assay.

3: Dispense Using 150 µl of prepared streptavidin in each well of the plate.

4: Shake for 30 min at room temperature.

5: Wash the plate 4 times.

6: Preparation of TMB solution by adding 295 µl TMB in 20 ml of Buffer substrate (x1).
7: Dispense 150 µl of tetramethylbenzidine (TMB) solution in each well.
8: Shake the plate at room temperature and in the dark until the zero well gave a blue colour equivalent to an optical density of approximately 1.0 (around 35 min), as a result of the reaction between the peroxidise and TMB.
9: Stop the reaction by dispensing 50 µl of 2M Sulphuric acid into each well.
10: Read the optical densities of each well using a plate photometer at a wavelength of 450nm, using the appropriate template in Ascent software, version 2.6.

Appendix A6: Urinary C-peptide assay preparation and procedure based on IBL international (C-Peptide ELISA; RE53011).

PREPARATION

Reagent Preparation

Standard: reconstitute the contents of the standard with 0.75 mL Aqua.

Wash Solution: 30 mL of concentrated wash solution with 1170 mL deionized water.

Sample preparation

Dilute samples in distilled water. Ranging from 1:1 to 1:100.

All reagents and specimens must be put at room temperature before use.

ASSAY PROCEDURE

1: Dispense 100 µl of each standard, controls and samples in appropriate wells.
(150 µl Standard A in Blank well).

2: Dispense 50 µl Antiserum into each well (NOT in Blank).

3: Dispense 100 µl Enzyme conjugate into each well. Mix for 10 seconds with multipipette.

4: Incubate for 60 min at room temperature.

5: WASH the PLATE (really sensitive step).

6: Add 100 µl of Enzyme complex to each well (TMB substrate).

7: Incubate for 30 min at room temperature.

8: WASH the PLATE (see above).

9: Add 100 µl of substrate solution to each well.

10: Incubate for 20 min at room temperature.

11: Stop the enzymatic reaction by adding 100 µl of stop solution to each well.

12: Read the absorbance of each well at 450 nm (within 10 min after adding the stop solution).

Appendix A7: UCP results which do not include samples below C-peptide assay sensitivity

Prediction 1vii: Animals in the Tourist Group have higher UCP levels than those in the Green Group.

Comparison of UCP levels between groups, data averaged over the 10 months of the study

There was no significant difference between groups in UCP levels for females (Independent t test: TG gave birth vs. GG: N=9 (3 TG/6 GG), U=7.000, P=0.606; TG did not give birth vs. GG: N=12 (6 TG/6 GG), U=14.000, P=0.522). However there was a significant difference between groups in Male UCP levels (Mann-Whitney test: N=13 (8 TG/5 GG), U=5.000, P=0.028, Figure A5-1).

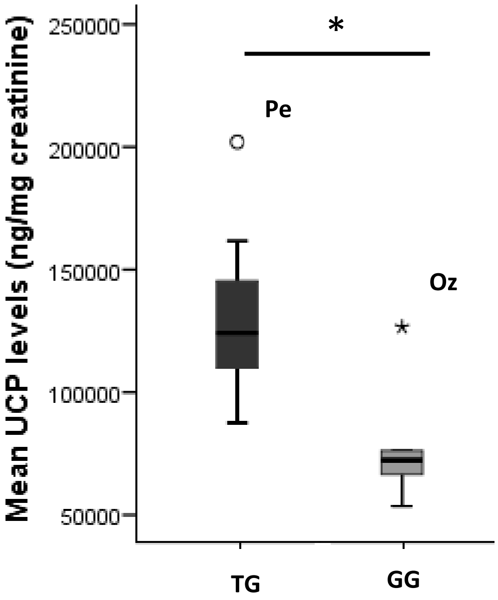


Figure A5-1: Box-plot showing the mean UCP levels over the 10 month period (from March until December 2012) in TG and GG for males. The outliers Pe and Oz are presumed to be the oldest males in each group.

Females

There was a significant difference in UCP levels only in March between TG females who gave birth and both GG and TG females who did not give birth, with GG females and TG females that did not give birth having lower UCP levels than TG females who gave birth (Table 5-12, Figure 5-16).Nevertheless these differences were not significant after correction for multiple testing.

Table A5-1: Monthly comparison of female UCP levels (ng/mg creatinine) between groups. t is associated with the independent t-test and U with Mann-Whitney test. Values in red were not significant after sequential Bonferroni corrections.

	March	April	May	June	July	August	September	October	November	December	
t/U	U=0.000	U=13.000	t=-0.326	t=-0.259	U=8.000	t=0.656	U=10.000	t=-1.648	t=-0.872	U=14.000	TG gave birth vs. GG
P value	**0.046**	0.715	0.752	0.802	0.394	0.536	0.602	0.13	0.409	0.522	
t/U	U=2.000	U=5.000	t=-0.543	t=0.411	U=5.000	t=1.734	U=4.000	t=-0.703	t=-1.527	U=4.000	TG did not give birth vs. GG
P value	0.564	0.456	0.607	0.695	0.724	0.158	0.699	0.505	0.187	0.197	
t/U	U=1.000	U=6.000	t=0.522	t=-0.654	U=6.000	t=-0.081	U=4.000	t=-1.074	t=0.305	U=5.000	TG gave birth vs. TG did not give birth
P value	**0.039**	0.439	0.618	0.534	0.439	0.938	0.699	0.318	0.769	0.302	

Males

There was a significant difference between groups in male UCP levels in March, May, and July when TG male UCP levels were significantly higher than GG males (Table 5-1), but neither was significant after sequential Bonferroni correction.

Table A5-2: Monthly comparison of male UCP levels (ng/mg creatinine) between groups. U with Mann-Whitney test. Values in red were not significant after sequential Bonferroni corrections.

	March	April	May	June	July	August	September	October	November	December
U	1	2	0	10	9	0	6	9	8	10
P value	**0.025**	**0.053**	**0.014**	0.143	0.107	**0.037**	0.089	0.234	0.394	0.223

Prediction 2iv: UCP levels are positively related to amount of provisioning.

Females

UCP levels of TG females were not significantly associated with percentage of provisioning (Table A5-).

Table A5-3: Results of GLMM testing the relationships between female UCP levels and provisioning in TG, and related GLMM run for female GG. x indicates that the variable was not included in the model.

	Model **TG** female UCP levels				Model **GG** female UCP levels			
Null vs.	N	df	χ2	P	N	df	χ2	P
full model	159	7	20.565	**0.004**	77	5	15.743	**0.008**
	Estimate	±SE	t	P	Estimate	±SE	t	P
Intercept	-14846.930	9893.260	-1.501	0.191	12042.429	3510.271	3.431	**0.007**
Gave birth vs. Did not give birth	7762.070	3911.520	1.984	0.138	x	x	x	x
Provisioning	50.500	36.340	1.390	0.169	x	x	x	x
Environment								
rainfall	1898.960	788.370	2.409	**0.023**	4.374	500.053	0.009	0.809
Social								
Rank	-2619.490	1781.290	-1.471	0.228	3506.380	1540.959	2.275	0.168
Season								
Birth vs Mating	-4380.780	5506.080	-0.796	0.431	9776.454	5173.799	1.890	**0.047**
Birth vs. PostBirth	9959.370	8400.050	1.186	0.257	-2453.059	4095.091	-0.599	0.572
Birth vs. PreBirth	22034.410	8427.810	2.614	**0.012**	6877.020	10039.971	0.685	0.592
Mating vs. PostBirth	14340.150	9056.900	1.583	0.119	-12229.513	5717.446	-2.139	**0.030**
Mating vs. PreBirth	26415.190	8907.770	2.965	**0.002**	-2899.434	11112.995	-0.261	0.636
PostBirth vs. PreBirth	12075.040	4364.340	2.767	**0.008**	9330.080	9823.722	0.950	0.445

Males

UCP levels of TG males were not significantly associated with provisioning (Table A5-).

Table A5-4: Results of GLMM testing the relationships between male UCP levels and provisioning in TG, and related GLMM run for male GG. x indicates that the variable was not included in the model.

	Model **TG** male UCP levels				Model **GG** male UCP levels			
Null vs.	N	df	χ2	P	N	df	χ2	P
full model	130	6	8.959	0.176	68	5	14.337	**0.014**
	Estimate	±SE	t	P	Estimate	±SE	t	P
Intercept	5068.526	1846.208	2.745	**0.009**	4021.100	1071.860	3.752	**0.005**
Provisioning	-6.289	7.842	-0.802	0.430	x	x	x	x
Environment								
rainfall	365.536	180.899	2.021	0.050	413.490	176.460	2.343	**0.043**
Social								
Rank	438.633	475.919	0.922	0.409	-378.890	447.900	-0.846	0.557
Season								
Birth vs Mating	-2699.992	1548.358	-1.744	0.086	-1181.850	1934.870	-0.611	0.635
Birth vs. PostBirth	464.528	1728.769	0.269	0.794	-75.120	1227.600	-0.061	0.881
Birth vs. PreBirth	-513.589	1771.918	-0.290	0.780	45.430	2313.620	0.020	0.927
Mating vs. PostBirth	3164.519	2161.121	1.464	0.155	1106.700	2054.100	0.539	0.716
Mating vs. PreBirth	2186.402	2104.140	1.039	0.310	1227.300	2903.400	0.423	0.686
PostBirth vs. PreBirth	-978.117	1003.697	-0.975	0.346	120.560	2184.530	0.055	0.857

Appendix A8: Creatinine assay preparation and procedure.

