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Effects of tourist presence and activity on the behaviour of Zanzibar red colobus monkeys (*Piliocolobus kirkii*) at Jozani-Chwaka Bay National Park

Warkentin, Ann Sophie

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**Effects of tourist presence and activity on the
behaviour of Zanzibar red colobus monkeys
(*Piliocolobus kirkii*) at Jozani-Chwaka Bay
National Park**

Ann-Sophie Warkentin



PRIFYSGOL
BANGOR
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A dissertation submitted for the degree of Master of Science
by Research in the School of Natural Sciences

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“When you realize there is something you don't understand, then you're generally on the right path to understanding all kinds of things.” (Jostein Gaarder, Sophie's World)

Summary

Primate tourism has been practised since the 1970s and has since expanded to every primate-range continent. It provides valuable revenue for both governments and, through community revenue sharing, surrounding human communities. I conducted a systematic review of the literature to identify where and how the effects of primate tourism has been researched. The majority of publications were published after 2008, showing an increasing trend of primate tourism. Most studies were conducted in Africa (51%, n=102 publications) and if a study concerned a single genus, macaques (*Macaca*) attracted the most attention (34%, n=55 publications). I identified both positive and negative effects of primate tourism. Positive effects include a growing number of individuals in some primate genera, and benefits such as improved healthcare for surrounding human communities. Negative effects include the risk of disease transmission and an increase in aggression among the primates. The literature review presents ideas to reduce the effects of primate tourism and highlights the importance of educating tourists on the effects they can have on visited primates.

Following the literature review, I present data from my study on the effects of tourism on the behaviour of Zanzibar red colobus. This study is the first to examine the impact of tourism on Zanzibar red colobus, an endangered and endemic colobus species with less than 6,000 individuals left. Jozani-Chwaka Bay National Park on Zanzibar has been visited by tourists since the 1990s and numbers have reached nearly 60,000 per year. I collected data on self-directed behaviour, activity budget and travel distance on two colobus groups, one exposed to tourists and one not exposed to tourists. The tourist-exposed group showed higher rates of self-directed behaviour (8.29 ± 3.95 acts / hour) than the one not exposed to tourists (5.58 ± 3.91 acts / hour). The groups differed in time spent resting (tourist exposed group: $33.77\% \pm 18.02$, group not exposed to tourists: $51.59\% \pm 18.65$) but did not differ in distances travelled during focal observations. These observed differences between groups could be due to differences in group size, substrate use or tourist presence. The study provides valuable baseline data for future research on this heavily utilised but understudied primate species.

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Abstract

Primate wildlife tourism has become an important source of income for primate-range countries since its implementation in Asia in the 1970s. Today, primate tourism utilises multiple species of primates in multiple locations across the world, wherever primates exist. While the economic benefits are clearly detectable (including \$14 million of revenue in Rwanda in 2014 alone), research on the effects of tourism on primates can still be considered to be in its early phases. Since 63% of all primate species are currently threatened with extinction, the utilisation of tourism and its economic benefits could be crucial to their survival. A review of the literature resulted in 219 publications on the topic of primate tourism, with the majority published since 2008. Most studies were conducted in Africa (51%, n=102 publications) and if a study concerned a single genus, macaques (*Macaca*) attracted the most attention (34%, n=55 publications).

This review highlights both positive effects - such as an increase in numbers for some species and benefits to the surrounding human communities - and negative effects such as changes in behaviour and higher risk of disease transmission to the primates. It considers different strategies to reduce the negative impacts on primates, including the implementations of existing rules, creating new rules and considering how species-specific effects could make certain species more suitable for primate tourism than others. Finally, it reflects on the value of educating tourists in order to encourage them to change their behaviour when viewing primates in the wild, as well as using future research to inform and implement changes in management practises.

Introduction

Wildlife tourism, defined as “tourism based on encounters with non-domesticated (non-human) animals [that] can occur in either the animals’ natural environment or in captivity”

(Higginbottom, 2004) is part of ecotourism, which is the fastest growing subset of tourism between 1990 and 2000 (Blangy & Mehta, 2006). Tourism as a whole has generated \$1.34 billion in 2017 and was responsible for 1 out of every 10 jobs worldwide (UNWTO, 2018).

When using the term “wildlife tourism”, this review means non-captive wildlife tourism where the animals are roaming freely and are not restricted by fences (Packer & Ballantyne, 2012).

Within wildlife tourism, there is a bias towards seeing large and charismatic mammals. D’Cruze *et al.* (2018) found that 67% of wildlife activities advertised through the travel site TripAdvisor in South America involved mammals, and 57% of those mammals were primates. Tourists enjoy

watching primates as their behaviour is relatively easy to understand, even without a background in biology, they are charismatic mammals and familiar due to their appearances in media (McKinney, 2016).

Primate tourism has become both popular and an important income source to primate range countries. Since primate tourism started in the 1970s with orangutans in Asia and gorillas in Africa (Russon & Susilo, 2014; Kalpers *et al.*, 2003), it has expanded to include multiple species, ranging from the South America to Asia. As it has become popular, it has also provided an important source of income to primate range countries. In 1998/99, three national parks in Uganda shared \$83,000 of revenue between them, while in 2014, wildlife tourists alone brought \$14 million into Rwanda (Archbald & Naughton-Treves, 2001; Sabuhoro *et al.*, 2017).

While primate tourism generates revenue that can be used towards conservation of both species and habitats, it can also have detrimental effects on the primates visited. This review will analyse studies observing these effects and how they can be minimised to improve conservation through tourism, while also reflecting on the impact of primate tourism on the human communities living close to primate sites. With the numbers of tourists predicted to rise continuously in the future, we provide a timely overview of the topic by summarising previous findings and highlighting necessary future research. With 63% of all primate species currently threatened with extinction and many of the tourism sites focusing on great apes, which are classified as “vulnerable”, “endangered” or “critically endangered” (with one species being data deficient and therefore not classified) (Cotton *et al.*, 2016), understanding the impacts and risks of primate tourism should be a priority for conservation programmes.

Even though there are numerous studies on the effects of tourists on primates, there have not been many summaries of the findings. “Primate Tourism – A Tool for Conservation?” (Russon & Wallis, 2014) provides a good synthesis of the problems associated with primate tourism and the possibilities of utilising tourism revenue for primate conservation. The book draws on case studies and focuses on geographical regions (Asian primates, African primates, Neotropical primates) as well as reviewing broader issues such as pathogen transmission or best practise guidelines.

With these case studies in mind and utilising current literature, this review will focus on highlighting the effects of tourism on primates and how these effects could be reduced. It will

draw on new studies published since Russon & Wallis' (2014) book on this topic (n = 61 publications since 2014) and on methods to assess the effects on primates and conclude with suggestions of how to change current practises and educate tourists in order to increase the benefits of primate tourism by lowering its costs to primates. It will provide an overview of the research questions and primate groups studied previously and highlight research gaps regarding primate tourism.

Methods

We conducted a search on Web of Science with the keywords “Primate AND Touris*” and “All Fields” for all years (1979 to 2019) to pick up on articles containing primates and the mention of tourism or tourists. The resulting list of articles (n = 226) was examined and each article read. Articles about primates and at least one mention of tourism/tourists (n = 109) were added to a database and coded to include title, authors, date of publication, journal, region of study, family of primate species studied, genus of primate species studied, and research topic. We created an identical list for all publications (including book chapters) found through citations from publications and other search engines (such as Google Scholar), adding an additional 110 publications.

When coding publications into research topic, we only assigned one topic per publication. If publications dealt with multiple topics, we chose the main topic of discussion. Table 1 provides examples for each category. While multiple publications mentioned the topic of conservation, we only assigned “Conservation” if this was in fact the main topic. Publications dealing with behaviour but drawing on the need for conservation were categorised as “Behaviour”. We decided on “General Research” if the main topic did not clearly fit into any other category.

Table 1: Example publications for each category of “research topic” used to code publication list

Category	Example publications	Authors
Behaviour	Dial and infradian rhythms; Activity budgets; Behavioural responses to tourists	Muñoz-Delgado <i>et al.</i> , 2018; Ilham, Nurdin & Tsuji, 2018; Maréchal <i>et al.</i> , 2016

Conservation	Contribution of research to conservation; Primate conservation and local communities; Flagship species tourism and conservation	Pusey <i>et al.</i> , 2007; Hill, 2002; Xiang <i>et al.</i> , 2011
Disease	Coronavirus infection in baboons; Epidemiology of respiratory outbreaks in chimpanzees; Disease risk analysis	Olarinmoye <i>et al.</i> , 2017; Kaur <i>et al.</i> , 2008; Travis, Hungerford & Engel, 2006
Economics	Who is on the gorilla's payroll?; Tourism revenue sharing around national parks; Economic impact of ecotourism	Adams & Infield, 2003; Archabald & Naughton-Treves, 2001; Serio-Silva, 2006
General Research	Visitor perception of captive Barbary macaques; Wildlife tourism: Taxonomy and conservation status; Qualitative assessment of macaque tourism sites	Stazaker & Mackinnon, 2018; D'Cruze, Niehaus & Balaskas, 2018; Fuentes, Shaw & Cortes, 2007
Human Wildlife Conflict	Residents attitude towards black howler monkeys; Farmer-Green Monkey relations; Food competition between vervets and farmers	Alexander, 2000; Dore, 2018; Horrocks & Baulu, 1994
Physiology	Measuring hair cortisol to assess effect of anthropogenic impacts; Effects of habituation, research and ecotourism on faecal glucocorticoid	Carlitz <i>et al.</i> , 2016; Shutt <i>et al.</i> , 2014; Maréchal <i>et al.</i> , 2016

	levels; Assessing impact of tourist provisioning on health	
Population	How tourism and pastoralism influence population demographic changes; Changes in demographic parameters in relation to decrease of provisioned food; Population dynamics of the Virunga mountain gorillas	Ménard <i>et al.</i> , 2014; Kurita <i>et al.</i> , 2008; Kalpers <i>et al.</i> , 2003
Review	Feeding wildlife as a tourism attraction: a review of issues and impacts; The state of Ethnoprimateology;	Orams, 2002; McKinney & Dore, 2018
Rules & Regulations	Chimpanzee tourism in relation to the viewing regulations; The rules and the reality of mountain gorilla tracking	Nakamura & Nishida, 2009; Sandbrook & Semple, 2006

Results

The Web of Science search resulted in 109 relevant articles on primate tourism. When combined with other publications (total n = 223, Figure 1), most publications on primate tourism have been published since 2008 (n=149). As of October, the number of publications in 2019 (n=13) are already as high as those in 2018 (n=13).

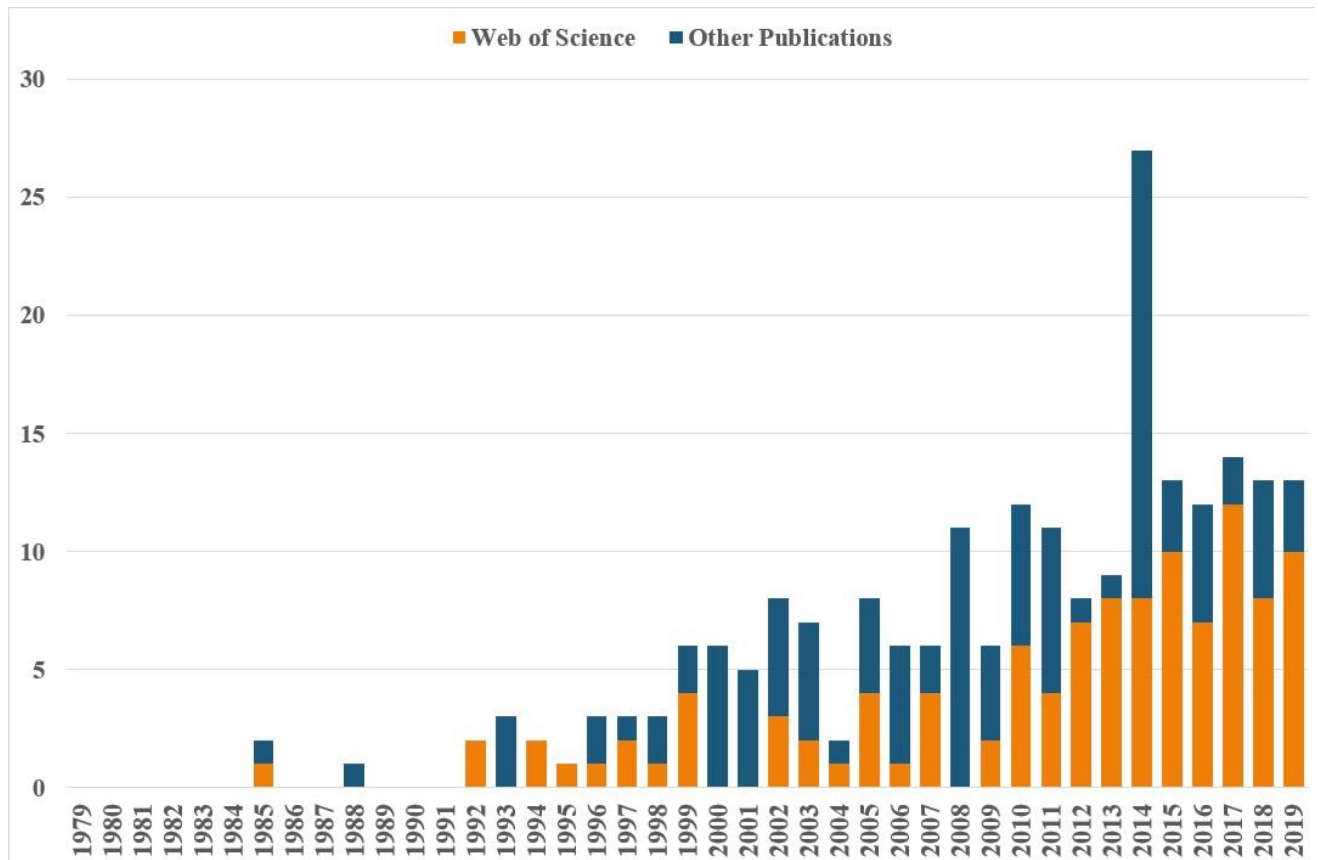


Figure 1: Numbers of articles published per year as identified through both Web of Science (search term “Primate AND Touris*” under “All Fields” and for all years (1979 – 2019)) and other publication sources, after checking for relevance (total n = 223)

The number of articles published sorted by region of research (Figure 2) shows that Africa is the region with the highest number of publications (n=102), with nearly double the number of articles as the next highest-ranking region (Asia, n=55). Four publications examine primate tourism on Madagascar and nine examine primate tourism on introduced species. The articles about introduced species include regions such as North America and the Caribbean.

