Ecological and Behavioural Adaptations of the Endangered Lion-Tailed Macaque to a Rainforest–Anthropogenic Habitat Matrix in India: Implications for Management

Preliminary Project Report submitted to Rufford Foundation, UK

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Scientific Publications

(a) Dhawale AK, Kumar MA, Sinha A. Changing ecologies, shifting behaviours: Behavioural responses of a rainforest primate, the lion-tailed macaque Macaca silenus, to a matrix of anthropogenic habitats in southern India. PloS one. 2020 Sep 23;15(9):e0238695.

Abstract

Primates are amongst the many taxa known to have direct, often detrimental, interactions with humans, particularly in anthropogenically-modified habitats. Such interactions are escalating globally making it crucial to understand them for the management and conservation of these often-threatened species. A unique case of potentially detrimental human-primate interaction is that of the endemic, habitat-specialist lion-tailed macaque *Macaca silenus* and the resident local community, which has developed in recent years in the Western Ghats mountains of southern India. Thus, we sought to understand the extent and nature of behavioural changes exhibited by the endangered lion-tailed macaque, as it explored and utilised relatively novel anthropogenic habitats in the human-dominated landscape of the Valparai Plateau in the Western Ghats of Tamil Nadu, India. We particularly documented behaviours, including foraging and social interactions, which would best reflect decisions made by the macaques as they utilised the new habitats, taking into account the structural features of the habitats, availability of food resources and the presence of humans. The availability of provisioned food in the human-dominated habitats appeared to significantly reduce the time spent by the troop in foraging, allowing them to engage in other behavioural activities, such as resting. Furthermore, the nature and rates of social interactions were unexpectedly different in natural and anthropogenic habitats, and individuals seemed to have adopted novel behavioural strategies, leading to altered social dynamics in the troop, possibly in response to provisioning. This study thus highlights the importance of understanding behavioural changes displayed by a primate species in response to novel ecologies, especially involving human-wildlife interactions; such knowledge could be crucial for the planning and implementation of management and conservation strategies for endangered species such as the lion-tailed macaque and other primates in anthropogenic landscapes.

(b) Dhawale A K and Sinha A. 2020. City lights: The synurbisation of a rainforest-adapted primate, the lion-tailed macaque *Macaca silenus* and its adaptation to anthropogenic habitats. *Journal of Biosciences*, submitted.

Abstract

The lion-tailed macaque is an endangered species, endemic to the Western Ghats mountains of southern India. The Anamalai hills harbour 63 groups of lion-tailed macaques, many of which occur in rainforest fragments amidst tea- and coffee plantations on the Valparai plateau. Being highly arboreal, these populations have always been assumed to be largely restricted to their fragmented forest patches and possibly unable to navigate successfully through the tea-plantation matrix. While adult males have occasionally been recorded along roadsides between forest fragments, we provide evidence for the migration of an entire troop out of a forest fragment into adjacent human settlements, leading to the inclusion of areas completely devoid of natural vegetation into the core home range of this troop. We argue that a combination of hostile inter-troop encounters, a natural urge to expand their range and the discovery of novel and relatively easily accessible food resources may have led to such an unusual ranging pattern, accompanied by significant changes in individual behavioural profiles, which we classify under inexorable processes of synurbisation.

(c) Dhawale A K and Sinha A. 2020. Gemini calling! Successful twinning in wild, endangered lion-tailed macaques *Macaca silenus* in the Anamalai hills of the Western Ghats, India. In preparation.

Abstract

We have recorded the first occurrence of surviving twins in the endangered lion-tailed macaque *Macaca silenus* from the Anamalai hills of the Western Ghats, India. We also recorded a second set of twins from the same population within six months of our first record. Only two previous cases of twinning had been observed in this population since 2000; in both cases, however, the twins did not survive beyond a few weeks. We followed and opportunistically collected behavioural data *ad libitum* on both sets of twins for seven months between April and October 2019. Although this particular subpopulation of lion-tailed macaques has historically been restricted to a rainforest fragment measuring 92 ha, adjacent to human settlements, direct interactions with humans have been observed only over the last ten years. The study troop, however, now visit settlements at a rate of 0.52/ day and exploits human-source foods. Both mothers, carrying the twins, were extensively terrestrial in their movement though the mother with the younger set of twins also used the canopy and certain precarious substrates, such as cable wires, to traverse her home range. Our report thus establishes conclusively that twinning does occur in this endangered species and that twins are able to survive successfully to become juveniles. Our report also supports previous evidence that twinning may occur in higher frequencies as a direct

response to provisioning while the mothers' behavioural adaptability may ensure the successful survival of twin offspring.

Introduction

I. Background

With a constant, unceasing increase in the expansion of human-dominated landscapes, especially in tropical countries like India, wild animals are increasingly observed to exist outside designated wildlife areas, often surrounded by high human densities (K. K. Karanth & Nepal, 2012). These wild animals face increasing human-induced pressures such as deteriorating habitats, the extraction of resources essential to wildlife and processes of urbanization, leading to the direct interactions between humans and animals (Soulsbury & White, 2016).

At present, numerous studies focus on the resulting interfaces between humans and animals, often observed in the form of direct interactions between the two parties. Although some interactions may be entirely neutral, it is especially pertinent to give focus to the hostile interactions that may cause harm to one or both of the parties involved; these interactions, often called Human-Wildlife Conflict (HWC), are heightening globally. Human-wildlife conflict can have extremely negative consequences on people that are exposed to interactions with wildlife including loss of livestock, damage to crops or homes, competition for local resources and even loss of lives or injury by wild animals (Thirgood et al., 2005). Conversely, HWC can have detrimental effects on wildlife as well, often being cited as one of the critical threats globally faced by wildlife (Dickman, 2010), leading to retaliatory killing of animals, trapping, poisoning, and wildlife trade (Sillero-zubiri & Switzer, 2015).

Over 70 species of primates are known to crop raid from around the world (Wolfheim, 1983), making human-primate conflict one of most globally prevalent human-wildlife conflict interactions.Primates tend to be highly adaptable, and are known to frequently come into conflict with humans, particularly in anthropogenic situations (Lee & Priston, 2005). Many species, especially of the genus *Macaca*, are known to have adapted to a wide variety of habitats across Asia and Africa (Thierry et al., 2000), living in close proximity to human settlements; these species are also thought to contribute significantly to human-wildlife conflict (Pirta, 1997). Such macaque populations have traditionally been exposed to human presence are now commensal with humans across the Indian subcontinent.