PREPARATION

Standard curve preparation (range 0.078 – 10 ng/50 µl)

Label tubes for standard curve

Standard: Add 400 µl of water to 100 µl aliquot of standard (C=10 ng/50 µl)

Standard curve dilution

Take 250 µl of the standard and dilute with 250 µl water (C= 5 ng/50 µl).

Repeat the procedure until the lowest curve concentration of 0.078 ng/50µl.

Sample preparation

Dilute samples with distilled water.

ASSAY PROCEDURE

1: Dispense 150 µl of distilled water in the Blank (duplicates).

2: Dispense 50 µl of the standard curve in duplicates (lowest concentrations to highest concentrations)

3: Dispense 50 µl of QCs in duplicates.

4: Dispense 50 µl of each sample in the appropriate wells in duplicates.

5: Prepare Jaffe reagent:

4.58g of picric acid in 500ml distilled water in order to obtain 0.04 M picric acid.

15g of NaOH in 500 ml distilled water to obtain 0.75 M NaOH.

Then mix 5.5 ml of 0.04 M picric acid with 5.5 ml of 0.75 M NaOH (directly before use)

6: Dispense 100 µl of Jaffe solution in each well except the blank.

7: Incubate for 15 min on the shaker at room temperature.

8: Read the absorbance of each well at 490 nm (reference 630 nm).

Appendix A9: Correlations between the different predictor variables used in GLMM analyses, Chapter 4.

Table A9-1: Correlations between the different predictors used in GLMM analyses for macaques' elevated positioning, Chapter 4.

		Number of tourists in the nearest tourist group	Distance from the nearest tourist group	Noise	Season	Rank	
Number of tourists in the area	r_s	0.287	-0.304	0.564	0.045	0.018	Females
	P value	<0.001	<0.001	<0.001	<0.001	0.061	
Number of tourists in the nearest tourist group	r_s		-0.437	0.198	0.056	-0.021	
	P value		<0.001	<0.001	<0.001	0.030	
Distance from the nearest tourist group	r_s			-0.176	-0.063	0.043	
	P value			<0.001	<0.001	<0.001	
Noise	r_s				0.024	0.026	
	P value				0.017	0.009	
Season	r_s					0.075	
	P value					<0.001	
Number of tourists in the area	r_s	0.268	-0.300	0.547	0.036	-0.015	Males
	P value	<0.001	<0.001	<0.001	0.001	0.155	
Number of tourists in the nearest tourist group	r_s		-0.386	0.189	-0.015	-0.023	
	P value		<0.001	<0.001	0.151	0.027	
Distance from the nearest tourist group	r_s			-0.193	-0.029	0.026	
	P value			<0.001	0.006	0.012	
Noise	r_s				0.008	-0.021	
	P value				0.441	0.049	
Season	r_s					-0.024	
	P value					0.020	

Table A9-2: Correlations between the different predictors used in GLMM analyses for the presence of macaques in proximity of tree cover, Chapter 4.

		Number of tourists in the nearest tourist group	Distance from the nearest tourist group	Noise	Season	Rank	
Number of tourists in the area	r_s	0.295	-0.377	0.546	0.056	0.024	Females
	P value	<0.001	<0.001	<0.001	<0.001	0.045	
Number of tourists in the nearest tourist group	r_s		-0.390	0.204	0.026	0.001	
	P value		<0.001	<0.001	0.032	0.910	
Distance from the nearest tourist group	r_s			0.132	0.026	0.029	
	P value			<0.001	0.035	0.018	
Noise	r_s				-0.030	-0.066	
	P value				0.014	<0.001	
Season	r_s					0.018	
	P value					0.130	
Number of tourists in the area	r_s	0.258	-0.359	0.542	0.047	-0.006	Males
	P value	<0.001	<0.001	<0.001	<0.001	0.612	
Number of tourists in the nearest tourist group	r_s		-0.367	0.184	0.019	-0.012	
	P value		<0.001	<0.001	0.127	0.342	
Distance from the nearest tourist group	r_s			-0.216	-0.034	0.083	
	P value			<0.001	0.007	<0.001	
Noise	r_s				0.009	-0.096	
	P value				0.467	<0.001	
Season	r_s					-0.059	
	P value					<0.001	

Table A9-3: Correlations between the different predictors used in GLMM analyses for the distance between macaques and tourists on the ground, Chapter 4.

		Number of tourists in the nearest tourist group	Noise	Season	Rank	
Number of tourists in the area	r_s	0.155	0.531	0.035	0.031	Females
	P value	<0.001	<0.001	0.007	0.019	
Number of tourists in the nearest tourist group	r_s		0.131	0.030	0.030	
	P value		<0.001	0.025	0.023	
Noise	r_s			0.028	0.027	
	P value			0.035	0.040	
Season	r_s				0.082	
	P value				<0.001	
Number of tourists in the area	r_s	0.145	0.528	0.034	-0.009	Males
	P value	<0.001	<0.001	0.014	0.498	
Number of tourists in the nearest tourist group	r_s		0.125	-0.032	-0.010	
	P value		<0.001	0.019	0.466	
Noise	r_s			0.017	-0.027	
	P value			0.222	0.047	
Season	r_s				-0.060	
	P value				<0.001	

Table A9-4: Correlations between the different predictors used in GLMM analyses for the presence of a socially bonded partner, Chapter 4. In grey, predictor variable removed from analysis because it was highly correlated with one or more factors.

		Number of tourists in the nearest tourist group	Distance from the nearest tourist group	Noise	Season	Rank	
Number of tourists in the area	r_s	0.581	-0.235	**0.823**	0.112	0.029	Females
	P value	<0.001	<0.001	**<0.001**	<0.001	0.045	
Number of tourists in the nearest tourist group	r_s		-0.316	0.579	0.106	-0.003	
	P value		<0.001	<0.001	<0.001	0.773	
Distance from the nearest tourist group	r_s			-0.227	-0.180	0.002	
	P value			<0.001	<0.001	0.857	
Noise	r_s				0.106	0.023	
	P value				<0.001	0.043	
Season	r_s					0.014	
	P value					0.202	
Number of tourists in the area	r_s	0.600	-0.244	**0.830**	0.099	0.015	Males
	P value	<0.001	<0.001	**<0.001**	<0.001	0.231	
Number of tourists in the nearest tourist group	r_s		-0.312	**0.628**	0.110	0.012	
	P value		<0.001	**<0.001**	<0.001	0.306	
Distance from the nearest tourist group	r_s			-0.232	-0.201	-0.017	
	P value			<0.001	<0.001	0.153	
Noise	r_s				0.095	0.022	
	P value				<0.001	0.078	
Season	r_s					0.001	
	P value					0.915	

Table A9-5: Correlations between the different predictors used in GLMM analyses for displacement behaviours, Chapter 4. In grey, predictor variable removed from analysis because it was highly correlated with one or more factors.

		Number of tourists in the nearest tourist group	Distance from the nearest tourist group	Noise	Season	Rank	
Number of tourists in the area	r_s	0.335	-0.276	**0.683**	0.081	0.021	Females
	P value	<0.001	<0.001	**<0.001**	0.005	0.461	
Number of tourists in the nearest tourist group	r_s		-0.333	0.220	0.018	-0.009	
	P value		<0.001	<0.001	0.544	0.768	
Distance from the nearest tourist group	r_s			-0.166	-0.104	0.043	
	P value			<0.001	<0.001	0.141	
Noise	r_s				0.035	-0.001	
	P value				0.231	0.976	
Season	r_s					0.019	
	P value					0.515	
Number of tourists in the area	r_s	0.364	-0.264	**0.675**	0.006	0.037	Males
	P value	<0.001	<0.001	**<0.001**	0.851	0.245	
Number of tourists in the nearest tourist group	r_s		-0.346	0.243	-0.053	-0.020	
	P value		<0.001	<0.001	0.094	0.523	
Distance from the nearest tourist group	r_s			-0.158	-0.050	0.045	
	P value			<0.001	0.116	0.156	
Noise	r_s				-0.021	0.044	
	P value				0.520	0.164	
Season	r_s					-0.008	
	P value					0.810	

Appendix A10: Summary of the significant results of the relationships between tourist presence measures and female Barbary macaques' behavioural responses.