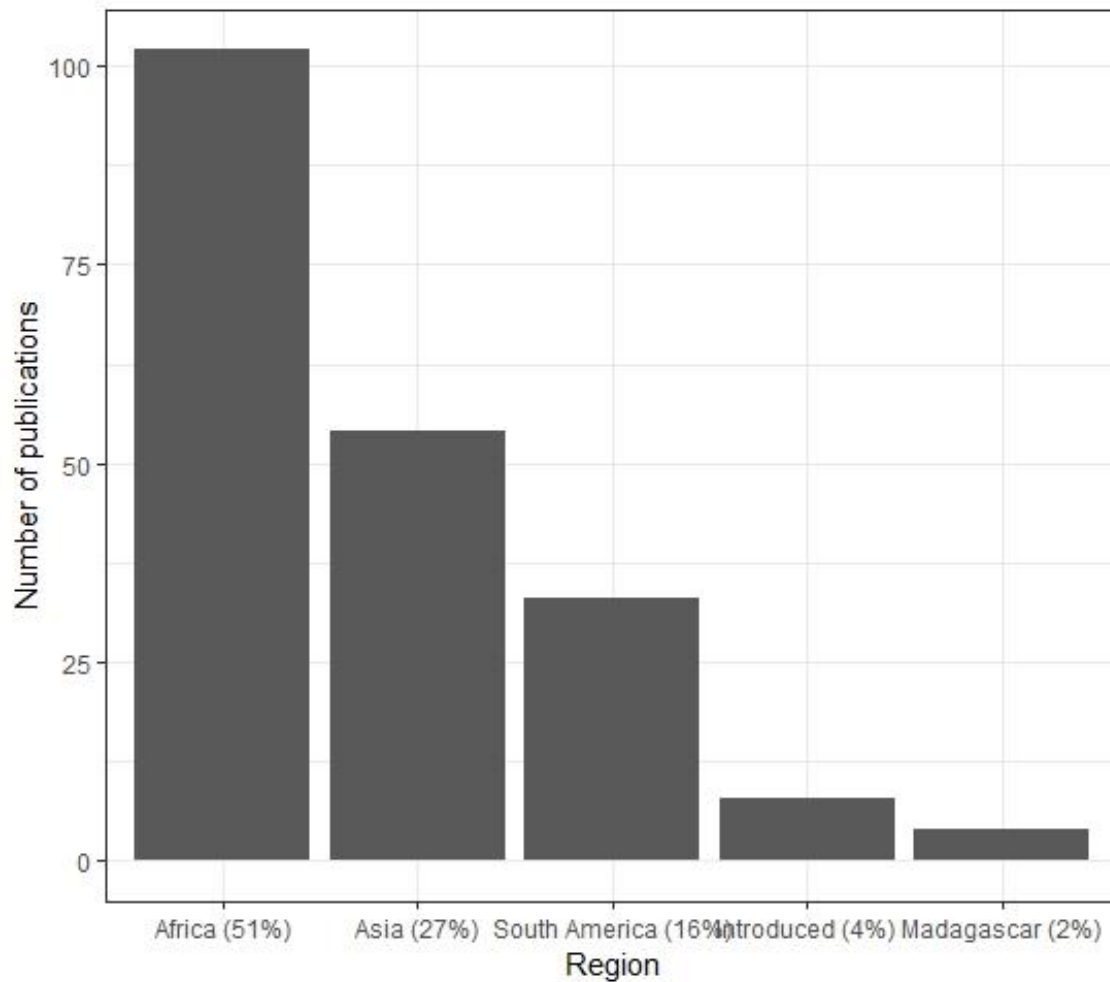


Figure 2: Number of publications on primate tourism per region if study was conducted in a single region (n=203)

Most articles on primate tourism studied primates of the genus *Macaca* (n=55, Figure 3). Combined with the second-highest rank, *Gorilla*, they account for more than 50% of articles published with a focus on one genus. The majority of genera only has one published article for its genus.

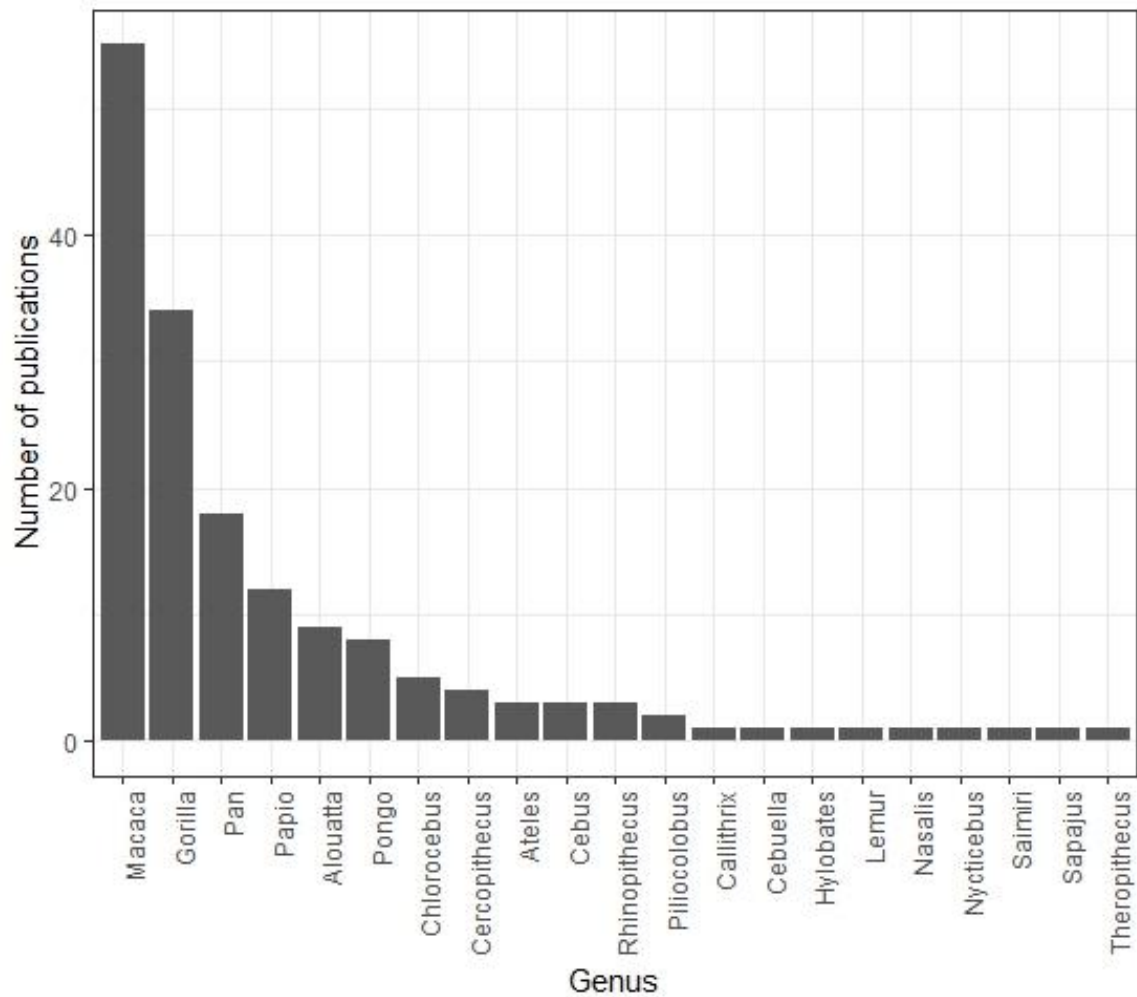


Figure 3: Number of articles published on primate tourism per genus if study was conducted on a single genus (n=167)

The topic of research within primate tourism is relatively balanced (Figure 4), with Behaviour (29%, n=64) being the most researched underlying question, followed by Disease (28%, n=62).

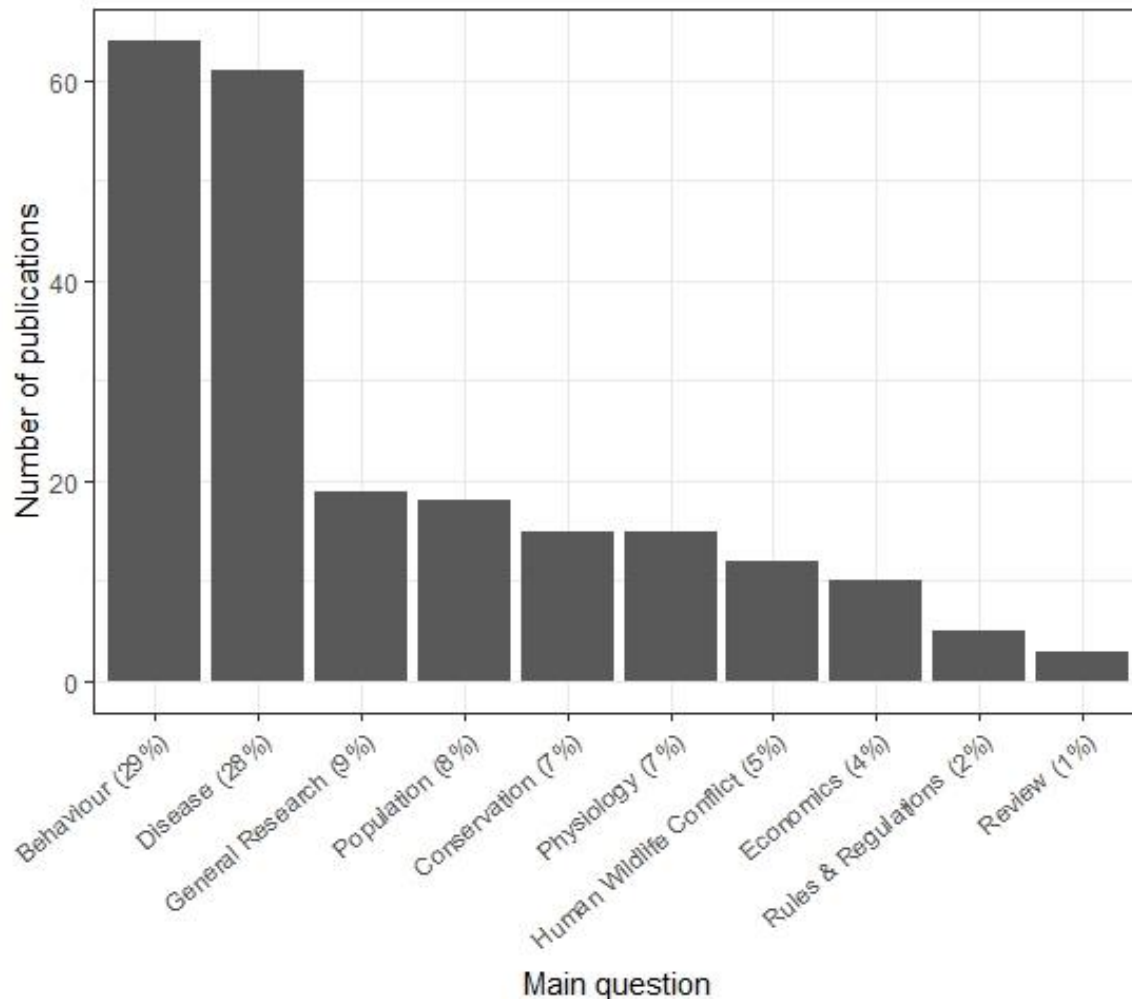


Figure 4: Number of articles published on primate tourism per main research question (n=223)

Discussion

Research bias within the primate tourism literature

The results from the literature review suggest a research bias within the topic of primate tourism, focussing strongly on primate tourism in Africa or Asia, on three genera (*Macaca*, *Gorilla* and *Pan*) and on disease or behaviour.

Within regions, Africa makes up more than 50% of the research. While Africa has numerous primate tourism sites, especially focussing on great ape tracking, it most likely does not host more than 50% of all sites. Madagascar, which is relatively popular with wildlife tourists (Wright *et al.*, 2014) only makes up 2% of the research on primate tourism. Asia is the second most

popular region to study primate tourism, which is possibly due to the large number of sites, especially with macaques (Yamagiwa, 2010).

When looking at genera, two larger-bodied and terrestrial primate genera (*Macaca* and *Gorilla*) are the focus of more than 50% (n=89) of the research articles. Only 17 out of 55 articles on Asia focus on a genus other than *Macaca*. Articles on great apes amount to 36% (n=60) of all articles with a focus on one genus, which could be explained by the history of primate tourism, which started with great ape tourism. While multiple genera only have one article on the topic of primate tourism published about them, this is a good indicator for the popularity of the topic. Research on primate tourism is moving on to new species on which the effects have not been studied before, which allows for better analysis of species-specific responses and conservation.

The two main focuses of research on primate tourism seems to be the topic of behaviour (n=64) and disease (n=62), which has been studied extensively since Wallis & Lee's paper (1999) highlighted the need for disease prevention when working with primates. One of the reasons for favouring a study on behaviour over a study of endocrinology (n = 9) could be the methods involved. Endocrinology studies can carry significant additional costs for sample shipping, processing and analysis, whereas purely observational behavioural studies are more affordable.

Overall, the analysis of current literature provides an overview of where the focus of studies on primate tourism currently lies and can help to identify gaps in our knowledge, both in questions asked and species studied.

Positive effects of primate tourism

Most studies observing effects of tourism on primates have primarily focussed on negative effects, as these can impact species survival. However, primate tourism can also have positive effects, both for the species and for human communities surrounding primate tourism sites.

Increase in numbers

Some primate tourism sites provision the primates with food to ensure primates are in view of tourists during certain times of the day (Yamagiwa, 2010). This can lead to increased birth rates in the provisioned primates, as seen in Japanese macaques at Takasakiyama where the population grew from 166 individuals before provisioning to around 1000 individuals after provisioning

started (Kurita *et al.*, 2008). In orangutans, females from rehabilitation centres at which they were provisioned had lower ages at first birth than those born and raised without provisioning, as well as shorter inter-birth intervals (Kuze *et al.*, 2012). While the authors highlight the possibility of incorrect age estimation at the rehabilitation centre as a potential issue in estimating age at first birth, the measurement of inter-birth intervals is more accurate and shorter inter-birth intervals could still lead to a quicker increase in population size in rehabilitated orangutans that were provisioned at the start of their lives.

Measuring direct impacts of tourism on primate conservation has proven difficult (HaySmith & Hunt, 1995), but one method to assess them can be population counts. Some primate populations seem to have increased since tourism started – mountain gorilla numbers have grown by nearly 400% between 1981 and 2018, from around 250 gorillas to just over 1000 gorillas (Hickey *et al.*, 2018). Robbins *et al.* (2011) found that while habituated gorilla groups that received various conservation measures increased in group size, unhabituated groups decreased in size. This indicates that habituated groups, which are often used for tourism, are benefitting from being utilised and therefore better protected, due to both veterinary interventions and protection from poachers through ranger presence.

Facilitating research

While historically, primate tourism sites were originally research sites later opened for tourism, it can work both ways: sites with infrastructure already in place for primate tourism can easily be utilised for scientific research. This allows an insight into conservation measures in place, provides an opportunity to study a primate species previously understudied, and enables measuring species-specific responses to anthropogenic disturbance.

Economic benefits for human communities surrounding primates

Through primate tourism, habitat necessary for the species' survival can be protected (Buckley, Morrison & Castley, 2016), as revenue from the site can be shared with the surrounding human community, therefore decreasing their need to utilise the land for farming. Since land surrounding wildlife tourism sites is currently often utilised as agricultural land (Lepp, 2007), crop-feeding by primates from the tourism site can be a problem. Crop-feeding is one of the major problems between humans and wildlife and can lead to the killing of the animals feeding

on crops (Meijaard *et al.*, 2011). While provisioned primates may feed less on crops (Fuentes, Shaw & Cortes 2006), the revenue from primate tourism can also be utilised to reimburse farmers for crop-feeding damage, as has been implemented in Bigodi (Lepp & Holland, 2006) and Mgahinga National Park (Adams & Infield, 2003). It has also been implemented on Zanzibar where farmers in the surrounding areas of the National Park are reimbursed for the damage from Zanzibar red colobus (*Piliocolobus kirkii*) which draw tourists to the park (Saunders, 2011). This reduces human-wildlife conflict and possibly increases a tolerance for the primates.

Tourists visiting a primate tourism site add a new market for the human community, as tourists are often willing to buy souvenirs or food offered by local people (Healy, 1994). Primates therefore have an economic value to the surrounding communities (Hill, 2002), which is often significant. In Rwanda, 5% of the profit from primate tourism are shared with the community, which between 2005 and 2009 resulted in over \$400,000 of revenue (Nielsen & Spenceley, 2010). This revenue can be used to improve infrastructure, education and health care. In Uganda, revenue was used to build 21 schools, four clinics, one bridge and one road between 1995 and 1998 (Archabald & Naughton-Treves, 2001). Considering the sharp rise in wildlife tourism in the past decade and the predicted future increase, money from tourism will be able to improve the quality of life in surrounding human communities significantly.

Negative effects of primate tourism

'Side effects' of habituation to human observers

In order to observe wild primates, it is necessary to habituate them to allow the presence of human observers without eliciting a fear response. Most primate species will flee upon first contact with human observers, and the time needed for the process of habituation varies between species – while nocturnal primates seem to be habituated within days, great apes can need up to 15 years to be fully habituated (Williamson & Feistner, 2003).