Given this urgent need to address the issues of conflict, a potential first step might be to examine the nature and patterns of human-animal interactions. In order to do so, we may first examine certain ecological and behavioural patterns displayed by animals when interacting with humans, as these are often the first responses that animals have to a changing environment (Tuomainen & Candolin, 2010).

A rapidly growing branch of animal studies, dealing with the expansion of human habitation and other forms of development, dubbed as urbanization, brings focus to the re-imagination of urban spaces from the perspective of animals (Barua & Sinha, 2017), understanding the challenges faced by wildlife in these novel ‘habitats’ and examining the extent to which humans and animals can, not only co-exist, but also benefit from one another (Soulsbury & White, 2016). In order to understand animal perspectives, especially in the context of exploring novel habitats, one may begin at examining the initial, biologically determined mechanisms: senses and movement. Senses “represent the interface between the anatomical environment and [a] behaving organism” (Dominy et al., 2004); these are essentially the first mode through which a being perceives its surroundings and include vision, audition, olfaction and gestation. In novel habitats, an animal encounters a plethora of previously unknown sights, sounds, smells and tastes, presenting them new modes of exploring, behaving and moving. Movement is perhaps the second stage required in facilitating an animal to 'explore' a habitat, by allowing it to physically interact with the surroundings and *utilise* potential resources. Often, animals acquire resources from anthropogenic habitats (Soulsbury & White, 2016); although biologically determined mechanisms such as ability to perceive a resource (through senses) and ability to access the resource (through movement) are crucial, various other socio-ecological factors play an equally important role. Some animals, such as primates, depend on social interactions with members of their troop, to function in various aspects of life such as foraging for food, watching out for predators, learning new skills and establishing hierarchies. Social interactions can often determine the fitness of an individual in a troop as these interactions are hypothesised to be influenced by various external factors such as the immediate environment, habitat structure, presence of predators and even other members of the troop (C. P. Van Schaik & Hooff, 2015). Social interactions can also inform us about the evolution of cognitive abilities in primates (Sinha, 1998), which may be especially required in the exploration of novel areas. Further, animals must inevitably interact with other species in anthropogenic habitats, such as humans; these interactions may be aggressive, affiliative or neutral. Anthropological studies hypothesise that these interactions shape not only the lives of animals, but also human, often influencing the evolution of culture in both parties (Wolch, 2002). Such cultural knowledge may be passed on amongst individuals, leading to the emergence of alternative behavioural strategies that aid in best adapting to external habitats (Sinha, 2005).

In order to understand such behavioural adaptability in a species that has only recently begun to explore a novel habitat, it is crucial to seek information from studies conducted on species in other similar contexts.

II. Literature Survey

Studies conducted on many species of primates indicate the potential for adaptability to anthropogenic habitats, where some even exhibit altered behavioural strategies that are largely influenced by the structure of the habitat (Ripley, 2008) and the availability of resources (Fleagle et al., 1999). Supporting evidence can be found in certain populations of olive baboons *Papio hamadryas anubis* of the Gashaka Gumti National Park, Nigeria: these baboons raid cultivated crop fields as a means of efficient foraging and appear to have shorter inter-birth intervals and reduced infant mortality (Warren et al., 2011). This altered behavioural pattern is attributed to the theory that benefits from the 'higher-quality' foods acquired by crop raiding outweigh the associated costs, such as being chased by farmers (Warren et al., 2011). Some populations of baboons and several other species have thus begun to use this strategy preferentially over their natural foraging strategies, although some studies have shown that certain primate species are more vulnerable in anthropogenic habitats as compared to undisturbed forests (e.g., Singh et al., 1998). A study on the bearded saki *Chiropotes satanas* showed that troops resident in habitats with stark structural differences exhibited variation in behavioural strategies such as change in group size and diet, allowing them to adapt to varying environmental conditions (Silva & Ferrari, 2009). These studies have, however, compared behavioural variation only across troops residing in locations that are isolated from one another. Very few studies have examined the behavioural flexibility displayed by primate individuals themselves. Although some investigations have documented the inter-individual variability in behavioural strategies within a group and demonstrated how these differences can influence the way these groups of primates utilise the landscape (Anderson et al., 2006), very few have examined inter-individual and inter-troop variability of a subpopulation of macaques that share a singular habitat, but vary in group size and social organisation.

A study on the forest-specialist Angola colobus *Colobus angolensis palliates* revealed that the species utilises a range of behavioural strategies in the matrix of habitats that surround the fragmented forest patches which it inhabits, including anthropogenic plantations and orchards (Anderson et al., 2006). It also observed a change in group structure across different habitats and was able to predict, on the basis of habitat structure and food availability, whether an individual colobus was likely to be present in a particular habitat, thus aiding in our understanding of how the species is able to disperse and use the habitat matrix in which it occurs. Another study on the Tonkean macaque *Macaca tonkeana* in Sulawesi discovered variation in the ranging behaviour of two troops of macaques, where those present in altered habitats decreased their ranging but increased the intensity of usage of the habitat; they also spent more time on the ground due to the lack of canopy in these habitats (Ripley, 2008).
In a study on bonnet macaques *Macaca radiata*, Ram et al., 2003 showed stark differences in the behavioural strategies of adult females, while foraging on natural and provisioned food, as did Sinha et al. (2005) in adult males. These studies observed a change in patterns of social interactions within the same individuals, the nature of change often being influenced by the position of the individuals in the social dominance hierarchy, under different conditions of foraging. Such evidence shows that resource availability can significantly alter individual behaviours, consequently leading to changes in social organisation and demography, with even significant population-level consequences for long-term survival (Sinha et al., 2005; Sinha & Mukhopadhyay, 2013).