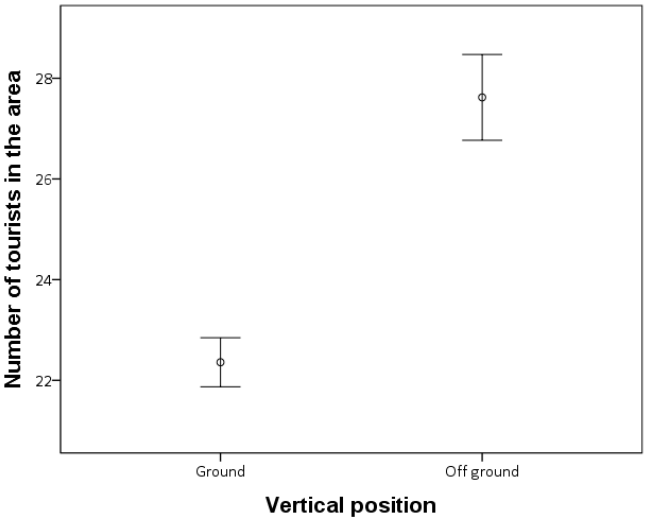


Figure A10-1: Bar graph for the number of tourists present in the area (mean and 95% confidence intervals) when females were on the ground or off the ground for the overall study period. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-5, page 150.

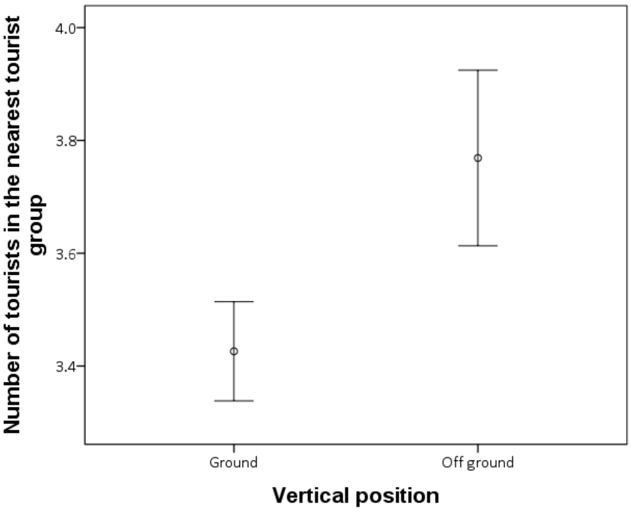


Figure A10-2: Bar graph for the number of tourists present in the nearest tourist group (mean and 95% confidence intervals) when females were on the ground or off the ground for the overall study period. The raw data used to construct this plot are not controlled for other variables, unlike in do the statistical models presented in Tabl 4-5, page 150.

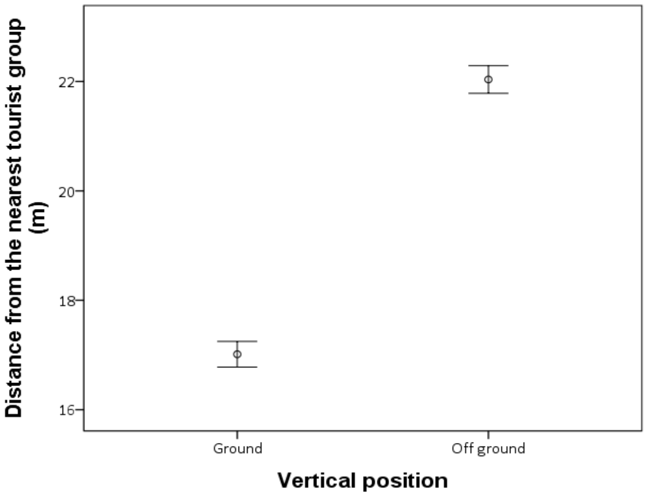


Figure A10-3: Bar graph for the distance from the nearest tourist group (mean and 95% confidence intervals) when females were on the ground or off the ground for the overall study period. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-5,page 150.

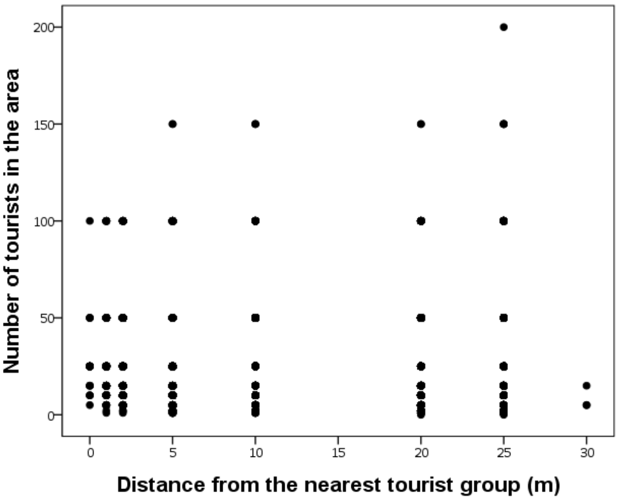


Figure A10-4: Scatterplots representing the relationships between number of tourists in the area and the distance from the nearest tourist group for the overall study period. Each dot represents one individual's datum for a day. Some data points may overlap. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-9, page 157.

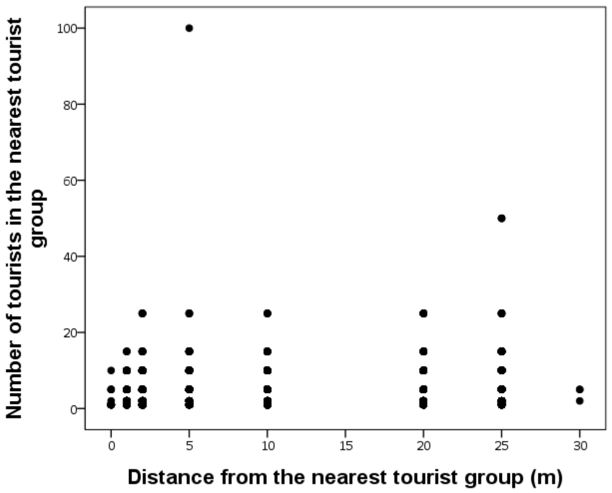


Figure A10-5: Scatterplots representing the relationships between number of tourists in the area and the distance from the nearest tourist group for the overall study period. Each dot represents one individual's datum for a day. Some data points may overlap. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-9, page 157.

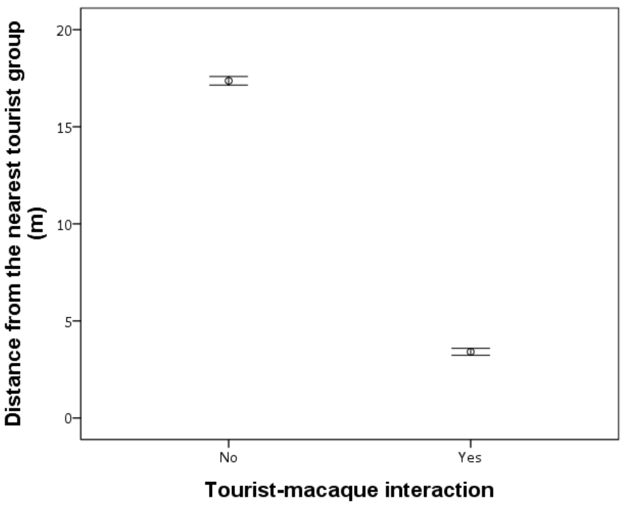


Figure A10-6: Bar graph for the distance from the nearest tourist group (mean and 95% confidence intervals) when females were interacting with tourists or not for the overall study period. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-9, page 157.

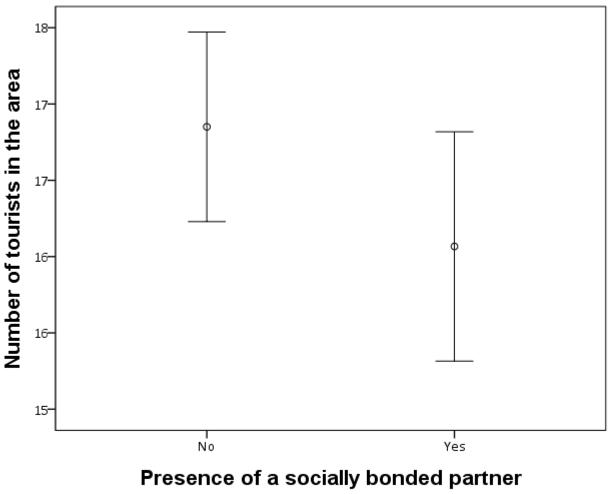


Figure A10-7: Bar graph for the number of tourists in the area (mean and 95% confidence intervals) when a socially bonded partner was present in close proximity to females for the overall study period. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-11, page 160.