While habituation is necessary for human observation, it can have negative effects on the primates. Shutt *et al.* (2014) found higher faecal glucocorticoid levels in habituated lowland gorillas (*Gorilla gorilla gorilla*) than in unhabituated ones, with the group undergoing habituation showing the highest levels. Faecal glucocorticoids are a measure of physiological stress (Keay *et al.*, 2006) and can have negative effects on immune function, reproduction and

even the survival of primates (Pride, 2005). Habituated primates may also be at a higher risk of poaching than unhabituated ones (Kasereka *et al.*, 2006; Ménard *et al.*, 2014), which can have detrimental effects on the population. Some primate species also show behavioural responses to habituation. One group of lowland gorillas increased their daily travel length during habituation and showed reactions of aggression towards the researchers (Blom *et al.*, 2004). But while there is evidence that habituation itself can have negative effects on primates, there are studies that show habituated primates to be less affected by visitors overall. Muehlenbein *et al.* (2012) looked at faecal glucocorticoid in habituated orangutans (*Pongo pygmaeus morio*) and compared their levels both before and after human contact, and then compared them with the levels of unhabituated orangutans. They found that while levels were higher after visitation than before, they were lower than those of unhabituated primates. Most studies looking at the effects of habituation focus on great apes, while very few studies look at the responses of other primate families on habituation. In one study, Souza-Alves & Ferrari (2010) observed three groups of unhabituated titi monkeys (*Callicebus coimbrai*) and found that each group reacted differently to observers, with one fleeing consistently and another one being habituated after only seven encounters. In another study, Jack *et al.* (2008) looked at both behavioural and faecal cortisol differences in habituated and unhabituated groups of capuchin monkeys (*Cebus capucinus*). The unhabituated monkeys showed higher levels of faecal cortisol upon human contact, though by the end of the study these levels were lower than at the beginning, showing the beginning of being habituated to human observers. Habituation was not fully completed after four weeks as the levels of faecal cortisol in the newly observed group were still higher than in the habituated group, but it highlights how quickly monkeys could be habituated both in terms of their behavioural and physiological reactions.

Current primate tourism utilises previously habituated primates, but with the projected growth of wildlife tourism, further habituation will be necessary in order to provide wildlife tourism experiences for the growing demand and to potentially spread the impact of being visited across multiple groups. When selecting a group of primates for habituation, current studies suggest that it would be beneficial to assure full funding and a quick and continuous process of habituation (Shutt *et al.*, 2014), as the habituation process seems to produce various stress responses in primates. Depending on the species, this could be a large upfront cost to the operator as constant observation of the primates would require many field assistants over a possibly long period of

time. One estimation of the cost of the habituation of a group of gorillas spanning two years is \$250,000 (Blom, 2001).

Behavioural changes

Exposure to humans has been proven to change certain behaviours in primates. Especially in areas where primates are hunted, they tend to react to humans by moving into hiding (Croes *et al.*, 2007) and reducing vocalisation (Papworth, Milner-Gulland & Slocombe, 2013). The exposure to tourists can also cause changes in behaviour. Some effects are seen regardless of whether tourists keep to the rules of visiting, others can be observed when rules are broken. Lowland gorillas in a group visited by tourists decreased their feeding time with an increase in observer numbers, while rates of aggression were higher when the distance to human observers was less than 10m (Klailova, Hodgkinson & Lee, 2010).

Ilham, Nurdin & Tsuji (2018) found that higher tourist numbers increased time spent foraging but decreased time spent grooming in provisioned long-tailed macaques (*Macaca fascicularis*). In vervet monkeys, a group feeding on human food spent less time foraging and more time resting (Saj, Sicotte & Paterson, 1999). Muñoz-Delgado *et al.* (2018) observed a difference in the pattern of activity between a group of spider monkeys living on an island with unsupervised feeding by tourists and those living in a forest enclosure of similar size and environmental conditions. The monkeys visited by tourists were most active during the days with highest tourist numbers (Saturdays and Sundays) while those in the forest enclosure showed a significant drop in activity on Sundays and Mondays, which could be explained by reduced staff activity on these days. While both groups showed changes in weekly activity patterns, the tourist group also showed more irregular daily patterns which are likely related to tourist presence and numbers. A study on pygmy marmosets (*Cebuella pygmaea*) found that pygmy marmosets spent less time in lower parts of the tree and reduced their social play time when tourists were present (de la Torre, Snowdon & Bejarano, 2000). Aguilar-Melo *et al.* (2013) showed that mantled howler monkeys (*Alouatta palliata mexicana*) spent less time on social activities when tourist numbers increased. Long-tailed macaques also spent less time grooming when tourists were present (Marty *et al.*, 2019). A recent playback study on pygmy marmosets showed that human noise exposure leads to a reduction in visibility (Sheehan & Papworth, 2019). Since pygmy marmosets moved away

from their feeding tree to be out of sight following exposure to noise, this can be a costly reaction.

Another observed effect of tourism, especially at sites with provisioning, is a higher rate of aggression. Higher rates of aggressive behaviour due to provisioning can be seen across species (Hamadryas baboons - Kamal, Boug & Brain, 1997; Japanese and rhesus macaques - Hill, 1999; bonnet macaques - Ram, Venkatachalam & Sinha, 2003) and can be directed at both other primates within the group and tourists. A study on Formosan rock macaques (*Macaca cyclopis*) showed that provisioned macaques had a four times higher rate of agonistic behaviour than those not provisioned (Hsu, Kao & Agoramoorthy, 2009), while a study on bonnet macaques showed a rate nearly three times higher during provisioning times than during natural foraging times (0.129 ± 0.048 acts/h during foraging, 0.349 ± 0.154 acts/h during provisioning – Ram, Venkatachalam & Sinha, 2003). Similarly, El Alami *et al.* (2012) showed that Barbary macaques in a semi provisioned group showed aggressive behaviour at more than double the rate of those in a non-provisioned group.

In a group of spider monkeys (*Ateles geoffroyi*) that receives food from tourists, higher rates of agonistic behaviour have been observed at times where food was provided, which resulted in females moving away from the feeding site more often, thus possibly having less access to food (Pérez-Galicia *et al.*, 2017). Brotcorne *et al.* (2017) even observed a new behaviour in long-tailed macaques at a temple site in Indonesia. The macaques robbed tourists of inedible objects and then used those to barter for food.

While higher aggression rates among the primates are often due to increased competition over the provisioned food (Self *et al.*, 2013), aggression towards tourists is often induced by tourists' gestures or noise levels. McCarthy *et al.* (2009) found that tourists pointing at macaques was one of the main behaviours that led to macaque threats, while Ruesto *et al.* (2010) found a significant correlation between decibel levels on the tourist platform and monkey threats. Snub-nosed monkeys (*Rhinopithecus bieti*) at a tourist site in China reacted to tourists with agonistic behaviour in over 80% of observed cases. Aggression towards tourists can have serious effects as seen in a study at a primate tourism site in China, Mount Emei. Within eight years, six visitors trying to retreat to avoid an aggressive primate fell down cliffs and died, with a further two dying as they tried to retrieve bags snatched by monkeys (Zhao & Deng, 1992).

Management practises can also affect rates of aggression and can have serious consequences as seen in Tibetan macaques (*Macaca thibetana*). Berman *et al.* (2007) observed higher rates of infant mortality during management than before management. While provisioned, the macaques were herded back into a certain area to be accessible to tourists. This range restriction led to a higher food competition within the provisioned area and adults attacked infants. Self *et al.* (2013) report similar results at the same site, showing that infant directed aggressions occur mostly within the provisioned area which is blocked off by tourists on two sites. Both studies suggest a change in management practise to allow more space for the macaques in order to reduce rates of aggression.

Food intake through provisioning or bin raiding

While provisioning can have positive effects on population growth, unsupervised feeding by tourists may come with negative consequences to the primates. Both studies by Borg *et al.* (2014) and Maréchal *et al.* (2016) found that Barbary macaques in a group visited and fed by tourists were larger in body size (measured as width of hips using photogrammetry) than those in a group not visited by tourists. This increase is most likely due to being fed anthropogenic food by tourists, which has higher calorie levels than natural food would have (Fuentes, Shaw & Cortes, 2007).

Similar increases in body weight have been observed in bin-raiding primates. These primates utilise food wastage left behind by tourists, a strategy that has been observed as early as the 1990s in Amboseli National Park (Altmann *et al.*, 1993). Access to food waste has led to obesity in yellow baboons (*Papio cynocephalus*), with females feeding from food waste weighing an average of 16.7kg (± 3.48) and females not feeding from food waste weighing an average of 11.0kg (± 1.94) (Altmann *et al.*, 1993). The same trend was observed by Banks *et al.* (2003) at the same study site (Amboseli National Park) nearly 20 years later. While Banks *et al.* could potentially have sampled some of the same individuals as Altmann *et al.*, this seems unlikely as studies on yellow baboons have shown a maximum age of 26.13 years (Rhine, Norton & Wasser, 2000). Therefore, the second study shows a consistency in obesity in baboons feeding on food waste. The same increase in body weight can be seen in vervet monkeys (*Cercopithecus aethiops*) where females in a group near a tourist lodge where they consumed human food were larger than those feeding exclusively on natural food (Turner, Anapol & Jolly, 1997).

Kemnitz *et al.* (2002) have shown higher serum insulin concentrations and cholesterol levels in bin-feeding baboons compared to wild-foraging baboons. These insulin and cholesterol levels can influence the development of problems with the cardiovascular systems, therefore having a potentially detrimental effect on the baboons. Another problem with bin raiding is the possibility of disease or parasite transmission. Sapolsky & Else (1987) observed an outbreak of bovine tuberculosis in a troop of baboons which they traced back to slaughterhouse offal containing cows infected with bovine tuberculosis. Since baboon to baboon transfer seemed to be very rare, the troops feeding on human food waste were much more susceptible to the disease. Foerster *et al.* (2015) found an increase in helminth infections in female forest guenons (*Cercopithecus mitis*) with food provisioning, possibly explained through increased soil intake when being provisioned, as soil contains helminth eggs which are then taken in by the primates. Provisioning also has an effect on activity budgets, as shown by Bronikowski & Altmann (1996). In their study, a troop of baboons feeding on refuse from a lodge spent half as much time foraging as troops with only natural foods in their diet.

Increased anxiety / stress levels

Primates at tourism sites can show stress responses to human observers, even after being fully habituated (Muehlenbein *et al.*, 2012). Self-directed behaviour, one of the displacement activities frequently seen in primates (Maestriperi *et al.*, 1992), has been utilised as a measurement of negative effects of tourists as it has been related to anxiety in primates (Schino *et al.*, 1996; Barros *et al.*, 2000). When given anti-anxiety medication, crab-eating macaques (*Macaca fascicularis*) showed a reduced rate of self-directed behaviour while showing an increased rate under anxiogenic medication (Schino *et al.*, 1996). Maréchal *et al.* (2011) found higher rates of self-directed behaviour in Barbary macaques to correlate with mean number of tourists present, as well as interactions between tourists and macaques. Pérez-Galicia *et al.* (2017) had similar results, with rates of self-directed behaviour being positively correlated with number of tourists visiting spider monkeys.

Additionally to self-directed behaviour rates, faecal glucocorticoids have been utilised to study the effects of tourism on the physiological stress of primates. Higher glucocorticoid levels can decrease immune functions and therefore increase susceptibility to disease (Hoffman *et al.*, 2011). Maréchal *et al.* (2011) found higher levels of faecal glucocorticoids in Barbary macaques

which were positively correlated with higher rates of aggressions between humans and macaques, but not to overall tourist numbers. Shutt *et al.* (2014) reported higher levels of faecal glucocorticoids in lowland gorillas for days during which human observers got closer than 7m. In black howlers (*Alouatta pigra*), higher glucocorticoid levels were positively correlated to tourist presence (Behie, Pavelka & Chapman, 2010).

Self-directed behaviour and faecal glucocorticoids are both valid methods to indicate an effect of tourism on primates, but we should be careful not to use them interchangeably as anxiety and physiological stress levels do not seem to correlate well in some studies (Higham *et al.*, 2009; Ellis *et al.*, 2011; Amrein, Heistermann & Weingrill, 2014).

Disease transmission

Close contact between tourists and primates can lead to disease transmissions, both from humans to primates and from primates to humans. Due to the close phylogenetic relationship, primates are susceptible to multiple pathogens affecting humans (Wolfe *et al.*, 1998). The risk of transmitting diseases to primates from researchers and tourists has been highlighted relatively early (Wallis & Lee, 1999) and certain rules and regulations are in place to avoid transmission of diseases from humans to primates, such as ensuring that humans with respiratory diseases are not allowed to visit primates (Sandbrook & Semple, 2006).

However, in a study that interviewed tourists about these rules, Hanes *et al.* (2018) found that 25% of tourists would still trek if ill, even though they were aware of the rules preventing this. Muehlenbein *et al.* (2010) found that 15% of tourists visiting an orangutan rehabilitation centre reported at least one symptom that should have excluded them from visiting, yet they did visit the primates. In another study, Muehlenbein (2017) conducted surveys with 3845 people and found that while most were aware of potential disease transmission, up to 65% of tourists would still feed or touch wild primates. Carne *et al.* (2017) observed high rates of close proximity and even physical contact between Barbary macaques and tourists when tourists were sneezing and coughing, thus increasing the risk of respiratory disease transmission to the macaques.

In the past, diseases spreading through primate groups have had detrimental effects. In 1988, six female gorillas in a habituated group died from a respiratory illness that was most likely transmitted by human observers (Butynski & Kalina, 1998). Habituated chimpanzee groups in

Tai Forest suffered from multiple outbreaks of respiratory diseases between 2004 and 2006, with mortality rates ranging from 3% to 18%. In all cases, tissue samples showed that the viruses affecting these chimpanzees were human-borne (Köndgen *et al.*, 2008). In the Kanywara community of chimpanzees in Kibale National Park in Uganda, respiratory diseases caused 27% of deaths over 31 years (Emery Thompson *et al.*, 2018). In 2003, a respiratory outbreak lethal to one chimpanzee in the same community was traced back to human rhinovirus C, which must have been transmitted from humans (Scully *et al.*, 2018). Between December 2016 and January 2017, the Kanywara and Ngogo chimpanzee communities suffered two simultaneous outbreaks of respiratory viruses that can be traced back to humans (Negrey *et al.*, 2019). While neither Kanywara nor Ngogo are tourist sites, Ngogo is bordered by a frequently visited tourist community and the authors highlight a possibility for complex cross-contamination through other primate species in Kibale National Park. In Gibraltar, a popular macaque tourism site, an outbreak of pneumonia in 1987 killed all infants of that year (O'Leary & Fa, 1993). While the pneumonia outbreak of 1987 can not be directly traced back to human origin, Köndgen *et al.* (2017) provided evidence for human origin of *Streptococcus pneumoniae* infection in chimpanzees. *S. pneumoniae* can spread to other individuals in a community and be carried into new communities when adult female chimpanzees disperse, infecting individuals without direct contact to humans. Similarly, *S. pneumoniae* of human origin was discovered in bonobos which were at the time in the process of being habituated to human visitors (Grützmacher *et al.*, 2018). While respiratory diseases often have a high mortality rate (possibly up to 47.7% in chimpanzees in Tanzania (Kaur *et al.*, 2008)), other diseases such as scabies also have the potential to be fatal. In 1996, an outbreak of scabies affected all four members of a habituated mountain gorilla group in Uganda, with the infant dying of the disease (Kalema-Zikusoka, Kock & Macfie, 2002).