III. **Research Gaps Identified**

While most of these studies have examined the behavioural variation displayed by species in response to change in habitats, there is, still, little known about the ability of individuals of particular primate species to alter their behaviour and adopt novel strategies in order to take advantage of a given environmental situation. Additionally, very few studies have attempted to evaluate the effects of direct interactions with humans on the behaviour of primate groups. While many studies have focussed on the transmission of disease between humans and non-human primates (e.g., Wallis, 1999), one study has examined how human presence results in decreased predation risks for vervet monkeys in the Amboseli National Park of Kenya (Isbell & Young, 1993). Yet, there appears to be a significant lack of studies that have quantified varying degrees and elaborated on the nature of human-non-human primate interactions, and examined their influences on the behaviour of the non-human species involved.
This is especially so for certain species like the lion-tailed macaque that are habitat specialists, primarily frugivorous, a species with rudimentary intra-group social interactions (Kumar, 2013), and with very little exposure to humans (Singh et al., 1997). This species has, however, in the recent past, due to intensive logging and other encroachments in its rainforest habitats in certain regions of the Western Ghats, become exposed to humans and has even begun frequenting their settlements (Singh et al., 2001). Although the lion-tailed macaque is otherwise a fairly well-studied species, there is considerable lack of information on the behavioural patterns displayed and the strategies adopted by particular individuals, especially when they range and forage regularly in anthropogenic habitats and interact with humans in these areas. What also remains unknown are potential changes in the social behaviour of these groups as they exploit their new habitats, particularly as social strategies in primates have been hypothesised to generally respond to selection pressures in their external environments (van Schaik & van Hooff, 1983). Further, there is considerable lack in information regarding the physiological response, such as stress, of a habitat specialist macaque in response to anthropogenic habitats. Knowledge in all these domains is, however, crucial not only to understand the behavioural adaptability of a species, traditionally confined to its rainforest

habitat, to a new anthropogenic landscape but also to inform potential management and conservation strategies for the species.
Thus my proposed project aims to set in place the long-term behavioural monitoring and management of a subpopulation of lion-tailed macaques residing in the Puthuthottam forest fragment, situated in the southern Western Ghats, on the Valparai Plateau, Tamil Nadu. The novel changes faced by individuals in this altered habitat and their behavioural responses are still relatively unknown. I propose an interdisciplinary approach which would first document shifts in ranging, foraging and intra- and inter-troop social interactions of this subpopulation of lion-tailed macaques in response to their altered habitats. Further, I propose to address the increasing conflict between the macaques and the local communities by initiating dialogues with concerned tea-estate managers, on-field forest department staff and residents of the surrounding human-inhabited areas to further understand how best to ensure the well-being of both macaques and people in the coming years.

IV. Objectives

The objectives of the proposed study are to uncover the demographic, ecological and behavioural responses of the lion-tailed macaque groups that are increasingly utilising the anthropogenic landscape surrounding their rainforest habitats on the Valparai Plateau and initiate long-term monitoring of the subpopulation of the Puthuthottam rainforest fragment. The Plateau is a landscape that has experienced large-scale expansion of tea and coffee plantations, and extensive clear felling over the last century; with the increasing fragmentation of its rainforests, Valparai is likely to provide an important model system to understand how currently threatened rainforest primate species respond to the loss and fragmentation of their natural habitats and increasing interactions with local human communities.

Objective 1: Gaining insight into the status lion tailed macaque subpopulation of the Puthuthottam rainforest fragment by documenting demographic factors such as troop numbers, sizes and age/sex compositions; estimating birth rates and mortality in adults and infants

Objective 2: Examining habitat use and competition across the multiple lion-tailed macaque troops residing in Puthuthottam forest fragment through ranging and movement behavior

Objective 3: Gaining insight into the adaptability of lion-tailed macaque troops that frequent human habitations by investigating behavioural variations in foraging and social interactions within and across interacting troops

Objective 4: Promoting co-existence between the liontailed macaques and the local human communities on the Plateau by implementing specific management strategies

V. Detailed Methodology

The study will primarily involve the non-invasive following and behavioural observations of specific habituated troops of lion-tailed macaques, the adult members of which would be individually identified by characterising their unique morphological features, wound marks and other infirmities, if any; GPS data with accuracy up to 3m; physiological data on stress levels collected from faecal samples of adult macaques; genetic data collected from faecal samples of adult macaques; non-participant observations of the local people, with which the macaques have begun to interact, often antagonisically, in recent years.

Study Site

The study will be carried out on the Valparai plateau 10˚ 19’ 39.22"N, 76˚ 57’ 18.98"E, located in the Anamalai hill range of the southern Western Ghats, in the state of Tamil Nadu. An expanse of around 220 km2, the Valparai plateau is a heterogeneous landscape of rainforest fragments interspersed with tea, coffee and Eucalyptus plantations. With an elevation ranging from 900 m to 1450 m, the plateau has a predominant native vegetation type of wet evergreen rainforest (Muthuramkumar et al., 2006). The Anamalai hills, separated from the Nilgiri hill range by the Palghat Gap, are important for the conservation of the endemic lion-tailed macaque, this being one of the only eight locations where the species is present (Kumara & Singh, 2003; Figure 1).