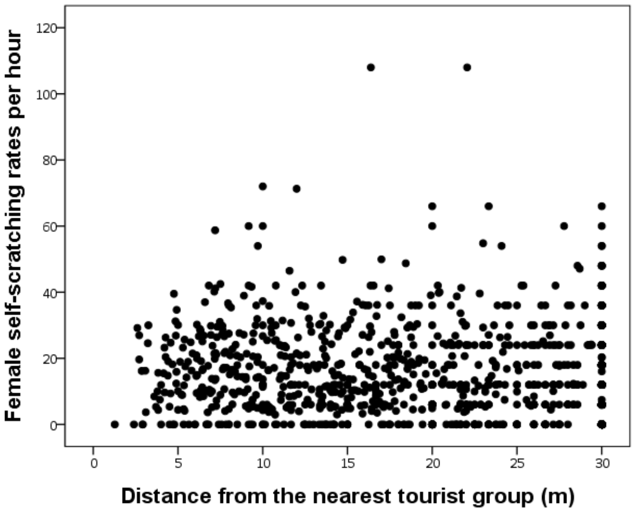


Figure A10-8: Scatterplots representing the relationships between females' self-scratching rates per hour and the distance from the nearest tourist group for the overall study period. Each dot represents one individual's datum for a day. Some data points may overlap. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-13, page 163.

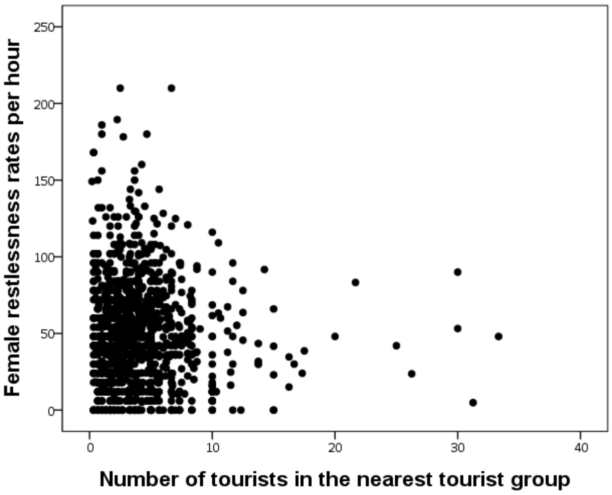


Figure A10-9: Scatterplots representing the relationships between females' restlessness rates per hour and the number of tourists in the nearest tourist group for the overall study period. Each dot represents one individual's datum for a day. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-15, page 166.

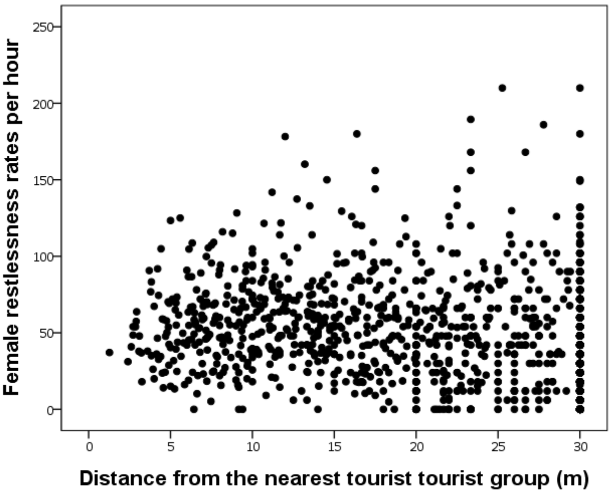


Figure A10-10: Scatterplots representing the relationships between females' restlessness rates per hour and the distance from the nearest tourist group for the overall study period. Each dot represents one individual's datum for a day. Some data points may overlap. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-15, page 166.

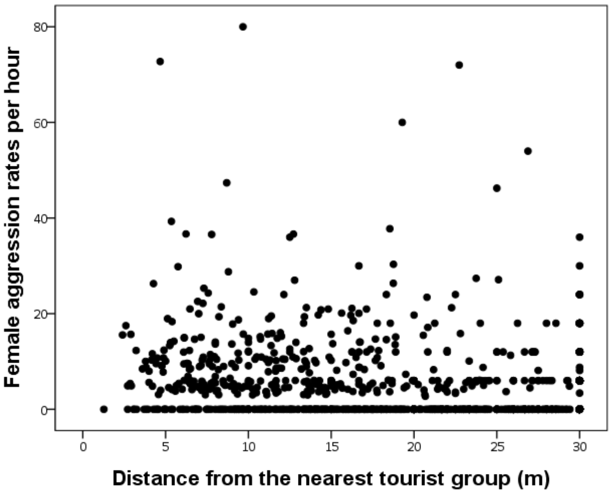


Figure A10-11: Scatterplots representing the relationships between females' aggression rates per hour and the distance from the nearest tourist group for the overall study period. Each dot represents one individual's datum for a day. Some data points may overlap. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-17, page 169.

Appendix A11: Summary of the significant results of the relationships between tourist presence measures and male Barbary macaques' behavioural responses.

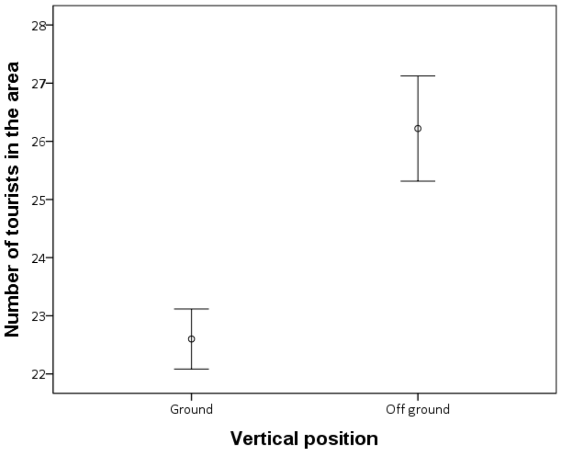


Figure A11-1: Bar graph for the number of tourists present in the area (mean and 95% confidence intervals) when males were on the ground or off the ground for the overall study period. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-5, page 150.

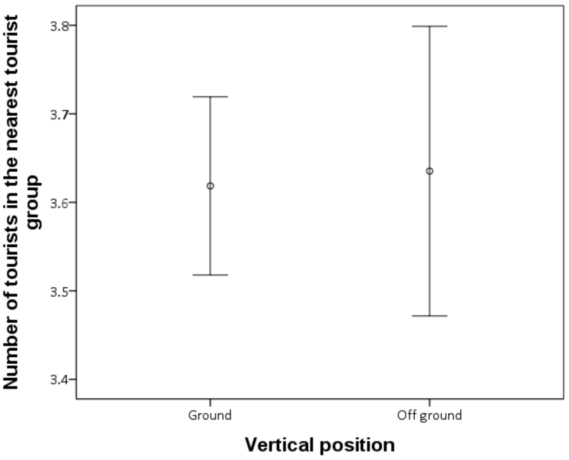


Figure A11-2: Bar graph for the number of tourists present in the nearest tourist group (mean and 95% confidence intervals) when males were on the ground or off the ground for the overall study period. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-5, page 150.

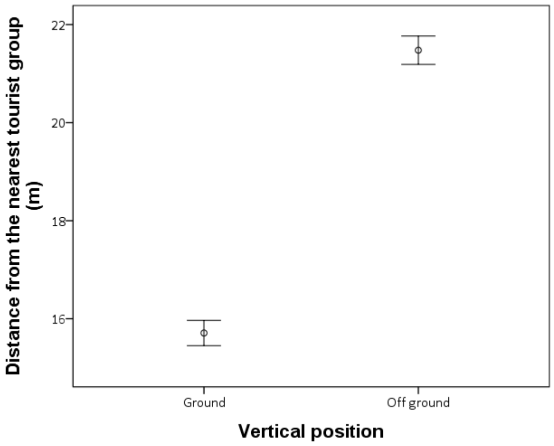


Figure A11-3: Bar graph for the distance from the nearest tourist group (mean and 95% confidence intervals) when males were on the ground or off the ground for the overall study period. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-5, page 150.

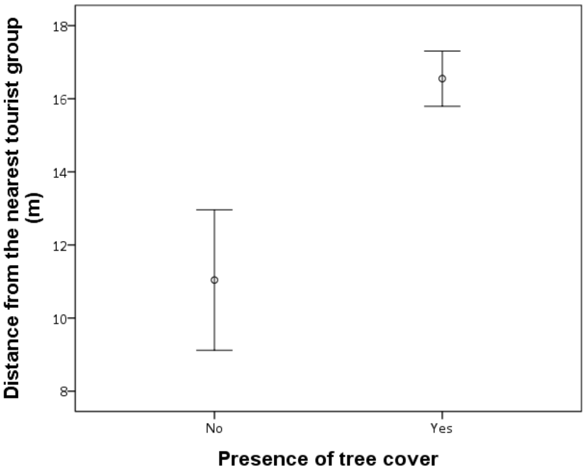


Figure A11-4: Bar graph for the distance from the nearest tourist group (mean and 95% confidence intervals) when males were under tree cover or not for the overall study period. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-7, page 154.