Dunay *et al.* (2018) found evidence for 33 occurrences of pathogen transmissions from humans to great apes in the literature, highlighting the risks humans pose to the primates they observe. Not all transmissions end in the death of primates but can still affect their overall health negatively. Sak *et al.* (2013) found the same strains of *Giardia intestinalis* in humans and human-exposed gorillas, suggesting a transmission from humans to gorillas. Similarly, Goldberg *et al.* (2006) found *E. coli* bacteria in chimpanzee faeces that were more similar to those present in researchers and tourists than those in humans living in surrounding areas, which indicates that chimpanzees are more at risk of disease transmission from tourists and researchers than from

local villagers. Bublitz *et al.* (2015) found enterobacteria only in lemurs living in fragmented and frequently visited areas, while they found no enterobacteria in lemurs living in an intact forest. Those enterobacteria were also found in humans and livestock surrounding the fragmented habitats, making it highly likely that they transmitted it to the lemurs. Further suspected examples of anthroponotic transmissions include *Giardia duodenalis*, *Campylobacter* spp., *Salmonella* spp. and *Shigella* spp. in mountain gorillas, Ebola in chimpanzees and gorillas and human herpesvirus type 1 in marmosets (Graczyk *et al.*, 2002; Nizeyi *et al.*, 2001; Huijbregts *et al.*, 2003; Costa *et al.*, 2011).

Transmissions from primates to humans can also have drastic consequences. Yong *et al.* (2013) found antibodies to six viruses in the blood of Tibetan macaques at a popular tourist site, while recording the frequency of physical contact resulting in scratches or bites by the macaques. Nearly 20% of interviewed tourists were scratched or bitten by macaques, which poses a serious risk of infection. Bites can happen frequently in tourist destinations, as a study by Brennan, Else & Altmann (1985) shows. During their study period from July to October, eleven guests at a lodge in Kenya were bitten by vervet monkeys (*Cercopithecus aethiops*). However, many primate species that are regarded as tourist attractions have not yet been screened for viruses or diseases that could be transmitted to tourists. Olarinmoye *et al.* (2017) conducted research on hamadryas baboons (*Papio hamadryas hamadryas*) in the Kingdom of Saudi Arabia and found that 22% of a group of baboons were seropositive to human coronavirus, while none of them showed the disease-typical lesions. While coronavirus is not fatal for humans, it can cause respiratory diseases. This study highlights the importance of health and safety measures when visiting primates since many potential zoonotic diseases could still be undetected.

The main threat to tourists is an infection with Herpesvirus B, which has a mortality rate of up to 70% in humans (Engel *et al.*, 2002). Primates can also be a vector for rabies – Kotait *et al.* (2018) found evidence of rabies transmission from white-tufted marmosets (*Callithrix jacchus*) to humans in at least 19 cases and highlight the potential threat of rabies transmissions to tourists, especially as tourism develops and numbers of tourists visiting primates increase. A survey in a rabies clinic in France showed 120 tourists injured by wild primates on holiday between 2001 and 2014 (Blaise *et al.*, 2015), and while none of the patients were infected with rabies due to post-exposure vaccinations, it highlights the risk of rabies transmission from

primates to humans. A review by Gautret & Parola (2014) using PubMed and Scopus search engines found that primates were responsible for nearly 30% of bites to humans, second only to dogs.

Abreu *et al.* (2019) documented a case of yellow fever in a deceased howler monkey (*Alouatta guariba clamitans*) in an area that had previously been yellow fever free for over 80 years but had multiple outbreaks since 2016. The authors hypothesise that yellow fever can remain in the same area for three transmission seasons through non-human vectors such as primates, which can then be transmitted across the country through unvaccinated tourists.

Parasites can also be transmitted from primates to humans, and while mostly not fatal, they can be rather unpleasant for human hosts. A study by Sricharern *et al.* (2016) found both *Giardia* spp. and *Cryptosporidium* spp., which can both cause intestinal diseases, in long-tailed macaques living near a human community and tourist sites.

Primates used for photo opportunities

In primate range countries visited by tourists, locals sometimes keep primates as pets to offer tourists an opportunity for paid photographs of the tourists with the primates (LaFleur *et al.*, 2019). This practise has been observed both with small species of primates that might be difficult to find for tourists, such as the slow loris (Nekaris, Rode & Nijman, 2015), and larger-bodied primates such as Barbary macaques (Stazaker & Mackinnon, 2018). While tourists may seize the opportunity to see and interact with a species they would not easily observe in the wild, interacting with larger-bodied primates which could be easily observed in the wild should not be as enticing. Stazaker & Mackinnon (2008) found that 88% of visitors to Marrakech did in fact not participate in presented photo opportunities and many visitors disapproved of captive primates. As the incentives for these often illegally kept pet primates is often money-making (Reuter & Schaefer, 2017), tourists could reduce this practise by not partaking in photo opportunities and thus not paying the owner of the pet primate.

Which primates are most affected?

While studies have shown that different primate species react differently to tourism or human presence (McKinney, 2014), it appears that some species are more at risk of being affected by tourism due to their size, diet or habitat use. Primate tourism usually focuses on primates that are

easy to find, observe and track in order to provide paying tourists with plenty of opportunities to watch the primates (Yamagiwa, 2010). Therefore, primate tourism could and does focus on larger-bodied primates (such as chimpanzees or gorillas), species who are partially or fully terrestrial (such as various macaque species) and have larger group sizes. This bias towards larger-bodied primates can be seen in the research on primate tourism as well. If even researchers tend to favour larger-bodied primates, possibly due to easier visibility, it is not surprising to see the same trend from tourists. However, not all primates that are larger-bodied, terrestrial and live in large groups are utilised for tourism. Geladas (*Theropithecus gelada*) in Ethiopia fulfil all of these criteria yet live in challenging terrain not suitable for physically unfit tourists and have therefore not been utilised intensively for primate tourism (Abie & Bekele, 2016). Primate tourism so far also rarely utilises nocturnal primates since they are challenging to find and observe, even for experienced researchers (Fernandez-Duque, 2007), and would therefore not be attractive to tourist groups.

Tourists tend to favour countries that are deemed safe when choosing a holiday destination (Mawby, 2000) so primates in more easily accessible and safe countries will be visited more often. Primates living closer to developed tourist areas or large cities are also more at risk of being visited frequently and by larger groups of people, since tour operators favour locations they can easily reach. Overall, the primates that will be most affected by tourism are those visited continuously and by high numbers of tourists, which is influenced by management decisions and tourist' interest.

How could the effects on primates visited by tourists be reduced?

All current options of viewing primates in the pose risks to both primates and humans. While the scope of negative effects on the primates visited is not yet fully understood, there are already suggestions of how to reduce the effects seen in current studies.

Rules and regulations are often already in place but in need of better enforcement and tightening. To aid in this, best practise guidelines have been created, both for general ecotourism (Samia *et al.*, 2017) and specifically great ape tourism (Macfie & Williamson, 2010). Research on the effects of primate tourism have highlighted species-specific responses and the need for studies on each species visited by primates to mitigate effects on them. Lastly, educating tourists on these effects and what they can do to reduce their impact on visited primates seems to be

necessary. This could be achieved through development of educational materials, having scientists talk to tourists at the site or showing the tourists a video on the impacts of tourism on primates.

Enforcing and tightening rules

When visiting primates, tourists are often told to keep a certain distance between themselves and the primates they visit. These minimum distances are in place to reduce the risk of disease transmission, rates of aggression towards humans and stress levels in primates. However, multiple studies found that tourists often disregard this rule and end up in close proximity to primates (Sandbrook & Semple, 2006; Nakamura & Nishida, 2009; Klailova, Hodgkinson & Lee, 2010). While this rule clearly needs better enforcement, there have been suggestions to increase the minimum distance overall. Klailova, Hodgkinson & Lee (2010) suggest increasing the minimum distance between human observers and primates from the current 7m to over 10m. The increase of minimum distance to over 10m is also encouraged by Shutt *et al.* (2014). Macfie & Williamson (2010) instead propose to either make surgical masks mandatory, with which a distance of over 7m would be acceptable, or to otherwise increase the distance to over 10m as well to reduce the risk of disease transmission. They also highlight the need to enforce the rule of not visiting primates at all when showing any signs of illness, a rule which studies have shown to be violated frequently as well (Nakamura & Nishida, 2009; Muehlenbein *et al.*, 2010; Hanes *et al.*, 2018).

As well as increasing the minimum distance, researchers have proposed smaller tourist group sizes to reduce the effects on primates (Klailova, Hodgkinson & Lee, 2010). While some primate tourism sites already have a limit on the number of tourists visiting primates each day, these rules are not always enforced. A study by Nakamura & Nishida (2009) found that tourist groups visiting chimpanzees (*Pan troglodytes*) were larger than allowed by park regulations on 23% of observation days. To prevent large numbers of people on the same day, Wright *et al.* (2014) suggest an online booking system to allow better control of group sizes and distribution throughout the day. This might not be suitable for every site, but it provides a good starting point for sites that need to diffuse tourist numbers throughout the day.

Species-specific responses

Research into species-specific responses could inform decision makers of which species to habituate or utilise for tourism. McKinney (2014) found a difference in response to humans between mantled howler monkeys (*Alouatta palliata*) and white-faced capuchins (*Cebus imitator*), with capuchins initiating contact with humans more often than howler monkeys. Howler monkeys also reacted more strongly to anthropogenic noise. A second study examining the species-specific differences in reactions to high human presence found higher faecal cortisol levels in golden-mantled howler monkeys (*Alouatta palliata palliata*) but not in ornate spider monkeys (*Ateles geoffroyi ornatus*) when comparing monkeys in areas of high human presence and low human presence (Vanlangendonck *et al.*, 2015). By repeating this approach for further species and using the results to inform management, strategies can be implemented to reduce negative impacts on each species visited and could aid in their conservation. Unwin and Smith (2010) discuss the idea that species-specific behaviour can influence whether primates show higher aggression rates when provisioned. They found no significant difference in aggression rates between a provisioned and unprovisioned group in Barbary macaques (*Macaca sylvanus*) and propose the idea that this is due to their highly cohesive social structure. McKinney (2014) found that while white-faced capuchins (*Cebus capucinus*) did adapt their diet to include human food resources, this did not change their activity budget compared to a group not feeding on human food resources.

Species-specific differences could therefore be used to decide on certain species to be used at new tourism sites to reduce the impact of tourists on these primates.

Mitigating effects of tourism can only be possible once we are aware of those effects. Sites with tourism and primate research could integrate research on the effects, as species-specific reactions to tourism might require species-specific strategies. By furthering our understanding of possible effects, we can incorporate plans to reduce these effects both at existing primate tourism sites and newly developed sites. While many sites of primate tourism have been utilised for research on the effects of tourism, multiple sites with tourism have had no research on the effects of those tourists on the primates visited. Jozani-Chwaka Bay National Park on Zanzibar has seen tourists since the 1990s (Carius & Job, 2019), but there are no studies on the effects of tourism on the endemic Zanzibar red colobus (*Piliocolobus kirkii*) published yet. Similarly, tourism around

Guizhou golden monkeys (*Rhinopithecus brelichi*) has been established and a ropeway system was added in 2009, yet there are no studies on the effects of tourism (Guo *et al.*, 2018).

Educating tourists

Educating tourists on both the effects they have on primates visited and on animal welfare could help them to make better choices in the future. Tourists currently rarely recognise bad animal welfare, as studies by Moorhouse *et al.* (2015; 2017) have shown. When scoring wildlife tourist attractions for negative impact on welfare, the authors scored 56% as having negative impacts, yet when looking at TripAdvisor reviews, only 7.8% of all reviews for these attractions highlighted negative welfare (Moorhouse, D'Cruze & Macdonald, 2017). They propose that educating tourists about animal welfare would reduce the number of tourists visiting attractions with negative welfare. Maréchal *et al.* (2017) found that humans without previous knowledge of Barbary macaques struggled to identify facial expressions correctly, which in case of aggression could lead to bites and scratches from the primates. Educating tourists on the meaning of facial expressions and the behaviour of primates could reduce aggressive interactions. Because wildlife tourism relies on the money generated from tourists, tourists themselves have a powerful tool of improving conservation and welfare of animals visited, simply by choosing to only visit sites with good animal welfare. Researchers can highlight effects and propose changes to current management in order to reduce these effects, but most effects mentioned previously are made by the tourists and can therefore most easily be reduced by tourists. Interdisciplinary work between social scientists and natural scientists could therefore help to understand motives behind tourists' behaviour, how these behaviours affect the primates visited, and how both could propose changes that would aid in their conservation.

Tourists should also be educated on the risks of disease transmission and how vaccinations could reduce the risk of infecting primates, as Muehlenbein *et al.* (2008) suggest in their study.

Respiratory diseases can often be fatal to primates, yet only 27.4% of interviewed tourists were vaccinated against influenza. Adams *et al.* (2001) conducted interviews with both tourists and locals. While locals had influenza vaccination rates of 50%, tourists only had rates of 6%.

Influenza vaccinations are often only recommended to people at risk of influenza (Nowalk *et al.*, 2010) but educated tourists could request the vaccination in order to protect the primates they visit.

Community-based health care

While primates utilised for tourism come in frequent contact with travellers, the human communities surrounding those parks may also be a source of disease transmission. Revenues from the parks could be used to build community-based health care centres and provide both vaccination and medication for the people living in close proximity to primates. Such community-based health care exists in Uganda at the edge of Kibale National Park (Chapman *et al.*, 2015) and has the potential to improve both the risk of disease transmission and the positive perception of primate tourism to the communities.

Overall, management at primate tourism sites should produce clear long-term conservation goals that focus on the protection of the species rather than the economic gains from primate tourism. Each site should produce a set of rules and regulations to protect the primates and should enforce these rules with tourists.

Ethics of primate tourism and decision-making

Primate tourism is a potentially very fast-growing industry, with visitor numbers doubling in a short time at some locations (Carius & Job, 2019; Nielsen & Spenceley, 2011). This growth could lead to the decision of opening or developing new primate tourism sites. During the decision-making process, ethical questions of primate tourism should be considered. While primate tourism has multiple benefits for local human communities, it can also have negative effects on primates as highlighted in this review. Who should be able to make decisions on whether or not benefits outweigh the negative effects on primates? If the revenue from primate tourism aids in the conservation and protection of the species overall, at what point do we reach an equilibrium of benefits and costs? How do we factor in the economic benefit to the people living in the area into this cost-benefit equation? Would it be worth to “sacrifice” a few selected groups for tourism in order to ensure the other individuals and groups can be undisturbed? If primate tourism affects animal welfare of individuals visited, can we argue that the reduced welfare in these individuals is made up by improved conservation of all other individuals? While this review cannot answer these questions, they are important to the future of primate tourism and should therefore be raised regularly.

Establishing a new site for primate tourism is never an easy task, and while many challenges will be of practical nature (providing infrastructure and appropriate waste disposal, training staff), these ethical questions should undermine the process of deciding on a new site.

Conclusion

Primate tourism already generates an important revenue for both governments and human communities in habitat range countries, and it is projected to further increase in the future. Multiple studies have looked at the effects of primate tourism on primates, and while they found both positive and negative effects on the behaviour, physiology and reproduction of certain species, the effects of tourism on other primate species are still understudied. While wildlife tourism has been highlighted as a possibility to aid in species survival and conservation, quantifying the effects of tourism on conservation has so far been proven difficult.

This review has highlighted the need for further studies into the effects on primates, conservation impacts and tourism behaviour. Educating tourists appears to be one of the easier ways to reduce impacts on primates, and enforcing rules more regularly seems necessary. Unsupervised feeding opportunities seem to pose the greatest danger to both primates and tourists and wildlife tourism would benefit from moving away from this practise, though this could prove difficult due to financial burdens associated. Future studies could highlight species-specific reactions to assess impacts on different species and inform individual management plans to reduce the impact of wildlife tourism on primates.