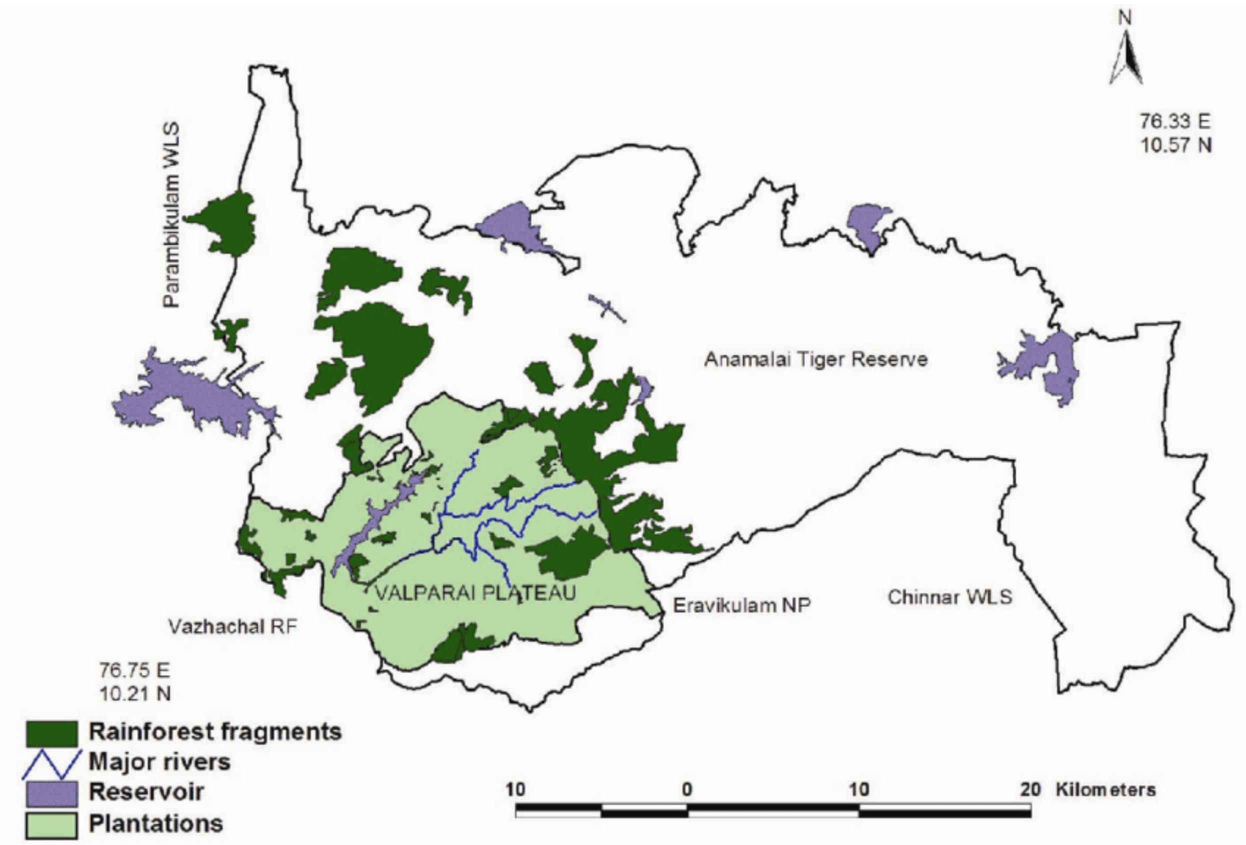


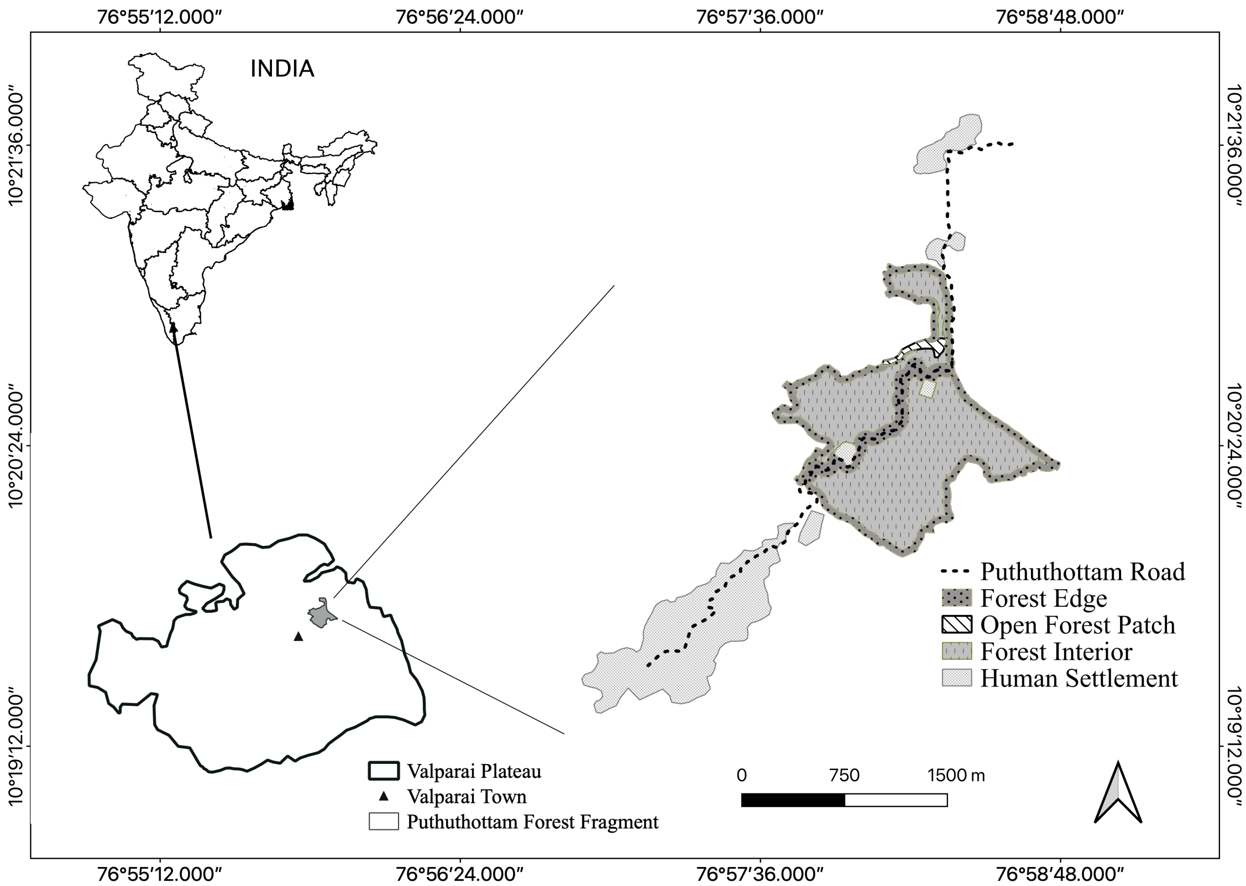
Fig 1. Map of Valparai plateau (light green) and surrounding Anamalai Tiger Reserve. Rainforest fragments are shown in dark green and water bodies in blue. Adapted from (Sidhu et al., 2015)

Since the early 1800s, extensive selective logging has led to the fragmentation and degradation of the native rainforest habitat. The lion-tailed macaque population is scattered in these remaining pockets of rainforest across the Valparai plateau (Figure 2).

One such rainforest fragment, the Puthuthottam forest fragment, with an area of 92 ha and neighbouring the town of Valparai, is of particular importance, as it harbours a subpopulation of macaques, consisting of five troops and c. 160 individuals. These troops spend significant periods of time in different anthropogenic habitats, visiting human settlements inside and around the fragment, including Valparai town, and traversing roads, orchards and plantations surrounding the fragment (Figure 2).

Fig 2. The study habitat types within the Puthuthottam forest fragment, located on the Valparai plateau in the Anamalai Hills, southern India.

Field Methods



Group Follows: Each of the groups residing in the Puthuthottam forest fragment will be followed for an extended period of time to ascertain absolute troop numbers, and age/sex composition. Each troop will be revisited at pre-determined intervals to collect data on birth and death rates of both adults and infants.