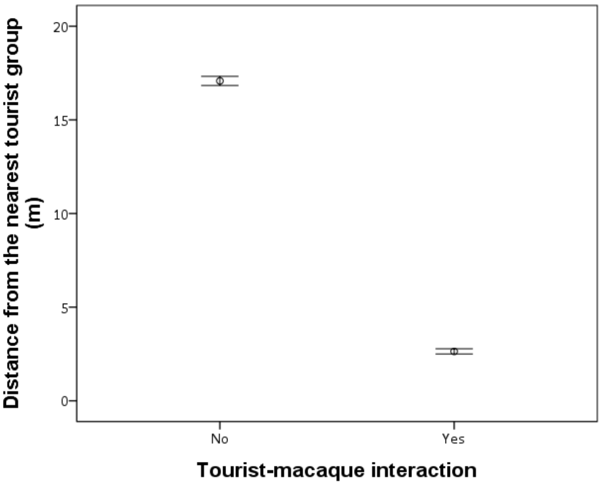


Figure A11-5: Bar graph for the distance from the nearest tourist group (mean and 95% confidence intervals) when males were interacting with tourists or not for the overall study period. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-9, page 157.

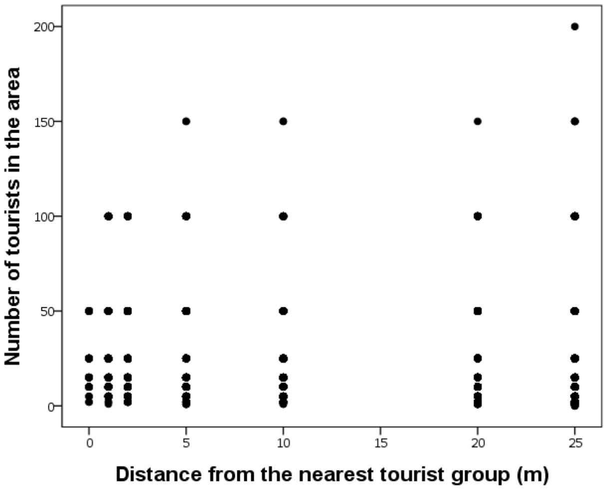


Figure A11-6: Scatterplots representing the relationships between number of tourists in the area and the distance from the nearest tourist group for the overall study period. Each dot represents one individual's datum for a day. Some data points may overlap. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-9, page 157.

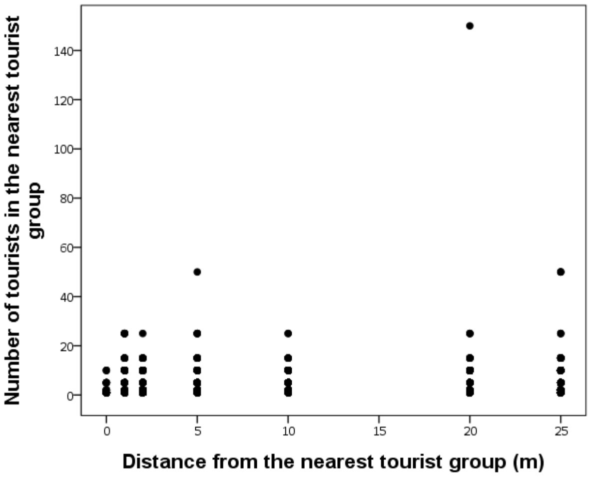


Figure A11-7: Scatterplots representing the relationships between number of tourists in the nearest tourist group and the distance from the nearest tourist group for the overall study period. Each dot represents one individual's datum for a day. Some data points may overlap. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-9, page 157.

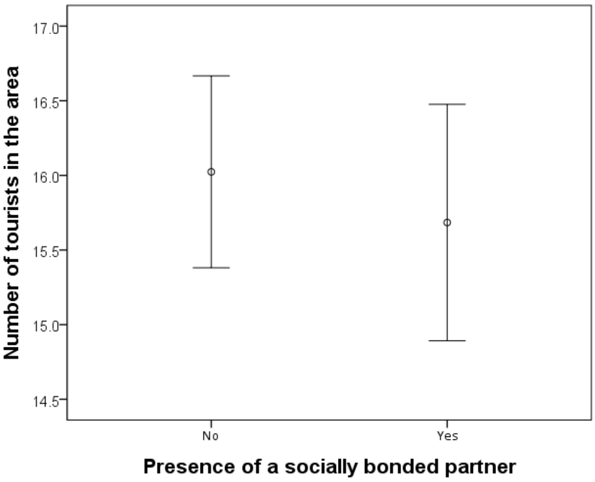


Figure A11-8: Bar graph for the number of tourists in the area (mean and 95% confidence intervals) when a socially bonded partner was present in close proximity to males for the overall study period. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-11, page 160.

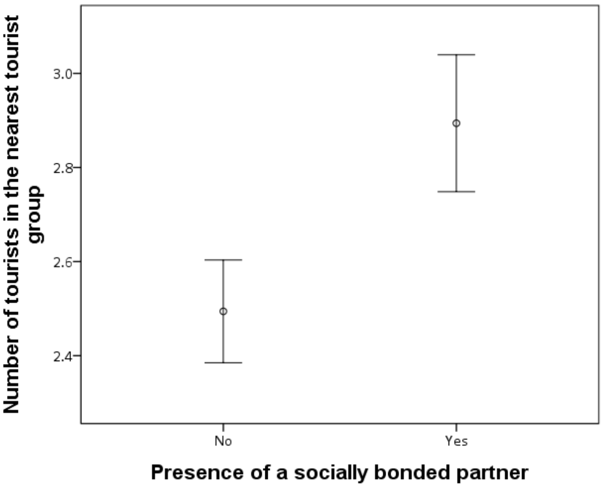


Figure A11-9: Bar graph for the number of tourists in the nearest tourist group (mean and 95% confidence intervals) when a socially bonded partner was present in close proximity to males for the overall study period. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-11, page 160.

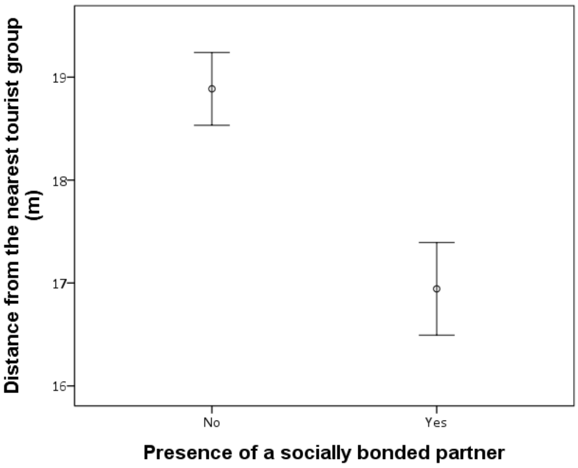


Figure A11-10: Bar graph for the distance from the nearest tourist group (mean and 95% confidence intervals) when a socially bonded partner was present in close proximity to males for the overall study period. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-11, page 160.

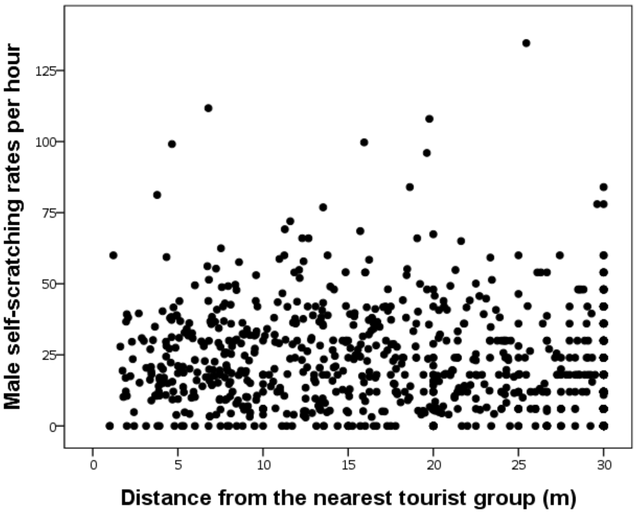


Figure A11-11: Scatterplots representing the relationships between males' self-scratching rates per hour and the distance from the nearest tourist group for the overall study period. Each dot represents one individual's datum for a day. Some data points may overlap. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-13, page 163.

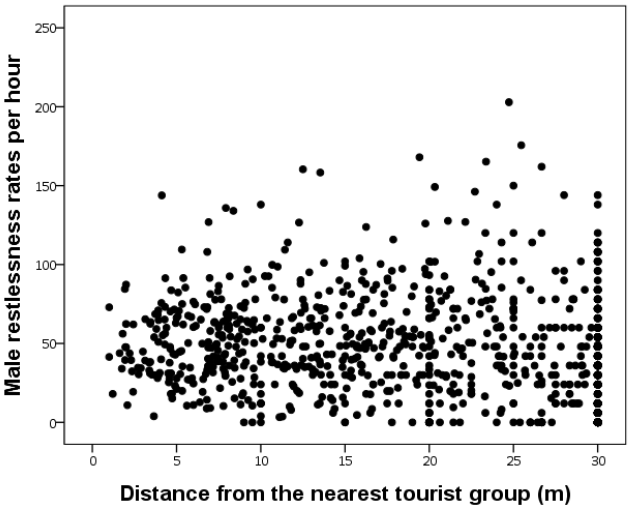


Figure A11-12: Scatterplots representing the relationships between males' restlessness rates per hour and the distance from the nearest tourist group for the overall study period. Each dot represents one individual's datum for a day. Some data points may overlap. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-15, page 166.