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Effects of tourist presence and activity on the behaviour of Zanzibar red colobus monkeys (*Piliocolobus kirkii*) at Jozani-Chwaka Bay National Park

Abstract

Primate tourism has been practised since the 1960s and growth has continued to this day. While the revenue created from primate tourism can be utilised for their conservation, negative effects such as disease transmission, higher levels of intragroup aggression and higher levels of stress and anxiety have been observed. Especially in endangered primates, effects of tourism should be studied to ensure primate tourism is beneficial. The endangered and endemic Zanzibar red colobus (*Piliocolobus kirkii*) at Jozani-Chwaka Bay National Park have been visited by tourists since the 1990s and visitor numbers to the park have reached nearly 60,000 per year. This study examines possible differences in behaviour between two groups with different tourist exposure. I collected data on self-directed behaviours, activity, movement and inter-individual spacing. Colobus monkeys showed higher rates of self-directed behaviour in the tourist group (8.29 ± 3.95 acts / hour) than in the non-tourist group (5.58 ± 3.91 acts / hour). Both group identity and the mean number of adult colobus within 1m of the focal animal were associated with higher self-directed behaviour rates. However, mean number of adult colobus within 1m of focal individual does not differ between the two groups and can therefore not be the sole reason for higher self-directed behaviour rates in the tourist-exposed group. Differences in group size, substrate use and tourist presence are likely reasons for the observed differences. There were no differences in activity budget or distance travelled during the focal observations between the two groups. This study provides valuable baseline data for future research on this heavily utilised for tourism but understudied primate species.

Introduction

Primate tourism has been practised since the 1970s in both Asia and Africa (Russon & Susilo, 2014; Kalpers *et al.*, 2003) and has since expanded to every primate-range continent and multiple genera of primates. It has generated valuable income to the surrounding human communities and for conservation since the start, with \$83,000 of revenue in Ugandan national parks as early as 1998/99 (Archabald & Naughton-Treves, 2001).

While primate tourism can have positive effects for surrounding human communities by generating revenue which can be used to improve infrastructure, healthcare or education at a community level (Chapman *et al.*, 2015), it can also have negative effects on the primates. These negative effects include risk of disease transmission, increasing the risk of higher levels of intragroup aggression, physiological stress and anxiety (Russon & Wallis, 2014).

Pathogens such as bacteria and viruses can be transmitted both from animal to human and human to animal. A recent study found evidence for 56 human-to-animal disease transmissions (Messenger, Barnes & Gray, 2014). Disease transmission from humans to primates is especially prevalent in great apes due to their close phylogenetic relationship (Wolfe *et al.*, 1998).

Transmitted diseases, especially those with respiratory symptoms, can have detrimental effects and even lead to the death of primates (Köndgen *et al.*, 2008) such as in Gibraltar, where an outbreak of pneumonia in 1987 killed all Barbary macaque infants of that year (O’Leary & Fa, 1993). Pathogen transmission from humans to primates can also negatively affect their overall health. *Giardia intestinalis* found in gorillas, *E. coli* found in chimpanzees and enterobacteria found in lemurs are all suspected to have been transmitted from humans to primates, often through tourists (Sak *et al.*, 2013; Goldberg *et al.*, 2007; Bublitz *et al.*, 2015). While no outbreaks of diseases related to these pathogens have been observed yet, the studies highlight the risk of future disease outbreaks through pathogen transmission from tourists to primates.

Aggression in group-living species can have negative consequences on both the group level and the individual level (Aureli, Cords & Van Schaik, 2002). Individuals leaving a group after aggressive interactions can lead to reduced group sizes and therefore reduced benefits of group-living, such as detection of predators (Majolo, de Bortoli Vizioli & Schino, 2008). Higher rates of human-directed and intragroup aggression have been observed both in provisioned groups and unprovisioned groups of primates. In unprovisioned gorillas, rates of human-directed aggression increased whenever human observers approached the gorillas within 10m (Klailova, Hodgkinson & Lee, 2010). In provisioned groups, higher rates of intragroup aggression due to feeding competition have been observed in multiple species (Hamadryas baboons - Kamal, Boug & Brain, 1997; Japanese and rhesus macaques - Hill, 1999; bonnet macaques - Ram, Venkatachalam & Sinha, 2003).

Higher levels of both stress and anxiety have been observed in primates visited by tourists. Anxiety is often measured through self-directed behaviours, a frequently observed displacement activity in primates (Maestripieri *et al.*, 1992). Rates of self-directed behaviours, such as yawning or self-scratching, increase under anxiogenic medication and decrease under anti-anxiety medication and are therefore utilised in behavioural studies on anxiety in primates (Schino *et al.*, 1996). Both barbary macaques and spider monkeys have shown increased rates of self-directed behaviour when visited by tourists (Maréchal *et al.*, 2011; Pérez-Galicia *et al.*, 2017).

Physiological stress can be measured through levels of faecal glucocorticoids, which have been utilised in primate tourism studies. Higher levels of faecal glucocorticoids in relation to tourism have been observed in barbary macaques (Maréchal *et al.*, 2011), lowland gorillas (Shutt *et al.*, 2014) and black howler monkeys (Behie, Pavelka & Chapman, 2010). While higher faecal glucocorticoid levels increase susceptibility to disease as they decrease immune functions (Hoffman *et al.*, 2011), they do not seem to correlate with higher rates of self-directed behaviours and therefore anxiety (Higham *et al.*, 2009; Ellis *et al.*, 2011; Amrein, Heistermann & Weingrill, 2014). Both measurements have been utilised in primate studies but should not be used interchangeably.

These negative effects of primate tourism might be offset by the positive effects on primate conservation through tourism. The revenue generated from tourists can be used for management plans and staff salaries and revenue sharing can lead to a positive attitude of residents towards wildlife (Lepp, 2007). Since the effects of tourists on primates could be species-specific (McKinney, 2014), some primates may not be affected as strongly and could benefit from primate tourism. Especially in endangered primates, where every individual counts towards species survival, the effects of tourism should be studied to ensure tourism is beneficial for their conservation.

The Zanzibar red colobus monkey (*Piliocolobus kirkii*) is an endangered and endemic primate native to the island of Unguja, Zanzibar. A recent census has estimated the population at 5862 individuals (Davenport *et al.*, 2017). More than 50% of these individuals live in Jozani-Chwaka Bay National Park or the surrounding agriculturally used lands (shambas).

Jozani-Chwaka Bay National Park (JCBNP) covers around 5000 ha with a variety of habitats, from plantation forests to mangrove and coral rag forests (Siex & Struhsaker, 1999). The park became Zanzibar's first national park in 2004 and has been visited by tourists since the 1990s with tourism numbers reaching nearly 60,000 tourists annually (Carius & Job, 2019). The main attractions for these tourists are the Zanzibar red colobus monkeys, which are advertised as the flagship species of Zanzibar and have been used to advertise other wildlife on the island (Saunders, 2011).

While there have been a handful of studies on the ecology, behaviour and conservation status of Zanzibar red colobus (Silkiluwashu, 1981; Struhsaker, Cooney & Siex, 1997; Siex & Struhsaker, 1999; Siex, 2003; Nowak, 2008; Nowak & Lee, 2011; Davenport *et al.*, 2017), none to date have been conducted on the effects of tourism on this species.

Considering the high numbers of tourists entering the park every year, and the potential to see a continued rise in numbers based on the growth in the past decade (Carius & Job, 2019), the effects of tourists on the Zanzibar red colobus is an important topic, especially since the revenue from tourists are currently used to aid colobus conservation. Park entry fees are shared among farmers whose *shambas* (agricultural fields) are within the park boundaries, as a compensation for occasional crop-feeding by Zanzibar red colobus. Before this compensation scheme was put in place, monkeys have been killed or chased away by farmers who lost crop yields to crop-feeding colobus (Saunders, 2011).

In this study, I focus on the impact of tourist presence and behaviour on the behaviour of Zanzibar red colobus. Negative effects due to feeding by tourists or provisioning by staff are unlikely to be observed in *P. kirkii*. The populations around the park are not provisioned and, due to their specialised diet of young and immature leaves and fruits (Siex, 2003), do not feed on food offered by tourists when these visitors occasionally break the park rules and try to tempt the monkeys with ripe fruit (personal observation).

I hypothesise that the presence and behaviour of tourists at Jozani-Chwaka Bay National Park affects the behaviour of the Zanzibar red colobus. While *P. kirkii* are largely arboreal, they move down to the ground from time to time, often to feed on terrestrial herbaceous vegetation or to consume charcoal (Struhsaker, Cooney & Siex, 1997). During these times on the ground, large

tourist numbers could be perceived as a threat, thus increasing their anxiety and self-directed behaviour rates.

I therefore predict: (1) the colobus in the group exposed to tourists will show higher rates of self-directed behaviour than the colobus in the group not exposed to tourists; (2) the colobus in the group exposed to tourists will show higher rates of self-directed behaviour in the presence of tourists than in the absence of tourists; (3) the colobus in the group exposed to tourists will spend less time resting and more time moving than the colobus in the group not exposed to tourists; (4) the colobus in the group exposed to tourists will travel further than the colobus in the group not exposed to tourists.

Methods

Study site

Jozani-Chawka Bay National Park (JCBNP) is located on Unguja Island in the Zanzibar archipelago, about 40km off the coast of Tanzania. The park stretches from the village of Jozani north to Chwaka Bay. JCBNP is composed of plantation forest, dryland and ground water forest as well as coral rag forest and is surrounded by agriculturally used land (Siex & Struhsaker, 1999). Zanzibar red colobus (*Piliocolobus kirkii*) populate both the National Park area and the surrounding shambas (Davenport *et al.*, 2017).

Behavioural observations

I conducted this study between July 2018 and November 2018. At the start of this study, I located two groups of *P. kirkii* on the southern edges of the National Park area – one exposed to tourists almost daily and one never exposed to tourists. I spent the first few weeks with these two groups to familiarise myself with the individuals and to take pictures for identification purposes. These pictures were used to compile group profiles. I started data collection when I was confident identifying the majority of the individuals but kept studying the pictures for further improvement in identification.

Study groups

The group exposed to tourists on an almost daily basis (Camp group) consisted of up to five adult males and up to 23 adult females. Due to their large group size, it was difficult to get a reliable count of group members on a daily basis. During the study period, the group included ten infants (of which one died during the study period and one was born during the study period) and at least three juveniles.

The group not exposed to tourists (ATG group) consisted of up to four adult males (one died within the first four weeks of the study period) and up to nine adult females. Four females had infants and one female had a juvenile.

Age classes were categorised into infants (black or red pelage, nursing frequently, smaller body size), juveniles (fully red pelage, nursing infrequently, larger body size close to adults) and adults (fully grown).

Observations

Focal observations lasted 20 minutes per focal and individuals were chosen based on previous amount of time spent on each individual – I aimed to sample each individual in each group for the same amount of time over the course of the study (see Table 1 for details on focal observations). However, especially at the beginning of the study, identifying individuals was not always possible, in which case I recorded them by age-sex class only (adult male, adult female). This resulted in two different data sets: The full data set with all focal observations regardless of positive ID, and the reduced data set with only those focal observations done on identified individuals.

Table 1: Overview of data collection and group composition per *P. kirkii* study group

	Camp group	ATG group
Group composition	≥ 5 Adult males / ≥ 23 Adult females	3-4 Adult males / ≥ 9 Adult females
Days spent with the group collecting focal data	16	17

Number of 20-minute follows conducted on adult males	25	23
Number of 20-minute follows conducted on adult females	150	96
Total hours of focal observations	43.29 hours	38.49 hours
Average daily group follow duration	7.19 hours \pm 0.79 hours	6.08 hours \pm 0.7 hours

At the beginning of the focal sample, I noted the date, time, individual's ID, age-sex-class and group ID. During the focal observation, I noted behaviour every minute on the minute (see Appendix 1.1 for detailed ethogram).

Every fifth minute, I recorded the location of the focal subject (with a global position system, GPS, using the Garmin GPSMAP64s), position of the focal (Ground, Shrubs, Tree lower crown, Tree top), whether the group was on the ground or in the trees (Trees = more than 50% of group in trees, Ground = more than 50% of group on ground, Mixed = approximately 50/50 between ground and trees), distance to researcher (in metres) and number of adult monkeys within 1m of the focal. During the twenty minutes of the focal follow, each instance of self-directed behaviour (rough self-scratching) was counted. A new instance was counted if the focal stopped scratching for at least 5 seconds.

Human presence data

Interactions with tourists and villagers were sampled through all-occurrences sampling. Tourists were only present in one of the two study groups. Whenever a tourist was present, the time, number of tourists and tour guides within 20m of the group was noted. If tourists were present during focal observations, the time, number of tourists within 20m of the focal, within 3m of the focal and within 1m of the focal as well as those trying to touch the focal were noted during continuous 5-minute intervals. I decided on these distances to get an overview of the number of people around the group (20m) as well as the number of people not following the rules (3m) and approaching the monkey very closely as if to touch it (1m). Every 5 minutes, level of noise

(human chatter) in the vicinity of the focal subject was scored on a 3-point scale (1=quiet chatting, 2=louder chatting, 3=laughing or shouting). Villager presence occurred in both groups and was noted whenever a villager was present around the group. Time, number of villagers and any reactions from the colobus group were noted.

Statistical analysis

The full data set includes focal observations on both identified and unidentified individuals. While aiming to identify all individuals, I decided to start collecting behavioural data before being able to identify every single monkey. With the full data set, I calculated average daily rates of self-directed behaviours and habitat use to compare these between groups using Mann-Whitney U tests.

Non-parametric tests do not require the data to fulfil assumptions and can therefore be applied broadly (Neuhauser, 2011, p. 1) and are more suitable for small sample sizes. Fitting mixed models can be difficult depending on the data set due to model assumptions and small data sets might lead to problems when calculating variances (Skene & Kenward, 2010).

To examine multiple predictors of self-directed behaviour rates, activity budget and travel distance, I also constructed linear mixed models on the reduced data set containing only focal observations on known individuals (ID data set: 163 observations; 71.5% of the full data set). This allowed me to gain a more detailed insight into the factors that could be affecting the differences shown at broader levels as tested by the non-parametric tests.

I tested the outcome variable (self-directed behaviour rate) for normal distribution and then log-transformed it. The variable did not show normal distribution due to a high number of zeros in the data set. However, I do not think that this results in zero-inflation which is defined as “more zeros than expected, based on the Poisson or negative binomial distribution” (Zuur *et al.*, 2009, p. 261). The variable seems to be nearly Poisson distributed, but because it includes non-integer values it can not be modelled in a GLM with Poisson family. Therefore, I log-transformed the variable which resulted in near-normal distribution and decided to analyse log-transformed self-directed behaviour rates through linear mixed-effects models in R (R Core Team, 2018) using the packages “lme4”, “lmerTest” and “car” (Bates *et al.*, 2015; Zeileis & Hothorn, 2002; Fox & Sanford, 2011).

I added both time of day (hour during which observation occurred) and focal identification (two-letter abbreviation) as random effects to account for individual variability and changes in activity level throughout the day (Gratton & Mundry, 2019). The full model tested for effects of age-sex-class (adult female, adult male), distance to researcher (in m), rate of aggression received by focal, number of villagers present during focal observation, number of tourists within three metres of focal individual, group ID (Camp, ATG), adult colobus monkeys within one metre of focal individual and maximum noise level during focal observation on self-directed behaviour rates. These predictors were chosen to analyse the effects of tourist behaviour (number of tourists within 3m of focal and maximum noise level), group cohesion (number of adult colobus within 1m of focal individual) or whether it is presence of any humans, regardless of whether they are tourists or not (distance to researcher and number of villagers present) that affect self-directed behaviour rates. After constructing the full model, I tested it against a null model containing only the random effects (time of day and focal identification) using a likelihood ratio test.

For analysis of activity budget, I ran five mixed models to test for predictors of each behaviour (Feeding, Resting, Moving, Grooming, Other). One of these variables (Moving) showed a Poisson distribution. I used glmer with family = poisson for this model (as recommended by Bolker *et al.*, 2009). In these full models I used the same predictors as in the self-directed behaviour models (age-sex class, distance to researcher in metres, rates of aggression received by focal, number of villagers present during focal observation, number of tourists within three metres of focal individual, group ID, adult colobus within one metre of focal individual, maximum noise level during focal observation and self-directed behaviour rate) to examine whether there was a direct effect of any of these variables on each behaviour.

I used ArcGIS (ESRI, 2018) on the GPS data to extract distances travelled during each 20-minute focal. I used the points-to-line function to connect the GPS waypoints chronologically, then measured the distance between each point and the next point for all waypoints taken during the 20 minutes of the focal observation. I then added the distances between all points to get the total distance travelled during each focal observation.