Ranging behaviour: GPS locations would be taken periodically at pre-determined intervals of space and time during the simultaneous and systematic following of all troops present in the Puthuthottam forest fragment, as they range over both natural and anthropogenic habitats. These points would later be mapped to calculate distances travelled, directions of movement and rates of ranging across the different habitats traversed by the study individuals. Such an analysis is essential to map the new-found home range of these macaque troops, particularly in so far as they overlap with human habitations, farms, orchards and roads, potential areas for escalated human-primate conflict. It will also provide insight into the competitive encounters between macaque troops and help establish determinants of habitat use.

Behavioural observations: The selected, identified macaque troops would be followed periodically from dawn to dusk for a period of about 15-20 days in a month for 20 months, from March 2018 to March 2020. Standard behavioural sampling protocols, including instantaneous group scans and focal animal sampling, would be conducted on identified adult macaques at specific pre-determined time intervals to assess their time-activity budgets and habitat and substratum use in different natural and anthropogenic environments. The proportion of time spent foraging on both natural and human-origin foods, other aspects of their foraging behaviour, including diet choice, searching and handling time for different food items, frequencies of intra-troop affiliative, agonistic and other social interactions, the nature and frequency of human-macaque interactions and the impact of such interactions on the ranging, foraging and socio-behavioural patterns of the macaques would then be evaluated and measured, as appropriate, from these observational data.

Habitat characterisation: Extensive surveys will be conducted across the Puthuthottam forest fragment, using the plot-less plant survey method to determine various structural and vegetational features.

Data Analysis

Quantitative behavioural data: Quantitative data will be analysed using standard non-parametric tests such as the Mann-Whitney U test, Kruskal-Wallis test and Kolmogorov-Smirnov test, matrix analysis using the Mantel test and regression analysis to appropriately determine behavioural changes in response to habitat characteristics. Generalised linear mixed effects models to quantify effect size of behavioural changes in response to anthropogenic habitats. All quantitative behavioural data analysis will be carried out in R (R Team, 2013).
Movement data: Kernel density estimation to delineate home range and core use area of all troops present in Puthuthottam. Habitat use selection ratios analysis to determine habitat use and selection by lion-tailed macaques. Movement data analysis will be carried out in R (R Team, 2013) and QGIS (QGis, 2011).

VI. Expected Outcomes

I. Mapping the distribution and demography of lion-tailed macaque groups that are increasingly interacting with people on the Valparai Plateau and characterising their natural and anthropogenic habitats

II. Continuous and long-term monitoring of lion-tailed macaque behavior, genetic and movement patterns to improve our overall understanding of a unique subpopulation of this species and to educate local stakeholders and the general public regarding lion-tailed macaque conservation

III. Engaging with the local communities to bring about change in their lifestyle by providing basic infrastructure that would help reduce human-macaque interactions

IV. Compilation and organisation of the data collected on this macaque population over time, in order to create an easily accessible database that may aid in the long-term understanding of lion tailed macaque demography, behaviour and their interactions with local human communities

VII. Importance of the proposed research

This project will provide us with vital insights into the changing behavioural patterns and adaptability of these macaques in response to novel food sources and unusual habitats, and inform potential management strategies for this population. Given the rise in human-wildlife conflict in such cases, I would also suggest methods of minimising negative macaque-human interactions, with the involvement of the local communities.

Education/ Public Information: Meetings would be held with tea and coffee plantation managers and local communities before the start of the project to explain the purpose of the project and another set of meetings conducted at the end of the project to share our findings with them and help them understand the threats faced by the species they coexist with. This, we hope, would significantly aid in the crucial involvement of the local communities in the conservation of the species in the future.

Involvement of Local People: A certain number of members of the local community would be asked, with consent, to participate in non-participant observation. They would be given a briefing on the purpose of the study and later be informed of the results of the study. I thus hope to raise crucial awareness of the threats faced by the endangered lion-tailed macaques in their vicinity and also obtain crucial insights into how people respond to the presence of home-raiding macaques, and how these macaque populations can be managed in the future.

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How many monkeys jumping in the trees?

Demography and population dynamics of a sub-urban population of lion-tailed macaques

I. Background

Very often, in the field of wildlife conservation and management studies, one of the preliminary objectives is to determine the population size (Cross et al., 2009) and other demographic parameters. Conservation strategies are usually implemented at the population level, making it crucial to have a thorough understanding of the dynamics at play. Largely, population studies attempt to describe the trends in growth, birth and death of individuals in the population of concern (Lebreton & Gaillard, 2016). For the management of wildlife, information on population structure becomes invaluable as it informs us of declining populations requiring special attention.

Population studies become especially important when attempting to understand the interactions between humans and wildlife. It is well known that wildlife exists outside protected areas, especially in tropical countries like India. These wild species face increasing human-induced pressures such as deteriorating habitats, the extraction of resources essential for their survival and the direct interactions between humans and wildlife. These interactions are escalating globally and it is crucial to understand them in order to aid the management and conservation of these often-threatened species. It is especially important to understand altered individual responses to changing ecologies and the resulting interactions of these individuals with different elements in their novel environments. Primates are amongst the many taxa known to have direct, often detrimental interactions with humans in such altered habitats. They also tend to be highly adaptable, particularly in anthropogenic situations, and many species, especially macaques, are now commensal with humans across the Indian subcontinent.

Populations of wildlife that have been negatively impacted by human activity, either directly through hunting or indirectly, are referred to as exploited populations (Lebreton & Gaillard, 2016). It is well known that globally, fish populations have been exploited and even overexploited almost entirely through processes of commercial harvesting (Reynolds et al., 2001). Increasing human populations, coupled with loss of native habitat has resulted in drastically altered population dynamics in primates the world round (Chapman et al., 2018). Primates existing today in fragmented landscapes are of special conservation interest, as these populations largely isolated populations are most vulnerable to extinction in the long term (Cowlishaw, 1999). In the Neotropic, populations of a species of spider monkey *Ateles geoffroyi* and two species of howler monkey *Alouatta palliata and A. pigra* have already become extinct in certain regions as a direct result of human activity and habitat fragmentation. Even closer to home, species like the endangered lion-tailed macaque have shown historical decline in their distribution congruent with the degradation of their native habitat across the Western Ghats (K. U. Karanth, 1992; Krishnamurthy & Kiester, 1998; Honnavalli N. Kumara & Sinha, 2009). Lion- tailed macaques populations that remain today are contained in pockets of rainforest fragments scattered across commercial plantations. These isolated populations have begun to explore and utilise human habitations in the last decade (Singh et al., 1998;

Jeganathan et al., 2018; Dhawale et al., 2020) and already exhibit signs of potential decline. Lion-tailed macaques living in forest fragments in the Anamalai landscape carry an increased parasitic load, many of which have been transmitted in the last decade directly from humans or livestock to the non-human primates (Hussain et al., 2013). This population also exhibits signs of inbreeding, a common phenomenon when the natural dispersal of animals is impeded by fragmentation, threatening the long term survival of the population (M. S. Ram et al., 2015).