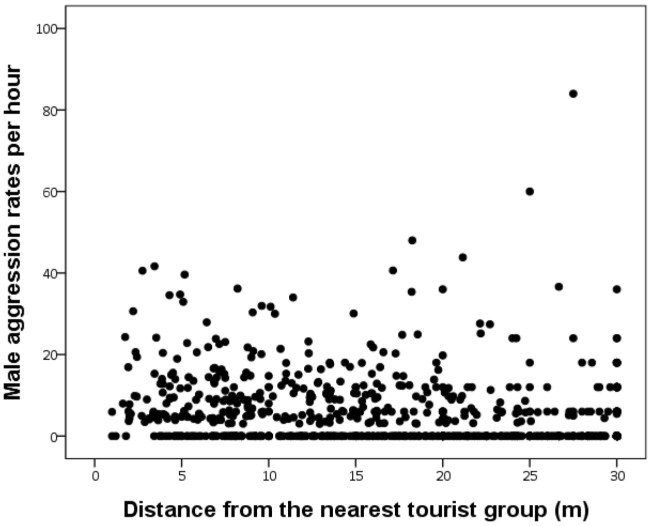


Figure A11-13: Scatterplots representing the relationships between males' aggression rates per hour and the distance from the nearest tourist group for the overall study period. Each dot represents one individual's datum for a day. Some data points may overlap. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-17, page 169.

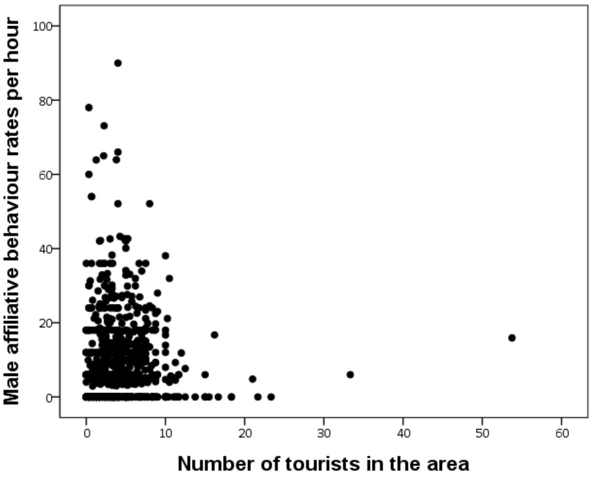


Figure A11-14: Scatterplots representing the relationships between males' affiliative behaviour rates per hour and the number of tourists in the area for the overall study period. Each dot represents one individual's datum for a day. Some data points may overlap. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-19, page 172.

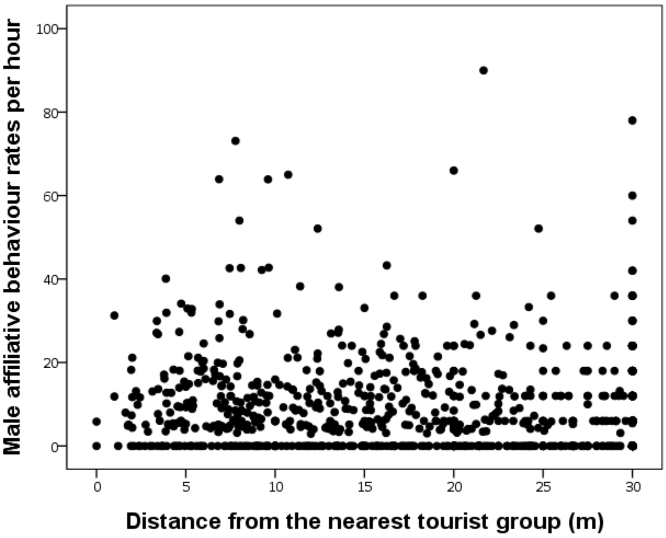


Figure A11-15: Scatterplots representing the relationships between males' affiliative behaviour rates per hour and the distance from the nearest tourist group for the overall study period. Each dot represents one individual's datum for a day. Some data points may overlap. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-19, page 172.

Appendix A12: Summary of the significant results of the relationships between tourist-macaque interaction measures and female Barbary macaques' behavioural responses during tourist-macaque interactions

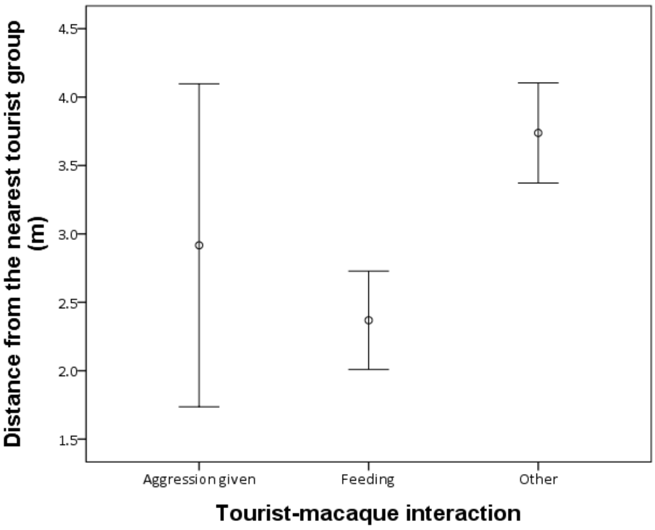


Figure A12-1: Bar graph for the distance from the nearest tourist group (mean and 95% confidence intervals) when females were interacting with tourists for the different types of interactions for the overall study period. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-10, page 158.

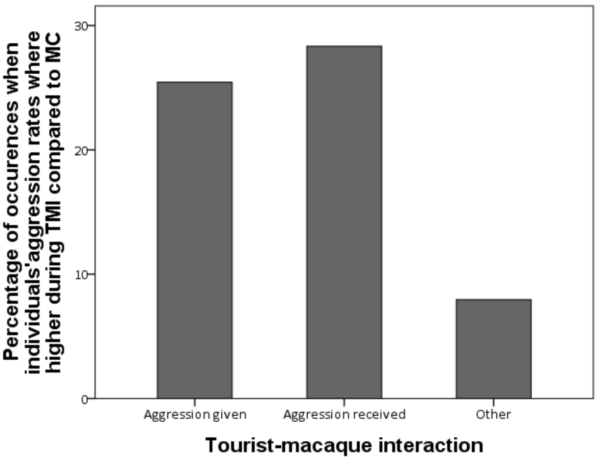


Figure A12-3: Bar graph for the percentage of occurrences when females' aggression rates were higher during TMI compared to MC for the different types of tourist-macaque interactions for the overall study period. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-18, page 171.

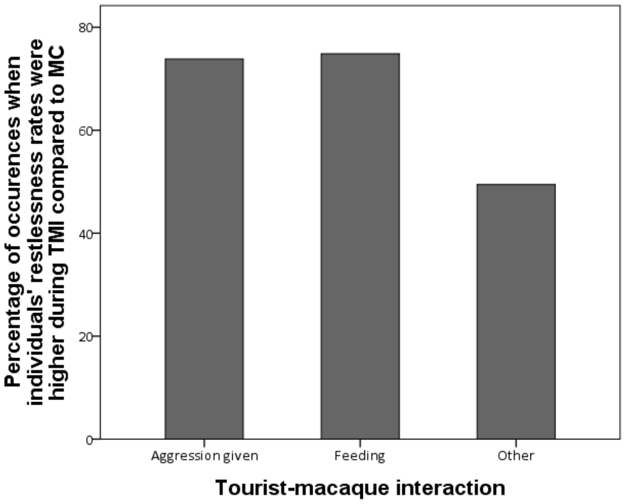


Figure A12-4: Bar graph for the percentage of occurrences when females' restlessness rates were higher during TMI compared to MC for the different types of tourist-macaque interactions for the overall study period. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-16, page 168.

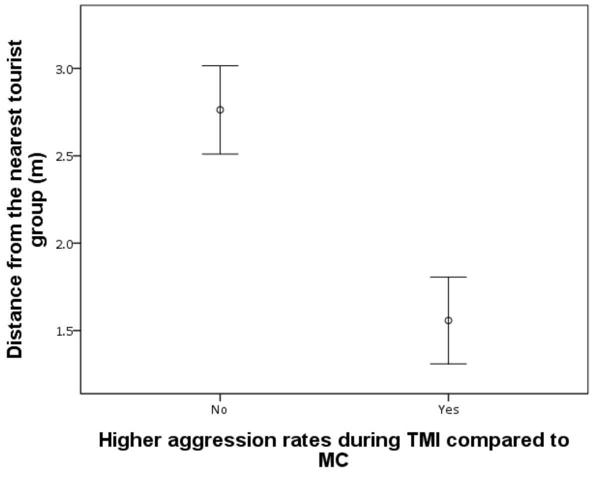


Figure A12-2: Bar graph for the distance from the nearest tourist group (mean and 95% confidence intervals) when females had higher aggression rates during TMI compared to MC for the overall study period. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-18, page 171.