I ran a mixed model on the distance travelled during the 20-minute observation to test if there was a difference between the groups. I used the same predictors as in the activity budget models. “Distance travelled per 20-minute observation” is not the same as “Percentage of focal

observation spent moving”. If a monkey climbed within the same tree during observations, it was recorded under Movement, but did not necessarily lead to a different GPS point, thus sometimes resulting in Movement while resulting in 0m travelled during the observations.

Results

Study groups

The two groups differed slightly in their use of habitat, both at the individual and group level, though only the difference in habitat use at group level was statistically significant. Camp group spent more time on the ground than ATG group (Figure 2, $n = 304$ observations in ATG, $n = 326$ observations in Camp, Mann-Whitney U: $U = 45472$, $p < 0.001$) at group level. There was no difference in the average number of adult colobus within 1m of the focal individual (Figure 3, mixed model: $t = -0.985$, $p = 0.368$). The two groups differed in their exposure to humans (see Table 2), with only Camp group exposed to tourists. Both groups were exposed to local villagers, with ATG exposed to a higher average number per day.

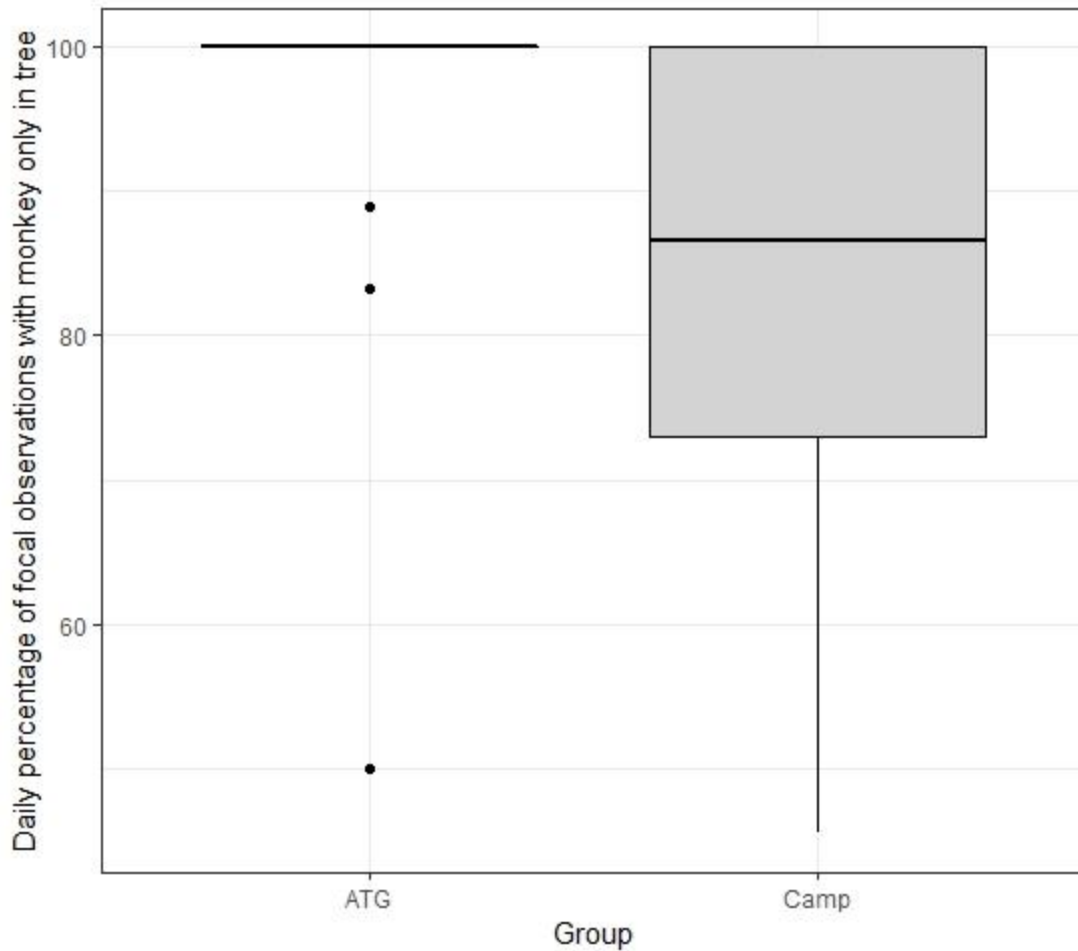


Figure 1: Daily percentage of focal observations per group where the focal individual stayed in the trees for the whole duration of the focal observation (ID data set: $n = 17$ days in ATG, $n = 16$ days in Camp). When running a mixed model to analyse predictors for the amount of focals spent fully in trees, the null model was not significantly better than the full model (X^2 ($df = 8$) = 8.52, $p = 0.38$).

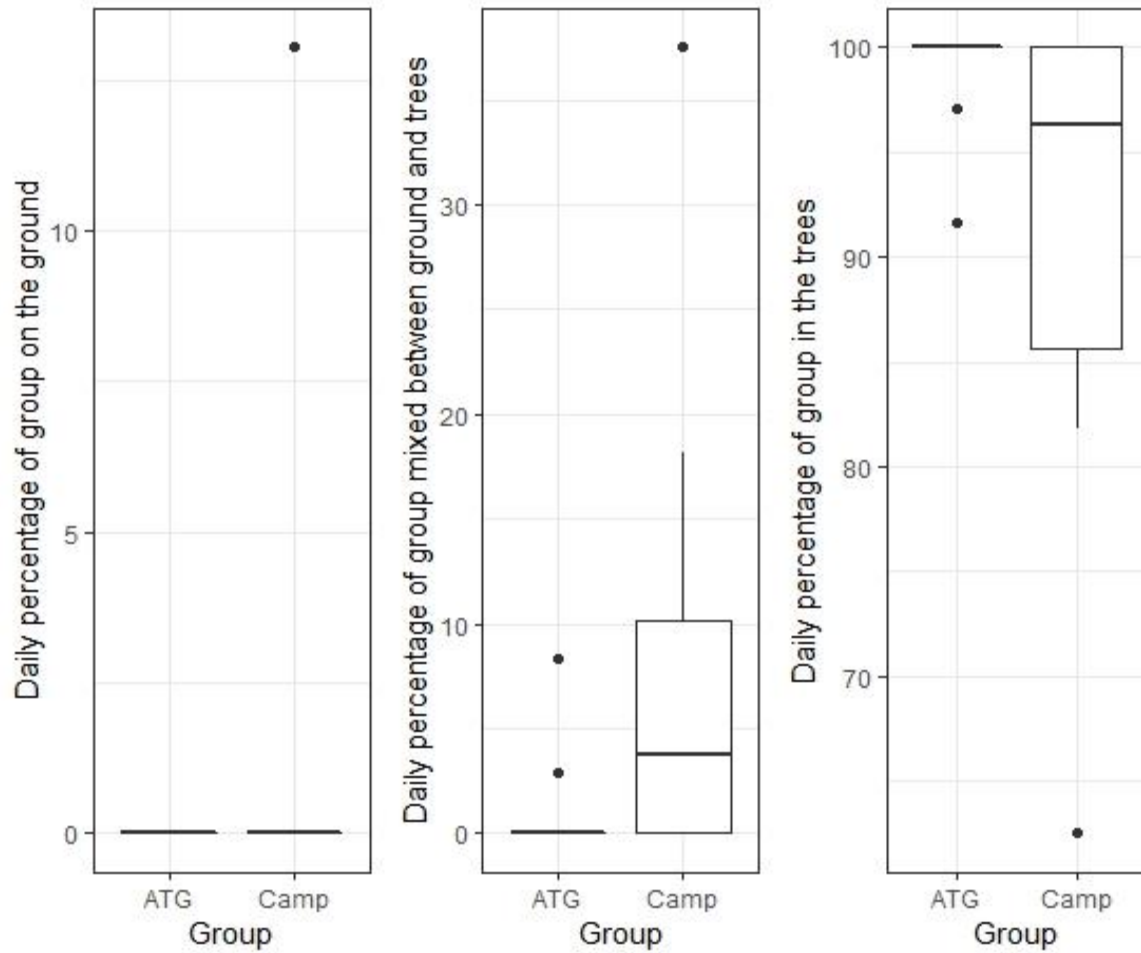


Figure 2: Position of group members during each 5-minute scans in each group: Ground = more than 50% of group members were on the ground, Mix = 50/50 between ground and trees, Trees = more than 50% of group members were in the trees (ID data set: n = 17 days in ATG, n = 16 days in Camp, Ground: Mann-Whitney U: U = 127.5, p = 0.77; Mix: Mann-Whitney U: U = 176.5, p = 0.02; Trees: Mann-Whitney U: U = 62.5, p = 0.02)

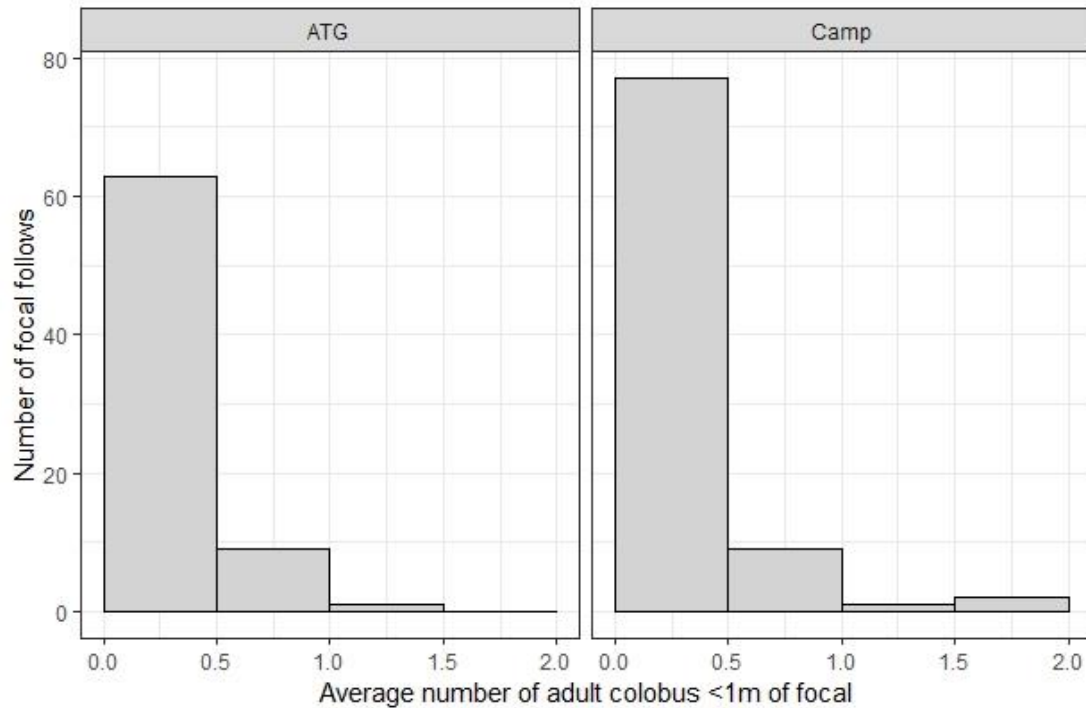


Figure 3: Average number of adult colobus within 1m of focal individual, based on up to 4 observations per focal follow. Group was not a significant predictor for number of adult colobus within 1m of focal individual (ID data set, mixed model: $t = -0.985$, $p = 0.368$, see Appendix 1.2 for full model)

Table 2: Overview of human presence in both study groups

	Camp group	ATG group
Tourists present on number of days	16/16	0/15
Average number of tourists per day	320.63	0
Number of days with tourists within 3m of focal	13/16	0/15
Villagers present on number of days	12/16	15/15

Average number of villagers per day	10.92	18.13
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Self-directed behaviour rates

Non-parametric tests

There was a significant difference in self-directed behaviour rates between the two study groups (Figure 4; $n = 17$ days in group without tourists, $n = 16$ days in group with tourists, Mann-Whitney U, $U = 190.5$, $p = 0.049$) when testing the full dataset. The group exposed to tourists on an almost daily basis (“Camp”) had a higher average hourly rate of self-directed behaviour (8.29 ± 3.95 acts / hour) than the group not exposed to tourists (“ATG”, 5.58 ± 3.91 acts / hour). This result supports the prediction of higher self-directed behaviour rates in the tourist exposed group (prediction 1).

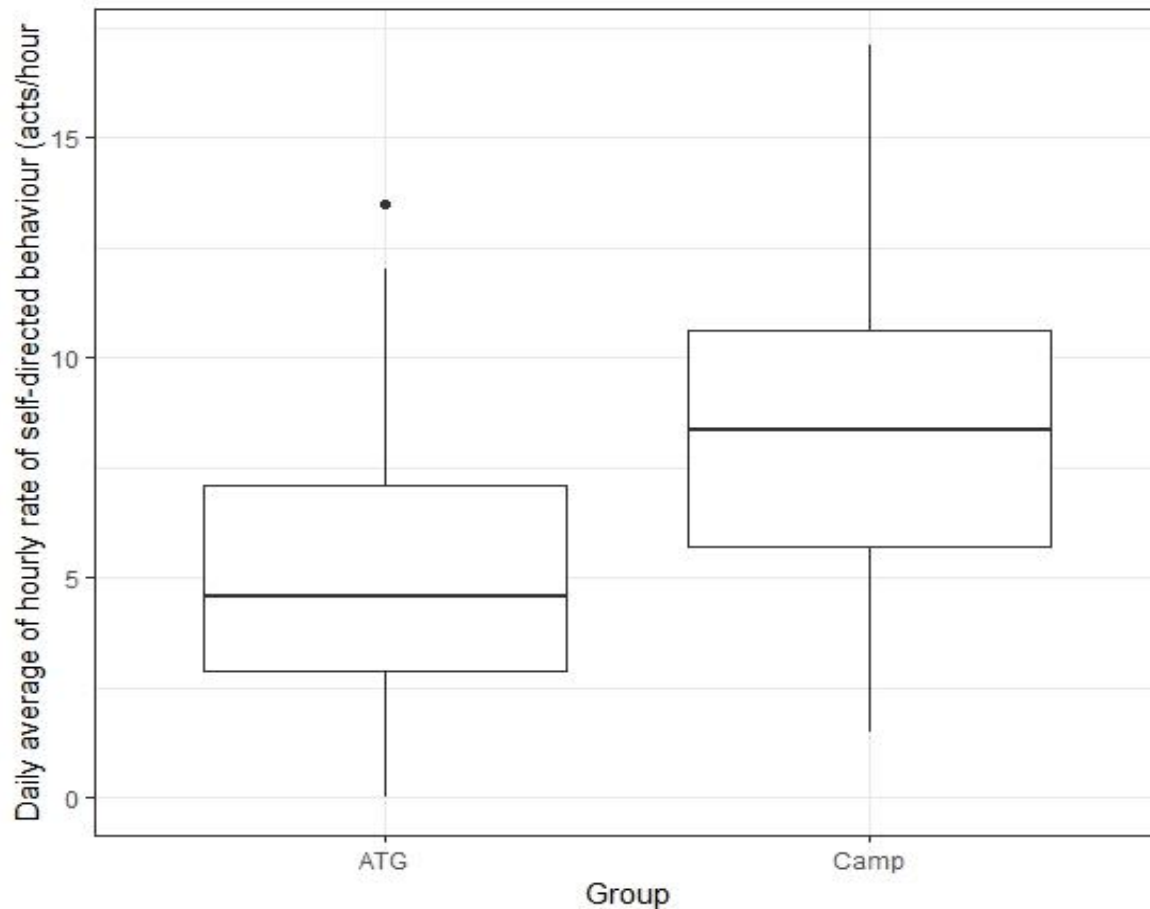


Figure 4: Daily average of hourly rate of self-directed behaviour in two groups of Zanzibar red colobus, one exposed to tourists and one not exposed to tourists (full data set; $n = 17$ days in group without tourists, $n = 16$ days in group with tourists, Mann-Whitney U, $U = 190.5$, $p = 0.049$)

When looking at self-directed behaviour rates within the full data set but filtered to Camp group only and differentiating between the rate at times with tourists present (8.38 ± 7.67 acts / hour) and at times with tourists absent (8.61 ± 8.66 acts / hour), there was no significant difference in hourly rate of self-directed behaviours (Figure 5; $n=43$ focal observations with tourists absent, $n=47$ focal observations with tourists present, Mann-Whitney U, $U = 1023.5$, $p = 0.915$). This does not support the prediction of a difference in self-directed behaviour rates between times of tourist presence and absence (prediction 2).