Lion-tailed macaque populations that interact frequently with humans and their habitation also show behavioural adaptations which include the consumption of an entirely new food resource, human-use foods. Previous studies have documented the population trends of the Puthuthottam group, depicting a steady rise in the population between 1998-2010 (Figure 1), however, we are as yet unaware of how the inclusion of human-use foods into the diet has affected these dynamics in the last decade. Thus, we aimed to update the existing demographic data, and monitor the Puthuthottam population between 2018-2020, to describe their growth-, birth- and death rates. While it was clear that the population seemed to be growing, we hypothesised that while the total population had nearly doubled in the last two decades, the active growth- and birth- rates would not be higher when compared to wild populations given the increased human-induced mortality of individuals.

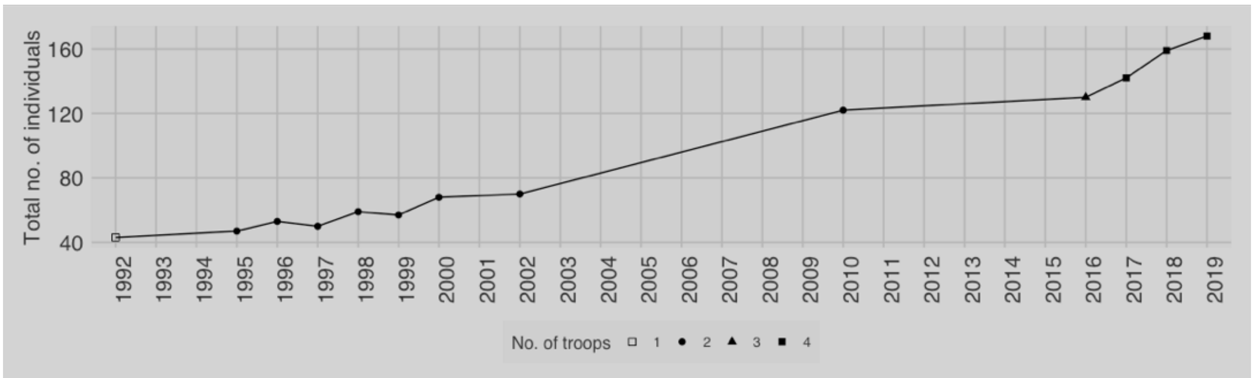

Fig 1. Population growth of the Puthuthottam lion-tailed macaques. Data from: (; Umapathy, 1998; Umapathy & Kumar, 2000; Singh et al., 2002)

II. Methods

Each of the groups residing in the Puthuthottam forest fragment was followed for an extended period of time (at least 3 continuous days) to ascertain absolute troop numbers, and age/sex composition. Each troop was revisited at six-monthly intervals to collect data on birth and death rates of both adults and infants. During each troop count, conducted at crossing zones, where individuals would move in a largely linear manner, the total number of individuals were counted, and divided into six age-sex categories (Table 1; adapted from Singh et al., 2002).

TABLE I. Age-sex Classification in Lion-Tailed Macaques

Age-sex class	Age range
Adult male	>8 years
Subadult male	4–8 years
Adult female	>6 years
Subadult female	4–6 years
Juvenile	1–4 years
Infant	<1 year

Our base assumption for the analysis of demographic data was that the Puthuthottam population was a closed population with close to zero emigration or immigration. We conducted a total of five counts per troop, between July 2018-July 2020. To describe troop composition, we have presented ratios of females to males and females to immature for each troop in each year. Birth rate was calculated as number of births per female-year, and all known instances of death (human-induced or natural) were recorded. We used an exponential growth model to estimate the growth rate of the population by year.

$$rN = dN / dt$$

where :

dN = change in number, dt = change in time, r = the per head maximum potential growth rate, N = number of individuals in a population.

III. Results

We conducted troop counts for each of the five troops, repeating each count in July and January of each year (Figure 2). A year-wise summary of the absolute troop counts is presented in Table 2. While we have differentiated across seven different troops, two of the troops have since merged to form a new group, resulting in a total of five troops.

Fig 2. Absolute troop count of all troops present in Puthuthottam between July 2018-July 2020

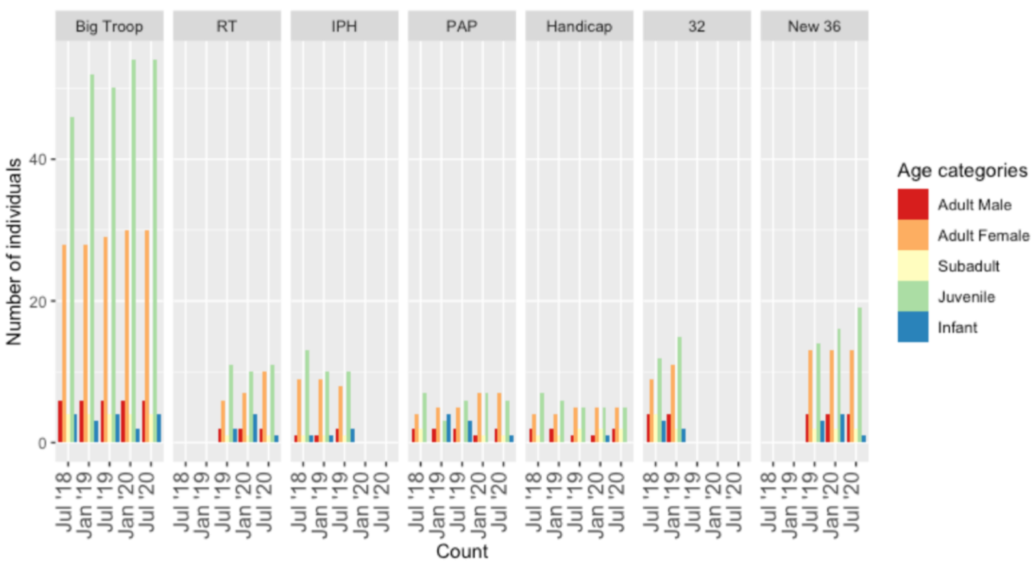

Table 2. A year-wise summary of the absolute troop counts of all Puthuthottam troops

The female- to male and immatures ratios for each troop across the study period are presented in Table 3.