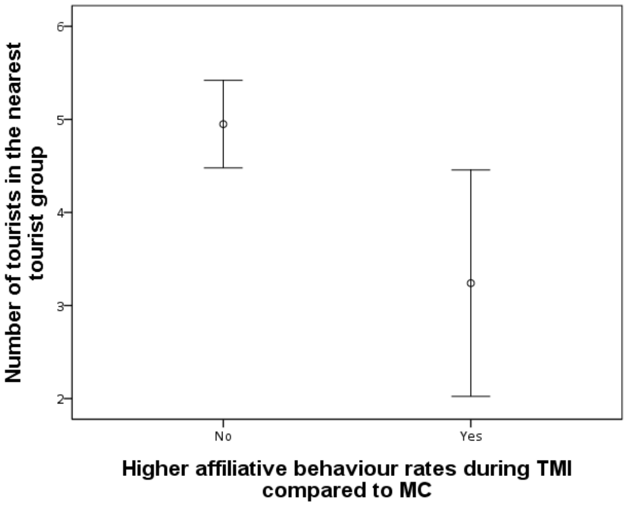


Figure A12-5: Bar graph for the number of tourists in the nearest tourist group (mean and 95% confidence intervals) when females had higher affiliative rates during TMI compared to MC for the overall study period. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-20, page 174.

Appendix A13: Summary of the significant results of the relationships between tourist – macaque interaction measures and male Barbary macaques' behavioural responses during tourist-macaque interaction

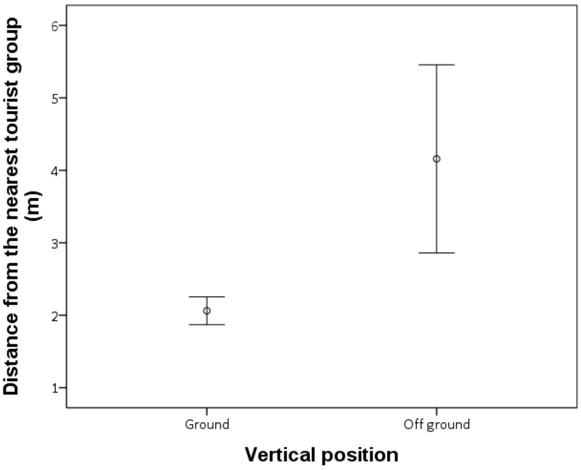


Figure A13-1: Bar graph for the distance from the nearest tourist group (mean and 95% confidence intervals) when males were on the ground or off the ground for the overall study period. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-6, page 152.

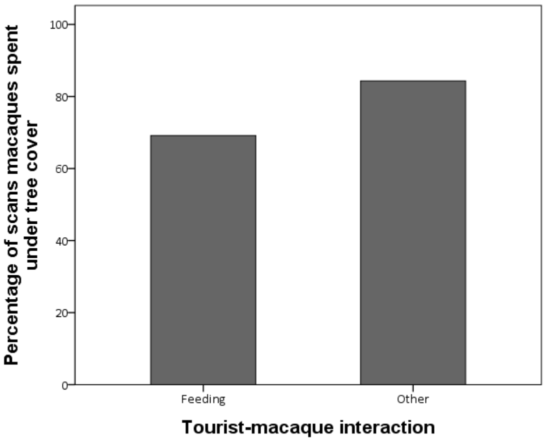


Figure A13-2: Bar graph for the percentage of scans males spent under tree cover for the different types of tourist-macaque interactions for the overall study period. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Tabl 4-8, page 156.

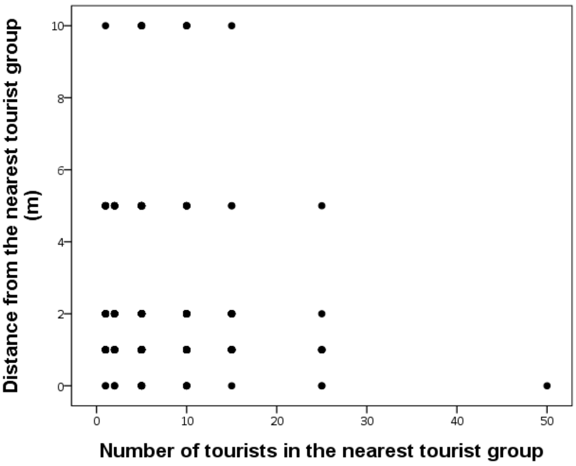


Figure A13-3: Scatterplots representing the relationships between number of tourist in the nearest tourist group and the distance from the nearest tourist group for the overall study period. Each dot represents one individual's datum for a day. Some data points may overlap. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-10, page 158.

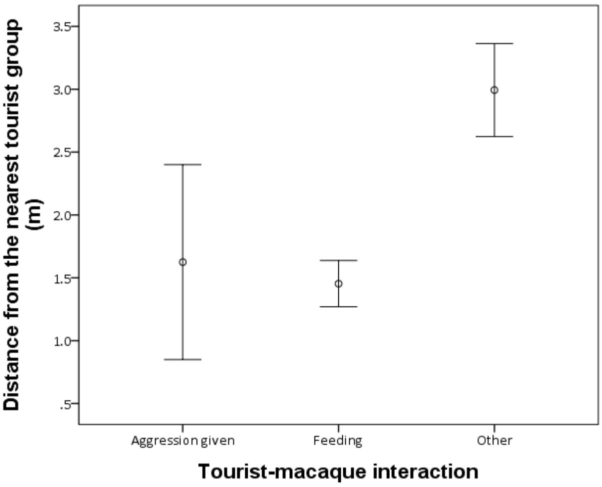


Figure A13-4: Bar graph for the distance from the nearest tourist group (mean and 95% confidence intervals) when males were interacting with tourists for the different types of interactions for the overall study period. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-10, page 158.

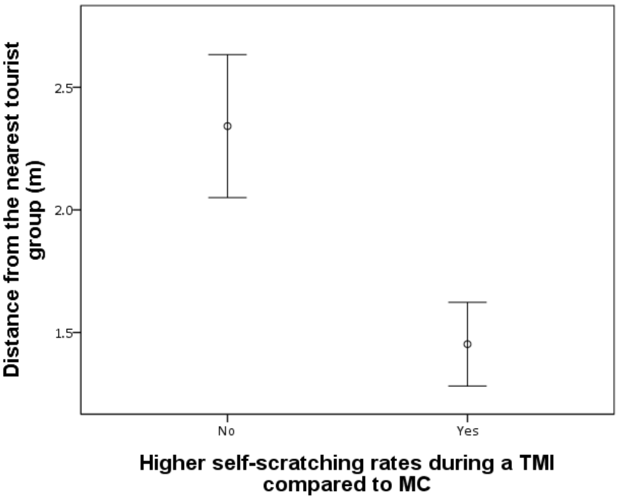


Figure A13-5: Bar graph for the distance from the nearest tourist group (mean and 95% confidence intervals) when males had higher self-scratching rates during TMI compared to MC or not for the overall study period. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-14, page 165.

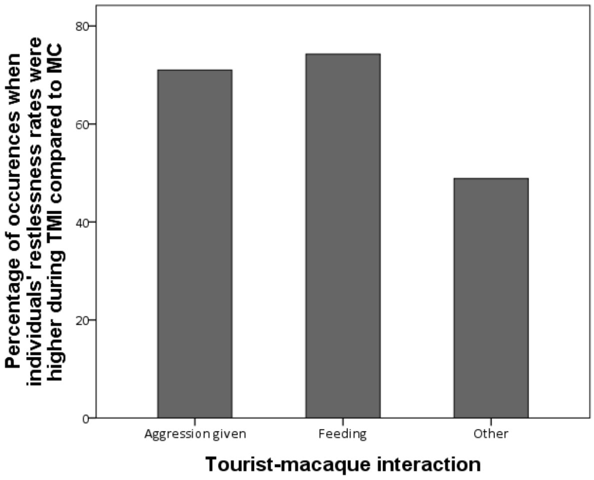


Figure A13-6: Bar graph for the percentage of occurrences when males' restlessness rates were higher during TMI compared to MC for the different types of tourist-macaque interactions for the overall study period. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-16, page 168.

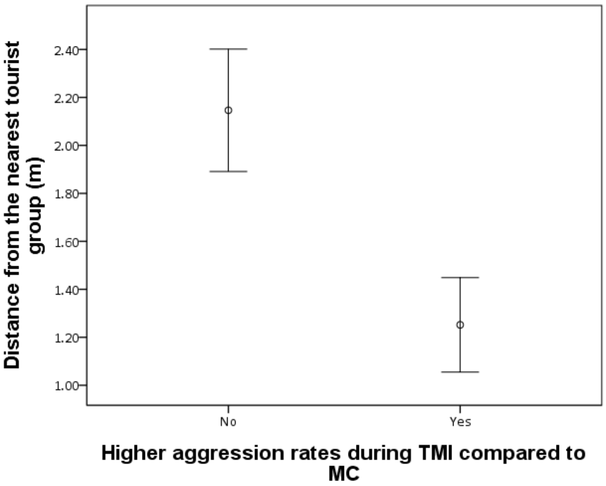


Figure A13-7: Bar graph for the distance from the nearest tourist group (mean and 95% confidence intervals) when males had higher aggression rates during TMI compared to MC or not for the overall study period. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-18, page 171.