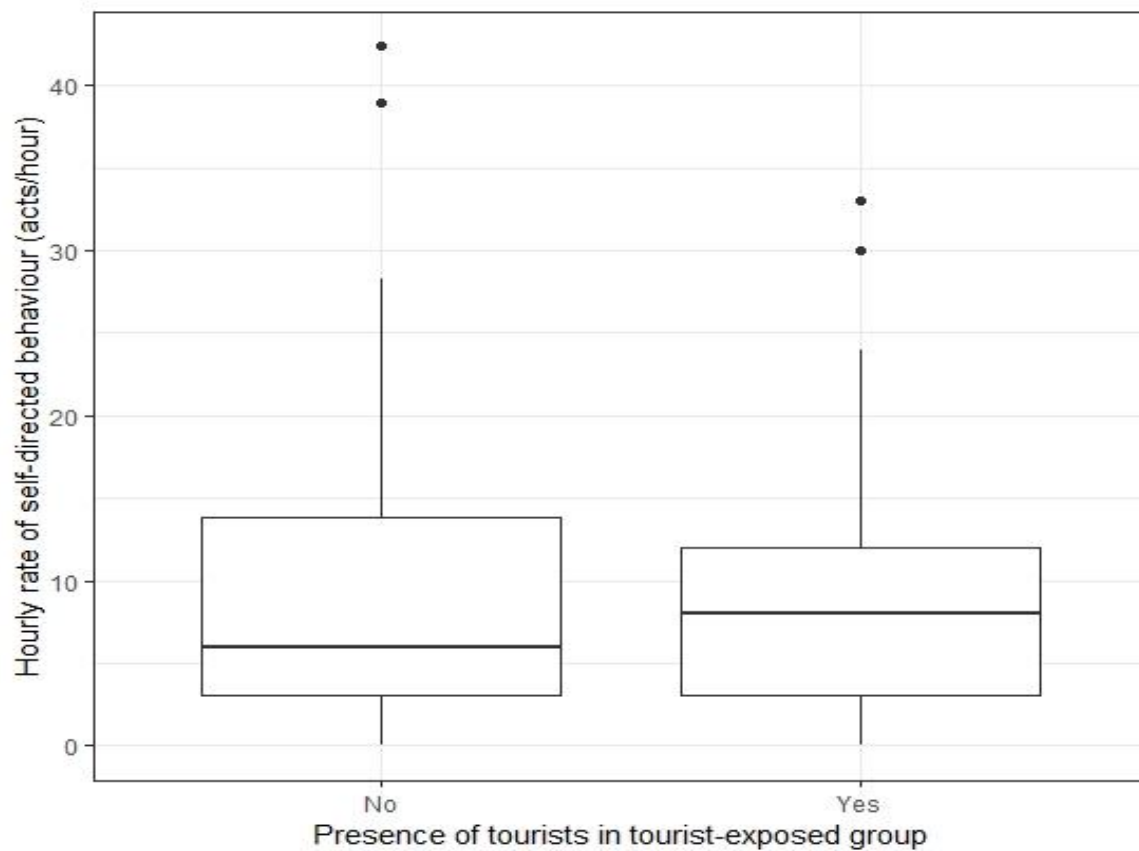


Figure 5: Average hourly rates of self-directed behaviour within the tourist-exposed group of Zanzibar red colobus, divided by tourist presence and absence during focal (full data set; $n=43$ focal observations with tourists absent, $n=47$ focal observations with tourists present, Mann-Whitney U, $U = 1023.5$, $p = 0.915$)

Mixed models

After conducting nonparametric tests on the full data set, I reduced the data set to individually identified individuals (163 out of 221 observations). This allowed for mixed models analysis, which accounts for pseudo replication by adding individual ID as random effect. From this mixed model, two of the seven tested predictors had statistically significant effects on self-directed behaviour rates (Table 3). One of these predictors was group. The monkeys in Camp group showed higher rates of self-directed behaviour, which is consistent with the findings from the non-parametric test conducted on the full dataset (Figure 4) and supports my prediction of higher rates of self-directed behaviour in the group exposed to tourists (prediction 1). Presence of

adult colobus within 1m of the focal individual was positively associated with rates of self-directed behaviour. However, since group was not a significant predictor for number of adult colobus within 1m of focal individual (mixed model: $t = -0.985$, $p = 0.368$, see Appendix 1.2 for full model), the number of adult colobus within 1m of the focal is not the reason for the difference seen in self-directed behaviour rates.

Table 3: Output from linear mixed-effect model on log-transformed self-directed behaviour rates with individual ID and hour of day as random effects, run on the dataset with identified individuals only ($n = 163$ focal observations). The full model provided a better fit to the data than the null model (X^2 ($df = 8$) = 21.77, $p = 0.01$).

Random effect	Variance	Standard deviation		
Individual ID	0.0005286	0.002299		
Time of day (hour)	0.130316	0.11416		
Predictor	Estimate	Standard error	t value	p value
Age-sex-class (Adult Male)	0.078751	0.091938	0.857	0.375
Distance to researcher (m)	-0.010149	0.023128	-0.439	0.658
Number of villagers present	-0.006692	0.031717	-0.211	0.842
Number of tourists within 3m of focal individual	0.016007	0.090463	0.177	0.850
Group (Camp)	0.196599	0.091330	2.153	0.028

Adult colobus within 1m of focal individual	0.185234	0.091349	2.028	0.039
Maximum noise level during focal observation	-0.009252	0.078564	-0.118	0.865
Rate of aggression received	0.026063	0.071244	0.366	0.688

Activity budget

The results from the activity budget models do not support my prediction of less time resting and more time moving in the tourist exposed group. The two groups did not differ in time spent on any of the behaviours (see Figure 5). Out of the five models tested, one was not stronger than the null model (Other: $X^2(df=9) = 3.92$, $p = 0.84$). The four other models did not show a difference between groups in either feeding (mixed model: $t = 0.69$, $p = 0.46$), resting (mixed model: $t = 0.08$, $p = 0.95$), grooming (mixed model: $t = -1.59$, $p = 0.10$) or moving (GLM with Poisson family: $z = -0.68$, $p = 0.50$; see Appendix 1.3 – 1.6 for full model outputs).

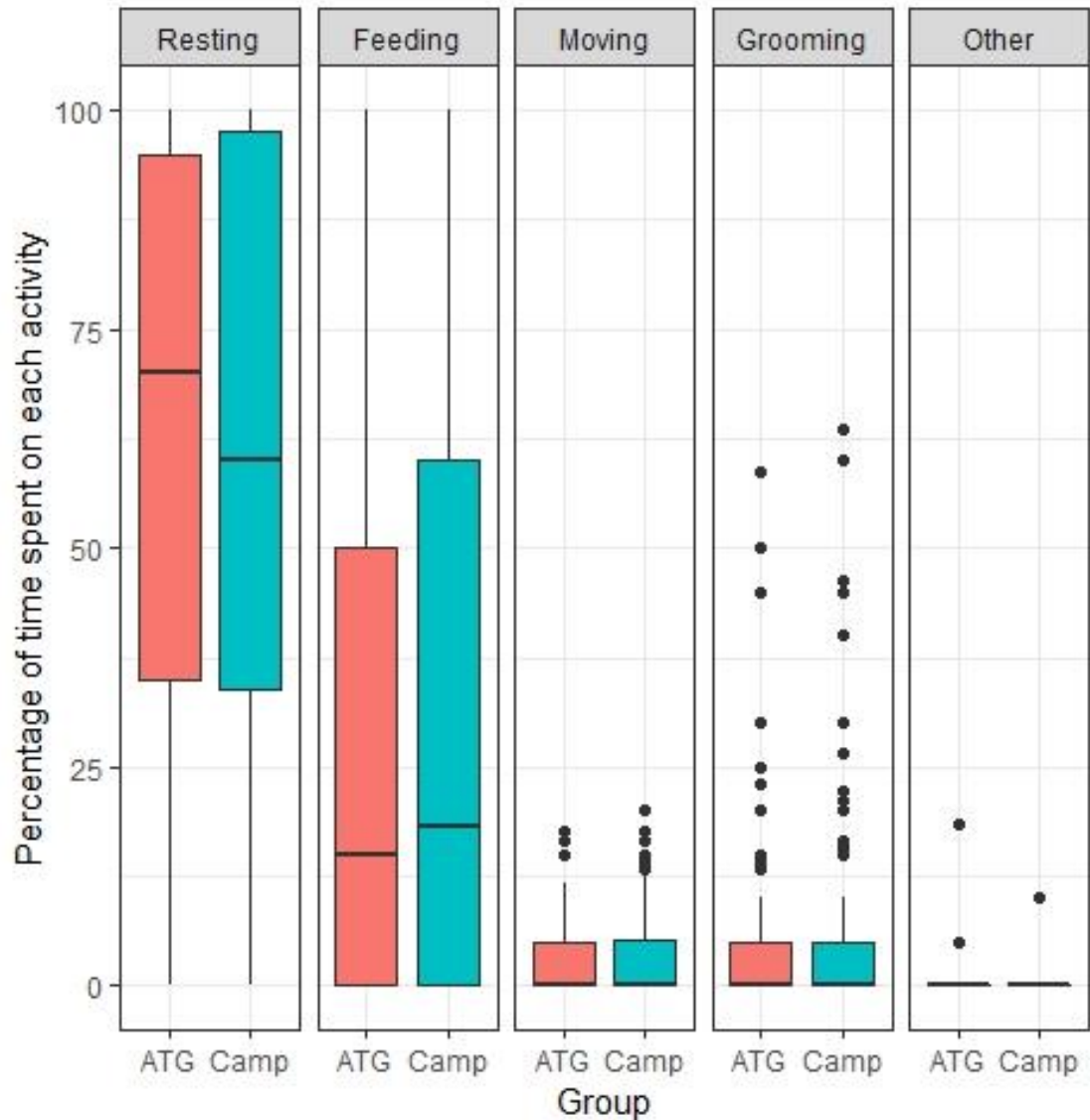


Figure 5: Activity budget from ID data set – percentage of each focal observation (n = 73 observations in ATG, n = 90 observations in Camp) spent on resting, feeding, moving, grooming and other in both groups

Travel distance

There was no difference in the distance travelled during focal observations between the two groups (mixed model, $z = -0.487$, $p = 0.67$; see Figure 7 and Appendix 1.7). The model was better than the null model (X^2 (df = 9) = 50.502, $p < 0.001$). This does not support the prediction

that colobus in the group exposed to tourists travel further than those in the group not exposed to tourists (prediction 4).

There is no correlation between the average number of tourists present and the average distance (m) moved per hourly segment ($r_s = -0.39$, $n = 12$ hourly segments, $p = 0.207$, see Figure 6).

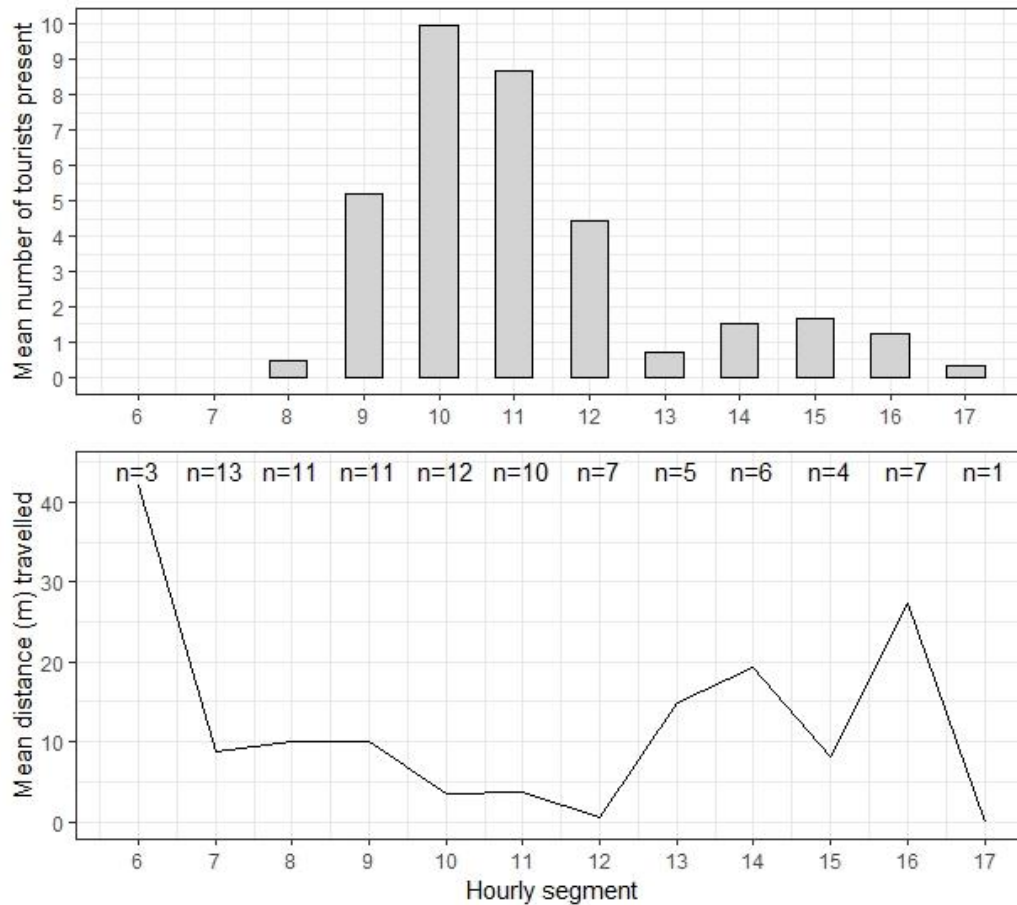


Figure 6: Comparison of mean number of tourists present in each hourly segment and mean distance travelled (m) by individuals in 20 minutes within each hourly segment in the tourist-exposed group (n = number of 20-minute focal observations per hourly segment).

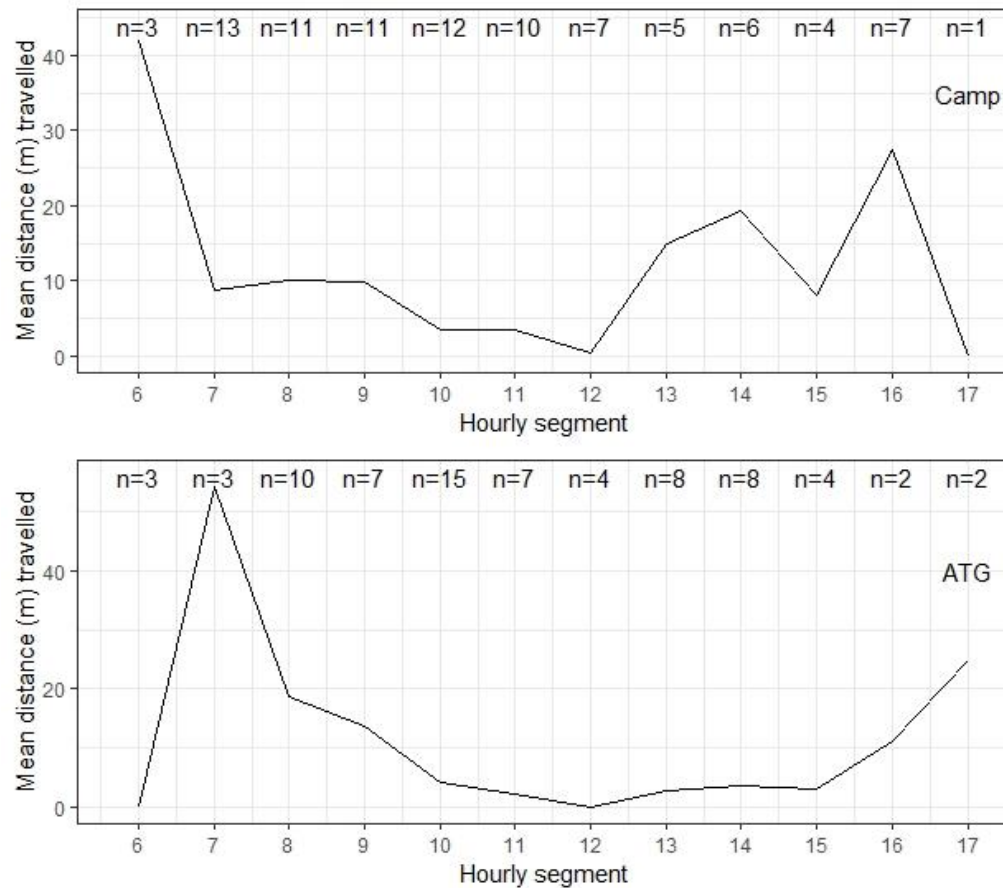


Figure 7: Comparison of mean distance (m) travelled in 20 minutes within each hourly segment between tourist-exposed group (top) and group not exposed to tourists (bottom; n = number of 20-minute focal observations per hourly segment in each group).