Table 3. Females to males and females to immatures ratios for Puthuthottam lion-tailed macaque troops

Troop ID	*Females: Males*	*Females: Immatures*
BT	1:0.20	1:1.58
RT	1:0.33	1:1.83
PAP	1:0.33	1:1.66
HAN	1:0.40	1:1.75
N36	1:0.30	1:1

We calculated a birth rate per year of 0.28 and an exponential growth rate of 7.8% over the study period with an exceptionally high mortality rate of 5% for the year 2018-2019.

Year	BT	RT	IPH	PAP	HAN	O32	N36	Total
2018	89	0	25	15	14	32	0	**175**
2019	93	22	0	16	13	0	36	**180**
2020	96	25	0	17	13	0	39	**190**

IV. **Discussion**

This population shows a drastically altered population density and age/sex composition. While in the wild a typical lion-tailed macaque troop would consist of a single adult male and multiple females, most troops in the Puthuthottam population contain multiple adult males. These results show both indicate the vulnerability of this species in disturbed habitat conditions.

Habitat change, or habitat deterioration, have drastic impacts on birth rates, survivorship and other demographic parameters of an animal population. In Puthuthotam, the population of the five lion-tailed macaque was calculated to have an exponential growth rate of about 7.8% per year. The growth rate indicated ina. Previous study conducted on the Puthuthottam population registered an exponential growth rate of 8% (Singh et al., 2001). While a growth rate of 7.8% is quite high for a rainforest-adapted primate species, there appears to be a slight reduction in this rate in the last decade ,indicating that certain features of the habitat or population limit the indefinite growth of the population. Additionally, even though the total number of individual present is the highest recorded to date, a majority of the population is made up of immatures.

The unusual troop composition of multiple males and multiple females is clearly evident in the female to male ratios across troops. Additionally, the ration of females to immatures indicate the high number of immatures present in the population. Male macaques typically disperse at sexual maturity (Greenwood, 1980), however, in fragmented landscapes, this migration is severely impeded (Singh et al., 2002), resulting in males staying back within the natal troop. Such an occurrence can have major implications on the behavioural profiles exhibited by these individuals and their ultimate survival ability.

A disproportionately large amount of the Puthuthottam population consists of immature individuals, while this pattern does not reflect, in time, in the increase of adult individuals in the population. This pattern can perhaps be explained by the relatively high mortality rates, especially of juvenile individuals. Most of the instances of death recorded during the study area were a direct result of collision with vehicles on the highway that cuts across Puthuthottam, or by electrocution on exposed electric lines that pass through the fragment, while the victims were almost always juvenile individuals. These individuals were slightly older juveniles that were not carried by adult individuals. We also recorded an increase instances of male-male aggression resulting in severe injury, and injuries to the hands and feet in members of troops that frequented human habitations across the study period.

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Who let the monkeys out?

Ranging and Habitat Use of a semi-urban population of lion-tailed macaques across a matrix of anthropogenic habitat

I. Background

Globally, populations of wild animals belonging to various taxa have shown a tendency to utilise ever-expanding urbanised areas, often in search of novel ecological opportunities (Griffin et al., 2017). This process by which wildlife adapt and continue to exist in urbanised or semi-urbanised (anthropogenic) environments is known as *synurbisation* (Andrzejewski et al., 1978; Babińska-Werka et al., 1979). From the wildlife perspective, anthropogenic habitats have been described as "new", "complex" and "strange" characterised by high degrees of anthropogenic pressures, and a host of associated threats to survival (Luniak, 2004). Conversely, urban areas also offer a novel food resource, human-use foods, which are abundantly available, easily accessible, and energy-rich (Griffin et al., 2017), making them attractive habitats for wild species to occupy. Populations of wild species that colonise anthropogenic habitats show a suite of ecological and behavioural adaptations including altered activity patterns (Altmann & Muruthi, 1988; Riley, 2007; Tracie, 2011; El Alami et al., 2012; Jaman & Huffman, 2013), drastically modified diets (Sinha et al., 2005; Tracie, 2011; Baruch-Mordo et al., 2014; Yirga et al., 2015) and increased mortality (Beckmann et al., 2008), that are consistent across taxa. Some species that exhibit these adaptations and thrive in anthropogenic areas, like the bonnet macaque *Macaca radiata* (Sinha, 2001; Radhakrishna et al., 2013), are often referred to as *synanthropic* while those that still remain largely isolated from humans are termed *non-synanthropic.* It is especially crucial to focus on species that classify as the latter, whose recent adaptations to anthropogenic habitats are still recondite.

The lion-tailed macaque *Macaca silenus,* for example, is a species endemic to the Western Ghats, existing today in 49 subpopulations, in only eight key locations, including the Anamalai Hills (Kurup & Kumar, 1993; Kumara & Singh, 2003; Molur et al., 2003). It is thought to be a highly arboreal, primarily frugivorous, habitat-specialist species, dependent on the wet evergreen native vegetation type of the landscape (Kumar, 2013).

Since the late 1800s, logging of the native vegetation for the expansion of commercially grown tea and coffee plantations on the Valparai plateau in the Anamalai hills has resulted in forest fragmentation and the isolation of lion-tailed macaque troops now scattered within these remaining pockets of rainforest (Singh et al., 2002; Jeganathan et al., 2018). Despite the degraded nature of these remaining habitats, the Anamalai hills, being contiguous with Parambikulam Tiger Reserve and Neliampathy in the North, and the Chalakudi hills in the south, has been identified as a crucial landscape for the conservation of the lion-tailed macaque (Singh et al., 2002).

The Valparai plateau is a matrix of tea and coffee plantations interspersed with 45 rainforest fragments ranging in size from <10ha to >100ha (Umapathy & Kumar, 2000; Mudappa & Shankar Raman, 2007). Of these, one particular forest fragment measuring 92ha, the Puthuthottam forest fragment, contains ~190 lion-tailed macaques in five troops (Dhawale pers. obs.). The Puthuthottam forest fragment neighbours the town of Valparai, and is surrounded on all other sides by tea-plantations (Figure 1).