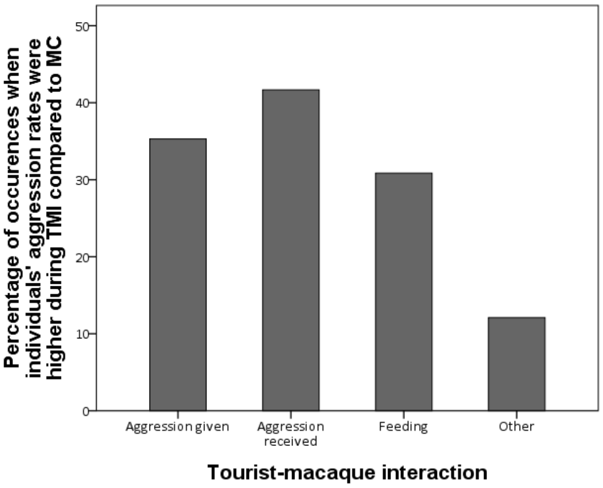


Figure A13-8: Bar graph for the percentage of occurrences when males' aggression rates were higher during TMI compared to MC for the different types of tourist-macaque interactions for the overall study period. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 4-18, page 171.

Appendix A14: Correlations between the different predictor variables used in GLMM analyses, Chapter 5.

Table 14-1: Correlations between the different predictor variables (monthly measures) used in GLMM for testing the relationships between provisioning and body size, coat quality, and alopecia for TG, Chapter 5.

		TG females (N=99)			TG males (N=86)		
		Provisioning	Rainfall	Rank	Provisioning	Rainfall	Rank
Rainfall	r_s	-0.471			-0.157		
	P value	0.001			0.151		
Rank	r_s	-0.220	0.000		0.077	-0.410	
	P value	0.029	1.000		0.481	0.711	
Social season	r_s	-0.317	0.494	0.000	-0.281	0.348	-0.008
	P value	0.010	<0.001	1.000	0.009	0.001	0.939

Table 14-2: Correlations between the different predictor variables (monthly measures) used in GLMM for testing the relationships between provisioning and body size, coat quality, and alopecia for GG, Chapter 5.

		GG females (N=60)		GG males (N=50)	
		Rainfall	Rank	Rainfall	Rank
Rank	r_s	0.000		0.000	
	P value	1.000		1.000	
Social season	r_s	0.516	0.000	0.325	0.000
	P value	<0.001	1.000	0.021	1.000

Table 14-3: Correlations between the different predictor variables (daily measures) used in GLMM for testing the relationships between provisioning and FGC levels for TG, Chapter 5.

		TG females (N=262)			TG males (N=309)		
		Provisioning	Rainfall	Rank	Provisioning	Rainfall	Rank
Rainfall	r_s	-0.051			-0.046		
	P value	0.413			0.420		
Rank	r_s	-0.119	0.010		-0.045	0.270	
	P value	0.055	0.867		0.433	0.639	
Social season	r_s	-0.204	0.079	0.038	-0.119	0.055	0.094
	P value	0.001	0.205	0.540	0.036	0.337	0.100

Table 14-4: Correlations between the different predictor variables (daily measures) used in GLMM for testing the relationships between provisioning and FGC levels for GG, Chapter 5.

		GG females (N=192)		GG males (N=149)	
		Rainfall	Rank	Rainfall	Rank
Rank	r_s	-0.028		-0.010	
	P value	0.700		0.872	
Social season	r_s	0.027	0.053	-0.100	-0.061
	P value	0.713	0.462	0.228	0.459

Table 14-5: Correlations between the different predictor variables (daily measures) used in GLMM for testing the relationships between provisioning and UCP levels for TG, Chapter 5.

		TG females (N=214)			TG males (N=164)		
		Provisioning	Rainfall	Rank	Provisioning	Rainfall	Rank
Rainfall	r_s	-0.208			-0.081		
	P value	0.002			0.305		
Rank	r_s	-0.113	0.006		-0.03	0.037	
	P value	0.099	0.928		0.707	0.64	
Social season	r_s	-0.226	0.093	0.061	-0.276	0.088	0.045
	P value	0.001	0.177	0.373	<0.001	0.262	0.568

Table 14-6: Correlations between the different predictor variables (daily measures) used in GLMM for testing the relationships between provisioning and UCP levels for GG, Chapter 5.

		GG females (N=112)		GG males (N=88)	
		Rainfall	Rank	Rainfall	Rank
Rank	r_s	0.030		-0.044	
	P value	0.756		0.683	
Social season	r_s	0.365	0.122	0.283	-0.033
	P value	<0.001	0.211	0.008	0.759

Appendix A15: Summary of the significant results of the relationships between macaques' health measures and percentage of provisioning.

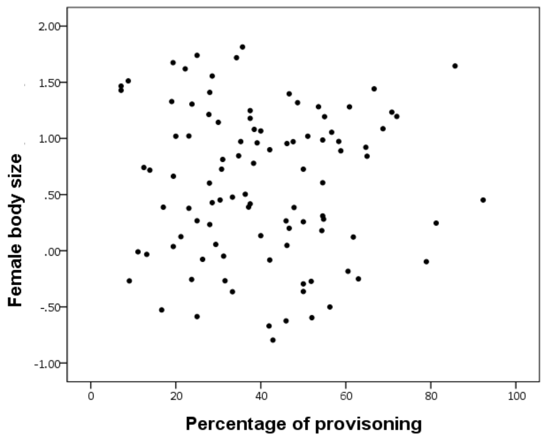


Figure A15-1: Scatterplots representing the relationships between females' body size (PCA 1 scores based on monthly data) and the percentage of provisioning for the overall study period. Eleven data points for each individual are plotted on the graph. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 5-16, page 252.

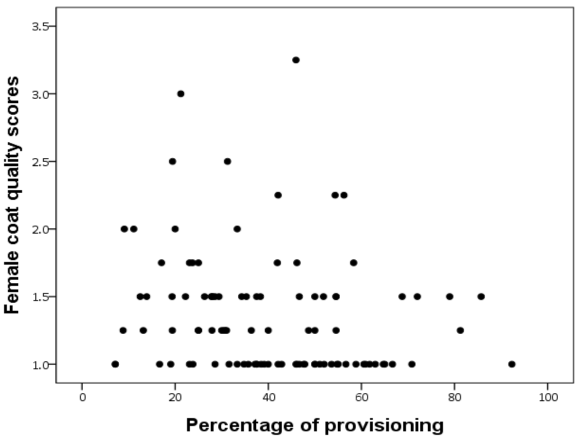


Figure A15-2: Scatterplots representing the relationships between females' coat quality (based on monthly data) and the percentage of provisioning for the overall study period. Eleven data points for each individual are plotted on the graph. Some points may overlap. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 5-18, page 254.

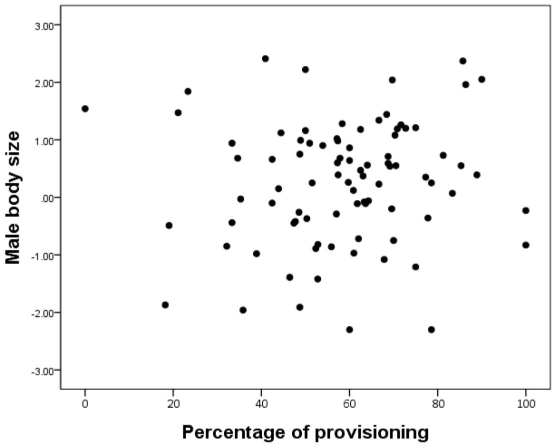


Figure A15-3: Scatterplots representing the relationships between males' body size (PCA 1 scores based on monthly data) and the percentage of provisioning for the overall study period. Eleven data points for each individual are plotted on the graph. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 5-17, page 253.

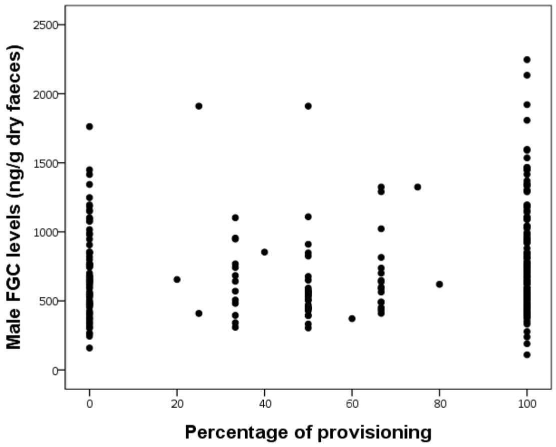


Figure A15-4: Scatterplots representing the relationships between males' FGC levels (based on daily data) and the percentage of provisioning for the overall study period. Some points may overlap. The raw data used to construct this plot are not controlled for other variables, unlike in the statistical models presented in Table 5-25, page 261.

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