Discussion

The two study groups differ in their rates of self-directed behaviour, with the tourist-exposed group showing higher rates, but show no differences in activity budget. They did not differ in distance travelled during each focal observation. This supports my first prediction fully but did not support the three remaining predictions.

Self-directed behaviour (Predictions 1 & 2)

While self-directed behaviour rates in the group exposed to tourists were higher than those in the group not exposed to tourists, these differences do not seem to be directly related to the number

of or proximity to tourists. The two predictors with a significant effect on self-directed behaviour rates were group and number of adults within 1m of focal individual. Manson & Perry (2003) have found higher rates of self-directed behaviour rates in capuchins when the focal individual was in proximity to other capuchins, which fits with what I have found here. However, since there was no difference in number of adults within 1m between the groups, the difference in self-directed behaviour rates between groups must be due to other causes.

One explanation for the differences between groups could be due to differences in group size. The group with higher rates of self-directed behaviour was more than double the size of the group with lower self-directed behaviour rates. While grouping has many benefits such as quicker predator-detection and food resource defence (Hill & Dunbar, 1998), it can also cause stress to the primates (Markham *et al.*, 2015). Larger groups experience intragroup aggression more often and have to compete with each other for food (Majolo, de Bortoli Vizioli & Schino, 2008). This could lead to higher rates of self-directed behaviour among the group members. However, in this study the inter-individual distance of group members was not different between groups – the mean number of adults within 1m of the focal individual did not differ. It is therefore possible that while individuals in Camp group lived in a larger group, they did not experience the pressures of living in a larger group.

A further difference between the groups that could explain the difference in self-directed behaviour rates is the use of habitat. Camp group comes down to the ground to feed (personal observation) which could expose individuals to parasites. Parasite load has been found to positively influence self-directed behaviour rates in Japanese macaques (Duboscq *et al.*, 2016) and could explain the difference in self-directed behaviour rates between the two *P. kirkii* study groups. In this study I did not include any measure of parasite load into the data collection and therefore cannot include this in my model. However, there was no difference in the time spent grooming between the two groups, which could have indicated a difference in parasite load since one of the functions of grooming is to reduce ectoparasite load (Akinyi *et al.*, 2013). Since Camp group did not spend more time on grooming than ATG group, I would tentatively rule out differences in parasite load as the main reason for higher self-directed behaviour rates in Camp group.

Utilising the ground for foraging could also increase self-directed behaviour rates due to higher predation pressure on the ground (Cowlshaw, 1997). Both car accidents and dog predation have killed monkeys from our study groups (Georgiev *et al.*, 2019). Therefore, foraging on the ground could increase self-directed behaviour rates due to the perceived threats of predation. At the same time, the tourists could act as a shield between the colobus and dogs or cars and could be the reason Camp group individuals utilise the ground for feeding at all. Berger (2007) has shown that prey species use human areas such as roads to shield their new-borns from predators. During the study period, I only witnessed one dog approaching Camp group while ATG group was approached twice, one of these resulting in the death of two group members (Georgiev *et al.*, 2019). Whether Camp group perceives tourists as a shield or threat is difficult to infer from this study and could be investigated further in future studies.

The most notable difference between the two groups is the exposure to tourists. Even if rates of self-directed behaviour did not differ within Camp group during times of presence and absence of tourists, the tourists could cause the observed difference in self-directed behaviour rates. Higher rates of self-directed behaviours in tourist-exposed groups have been found in various primate species such as Barbary macaques, Tibetan macaques and spider monkeys (Maréchal *et al.*, 2011; Berman *et al.*, 2014; Pérez-Galicia *et al.*, 2017).

At the study site, Zanzibar red colobus have been visited by tourists for decades and show signs of overhabituation – they do not move away even when tourists are within 1m of them or touch them. During the study period, I have observed 11 instances of tourists coming to within 1m of the focal individual, without observing any human-directed aggression. Human-directed aggression as a result of tourists approaching too closely have been observed in Tibetan macaques, mountain gorillas and long-tailed macaques (Ruesto *et al.*, 2010; Klailova, Hodgkinson and Lee, 2010; Fuentes and Gamerl, 2005).

However, this lack of reaction does not necessarily represent the lack of increased anxiety for the monkeys. The increase in self-directed behaviour rates in the tourist-exposed group could indicate that *P. kirkii* perceive the tourists as a constant threat, raising the baseline rate of self-directed behaviours in the group. This would explain why temporary absence of tourists does not decrease the rate of self-directed behaviours.

Activity budget (Prediction 3)

The differences in activity budget between the two groups were not as large as expected and did not support the prediction regarding activity budget differences. The two groups did not differ in any of their behaviours examined. Neither did the number of tourists within three meters predict any of the behaviours. Therefore, whether tourists have an impact on the activity budget of Zanzibar red colobus is unclear.

Since Camp group is larger than ATG, I would have expected to see a reduced time resting, such as Fashing *et al.* (2007) found in black-and-white colobus. At the same time, other studies on red colobus and ursine colobus have found no decrease in resting time in larger groups once the study controlled for food availability (Teichroeb *et al.*, 2003; Gogarten *et al.*, 2014). I did not collect enough food data to control for food availability differences between the groups and can therefore not identify whether there should be a difference in resting time due to the size of the groups, or whether food availability makes up for the difference and results in no differences in resting times.

Travel distance (Prediction 4)

The average travel distance during focal observations did not differ between the two groups, which does not support my prediction of increased travel of the tourist-exposed group. However, tourist numbers are highest around noon when travel distances are low in both groups. This might be the reason tourist presence does not affect travel distance: when tourist numbers are highest, *P. kirkii* are resting, for which they stay in the trees (personal observation). When they are in the trees, they might not perceive tourists as a threat and therefore not move away.

Statistical analysis

For this study, I used both nonparametric tests and mixed models. This was due to a difference in sample size between the data set on just identified individuals and the one including not-identified individuals. I wanted to maximise the use of data I have collected and at the same time account for individual variability. While both the non-parametric test and the mixed model shows a difference in self-directed behaviour between the two groups, I wanted to ensure this difference is actually present and does not just come up as significant in the mixed model due to modelling errors. While this is not ideal in terms of statistical testing, it is better than only

presenting a model that might not be a perfect fit for the data set due to problems with normal distribution.

Tourist behaviour

Although this study did not show a direct effect of tourist behaviour on *P. kirkii* behaviour, tourists should be educated and encouraged to follow the rules. The park has clear rules in place (minimum distance of 3m to any monkey) and tourists are made aware of these rules by park staff, yet do not always follow them. During 26% of focal observations, tourists were closer than 3m to the focal individual. Tourists approaching focal individuals within 3m happened on 13 out of 16 observation days (see Table 2). This increases the risk of disease transmission both to humans and colobus and instances of close proximity should be reduced. Tourists who do not follow the rules should be educated on the importance of the rules both for their own and the monkeys' health.

Tourist behaviour has also been shown to influence monkey behaviour, both in Tibetan macaques (where an increase in decibel level led to an increase in aggressive behaviours from the monkeys; Ruesto *et al.*, 2010) and Barbary macaques (where male self-scratching rates were positively correlated to the number of tourists and interactions with tourists; Maréchal *et al.*, 2011). While this study could not show a direct link between tourist numbers and self-directed behaviour rates, the tourist-exposed group did show higher rates of self-directed behaviour. Managing tourist behaviours could reduce both the risk of disease transmission and the possible influence on the colobus' behaviour.

Conclusion

This study found a higher rate of self-directed behaviours in the tourist-exposed group. Group size, habitat use and tourist presence could all affect self-directed behaviour rates. There were no differences in activity budget between the groups and travel distance does not seem to be affected by tourists either. Even though this study did not show direct effects of tourists on the behaviour of Zanzibar red colobus monkeys, the aim should be to reduce instances of close proximity between tourists and monkeys by educating tourists. This study provides a first insight into the behaviour of two groups of an understudied species heavily utilised for primate tourism.

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Appendix

1.1: Ethogram for behavioural observations

Behaviour	Description
Feeding	Chewing on food items
Resting	Eyes closed, not moving
Observing	Eyes open, not moving
Scanning	Looking around, scanning the environment, while not moving
Possibly nursing	No nursing directly observed but proximity and position to offspring makes nursing likely
Nursing	Offspring is suckling
Climbing	Moving above ground
Out of view	Focal is not visible
Out of view feeding tree	Focal is not directly visible but positioned in a feeding tree
Out of view THV	Focal is not directly visible but positioned on the ground in terrestrial herbaceous vegetation (THV)
Grooming	Focal grooms another individual
Being groomed	Focal is groomed by another individual

Mutual grooming	Focal and other individual groom each other at the same time
Selfgrooming	Focal grooms self in slow, considerate movements
Walk, ground	Moving on the ground
Play, adult	Focal interacts in non-aggressive contact or movement with another adult individual
Play, juvenile	Focal interacts in non-aggressive contact or movement with a juvenile individual
Cross Road, arboreal	Focal crosses a road while moving above ground (tree tops, cable across the road)
Cross Road, ground	Focal crosses a road while on the ground
Copulation	Focal is involved in copulation
Agonistic behaviour	Focal threatens, chases or bites other individual
Inspection	Focal inspects another individual

1.2 Full model for Average number of adult colobus within 1m of focal individual – the model was a better fit than the null model (X^2 (df = 8) = 322.64, $p < 0.001$).

Random effect	Variance	Standard deviation		
Individual ID	4.706	2.169		
Time of day (hour)	1.372	1.171		
Predictor	Estimate	Standard error	z value	p value
Age-sex-class (Adult Male)	1.197271	0.855893	1.399	0.16186
Distance to researcher (m)	-0.353157	0.030369	-11.629	<0.001

Number of villagers present	-0.001363	0.038117	-0.036	0.97147
Number of tourists within 3m of focal individual	-0.233306	0.139518	-1.672	0.09448
Group (Camp)	-0.756727	0.767915	-0.985	0.32441
Adults within 1m of focal	-0.798393	0.114608	-6.966	<0.001
Maximum noise level during focal observation	-0.272607	0.110754	-2.461	0.01384
Rate of aggression received	0.177297	0.046918	3.779	<0.001

1.3 Full model on Feeding – the model was a better fit than the null model (X^2 (df = 9) = 63.10, $p < 0.001$).

Random effect	Variance	Standard deviation		
Individual ID	76.36	8.738		
Time of day (hour)	50.77	7.125		
Predictor	Estimate	Standard error	t value	p value
Age-sex-class (Adult Male)	-1.10805	6.84196	-0.162	0.86350
Distance to researcher (m)	-0.80586	1.42891	-0.564	0.54207

Number of villagers present	-0.09336	1.97451	-0.047	0.99587
Number of tourists within 3m of focal individual	1.16834	5.65490	0.207	0.85416
Group (Camp)	4.47603	6.52381	0.686	0.45702
Self-directed behaviour rate	12.10952	5.02229	2.411	0.01297
Maximum noise level during focal observation	-7.06734	4.97904	-1.419	0.14122
Rate of aggression received	8.21437	4.41841	1.859	0.05439

1.4 Full model on Resting – the model was a better fit than the null model (X^2 (df = 9) = 63.78, $p < 0.001$).

Random effect	Variance	Standard deviation		
Individual ID	40.49	6.363		
Time of day (hour)	100.30	10.015		
Predictor	Estimate	Standard error	t value	p value
Age-sex-class (Adult Male)	2.7847	6.5383	0.426	0.65757
Distance to researcher (m)	0.1913	1.4869	0.129	0.87224

Number of villagers present	-0.3908	2.0589	-0.190	0.81923
Number of tourists within 3m of focal individual	-5.3309	5.8381	-0.913	0.34484
Group (Camp)	0.4796	6.4184	0.075	0.95496
Self-directed behaviour rate	-18.3212	5.2241	-3.507	0.00037
Maximum noise level during focal observation	1.3580	5.1758	0.262	0.76095
Rate of aggression received	-7.7341	4.6158	-1.676	0.08065

1.5 Full model on Grooming – the model was a better fit than the null model (X^2 (df = 9) = 74.873, $p < 0.001$).

Random effect	Variance	Standard deviation		
Individual ID	1.889e+01	4.346e+00		
Time of day (hour)	1.248e-08	1.117e-04		
Predictor	Estimate	Standard error	t value	p value
Age-sex-class (Adult Male)	-2.6544	2.8881	-0.919	0.33222
Distance to researcher (m)	1.0444	0.5492	1.902	0.05056

Number of villagers present	0.7165	0.7506	0.955	0.33628
Number of tourists within 3m of focal individual	3.5746	2.1991	1.626	0.09071
Group (Camp)	-4.2133	2.6458	-1.592	0.09719
Self-directed behaviour rate	5.8531	3.1010	1.887	0.05054
Maximum noise level during focal observation	6.0078	1.8869	3.184	0.00139
Rate of aggression received	-0.6948	1.6801	-0.414	<0.001

1.6 Full model on Moving – the model was a better fit than the null model (X^2 (df = 9) = 105.91, $p = 0.01$).

Random effect	Variance	Standard deviation		
Individual ID	1.8404	1.3566		
Time of day (hour)	0.7233	0.8505		
Predictor	Estimate	Standard error	z value	p value
Age-sex-class (Adult Male)	0.67171	0.54634	1.229	0.21890
Distance to researcher (m)	-0.13229	0.03622	-3.653	<0.001

Number of villagers present	0.03677	0.05183	0.709	0.47803
Number of tourists within 3m of focal individual	0.44651	0.12328	3.622	<0.001
Group (Camp)	-0.33331	0.49244	-0.677	0.49851
Self-directed behaviour rate	0.95395	0.13630	6.999	<0.001
Maximum noise level during focal observation	-1.09235	0.17823	-6.129	<0.001
Rate of aggression received	-0.11262	0.08461	-1.331	0.18318

1.7 Full model on distance travelled during 20-minute focal observation – the model was a better fit than the null model (X^2 (df = 9) = 50.502, $p < 0.001$).

Random effect	Variance	Standard deviation		
Individual ID	3.967	1.992		
Time of day (hour)	34.737	5.894		
Predictor	Estimate	Standard error	z value	p value
Age-sex-class (Adult Male)	-1.6732	3.4359	-0.487	0.79876
Distance to researcher (m)	-0.5768	3.4204	-0.169	0.00713

Number of villagers present	-1.2299	1.1516	-1.068	0.28720
Number of tourists within 3m of focal individual	-4.2446	3.2555	-1.304	0.17516
Group (Camp)	-1.6732	3.4359	-0.487	0.66850
Self-directed behaviour rate	4.4584	2.9199	1.527	0.10829
Maximum noise level during focal observation	0.6127	2.8777	0.213	0.84076
Rate of aggression received	3.9722	2.5830	1.538	0.11158
Adults within 1m of focal individual	-1.7076	3.3495	-0.510	0.64219