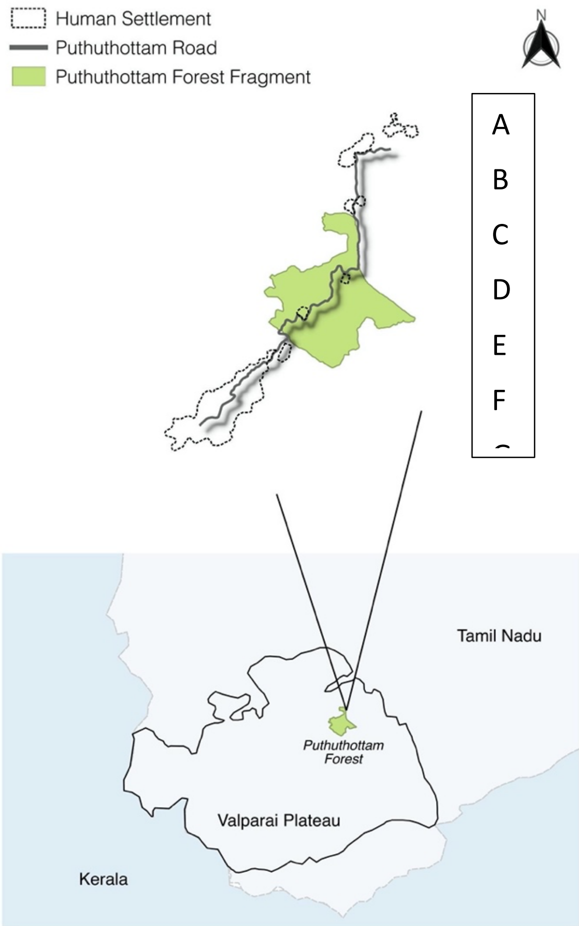


Fig 1. Human settlements within and surrounding the Puthuthottam forest fragment. A-Iyerpadi, B-Rottikadai, C-IPH, D-10 Acre, E-PTTM, F-PAP, G-Valparai Town.

All of the five troops present in the Puthuthottam forest fragment visit human habitations, either labour lines within the fragment or the neighbouring town of Valparai. Troops in this population already exhibit adaptations to these anthropogenic habitats, significantly reducing time spent foraging while increased time spent resting and display altered social dynamics under regimes of potentially perceived competition in the presence of human-use foods (Dhawale et al., 2020). Like many other macaque species (Greenwood, 1980), male lion-tailed macaques typically disperse from the natal troop at sexual maturity. This dispersal pattern is thought to reduce inbreeding in species (Moore, 1992), thus playing a crucial role in their long-term survival. In fragmented landscapes like the Valparai plateau, however, male migration in lion-tailed macaques is severely impeded (Singh et al., 2002). As a result, males tend to stay back in the natal troops, which has led to an unusual multi-male, multi-female social organisation in the troops present in Puthuthottam (Dhawale, pers. obs.). In this paper we present first evidence of an entire troop migrating out of the forest fragment across a seemingly impermeable matrix of anthropogenic habitats into novel human settlements, displaying significantly reduced daily movements and homerange size, a pattern congruent with those observed in other *synurbic* populations (Quinn, 1994; Parker & Nilon, 2012) .

II. Methods

Habitation Visitation Rate

The Puthuthottam highway and human settlements were monitored continuously for 12 months between October 2018-October 2019, with a GPS location recorded at every encounter with any troop present in Puthuthottam. If the troop continues to remain by the human habitation, the GPS record for repeated at 15 min intervals. These locations were later mapped to describe the patterns of road visitation by the lion-tailed macaques in the Puthuthottam population. A habitation visitation rate was calculated as the proportion of days over the entire study period during which lion-tailed macaques were encountered near roads or human settlements (adapted from Singh 2001).

Home range estimation and habitat use

GPS locations was taken at 15 min intervals during the simultaneous and systematic following of all troops present in the Puthuthottam forest fragment, as they range over both natural and anthropogenic habitats. Data was collected for 6±6 months (over 15±10 days/ month), on each of the five troops present in Puthuthottam between September 2018 to February 2020. We collected a total of ~8000 location data with 350±100 data points per month. These points were later be mapped to calculate distances travelled, directions of movement and rates of ranging across and outside the study area. Such an analysis is essential to map the new-found home range of these macaque troops, particularly in so far as they overlap with human habitations, farms, orchards and roads, potential areas for escalated human-primate conflict. It will also provide insight into the competitive encounters between macaque troops and help establish determinants of habitat use. A kernel density estimation (Laver & Kelly, 2008) allowed us to determine home range (95% use area) and core use area (50% use area) over the two field seasons, using an optimal bandwidth selection method to delineate kernels from Fotheringham et al., 2000. KDE calculations and visualisation were completed in QGIS (QGis, 2011 version 2.18.3) using the Heatmap plugin. Additionally we present the percentage overlap of home range across all troops in Puthuthottam to describe prevailing inter-troop competition

Human induced home range expansion: a case study

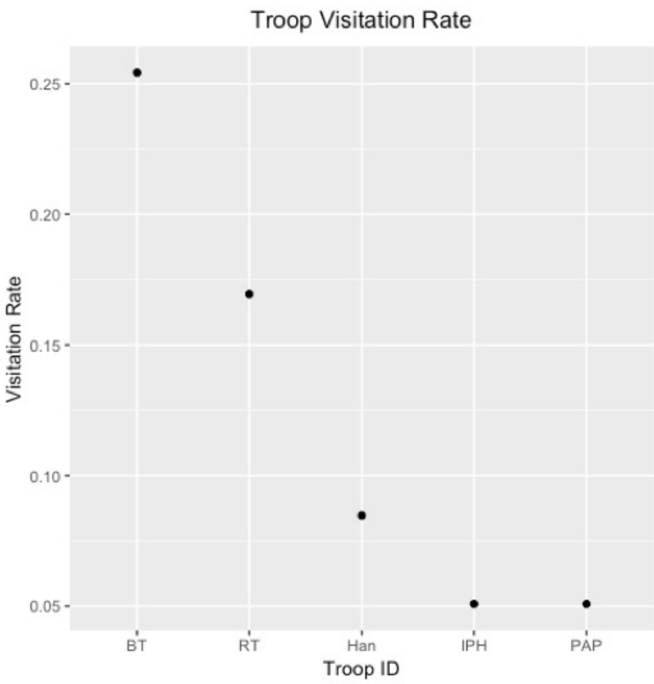
We observed the study troop exiting the forest fragment for the first time, as confirmed by our earlier records and on-ground informants, in September 2018, and then again in November 2018. On both of these occasions, the troop moved 1 km north of the forest fragment towards a dense human settlement, returning to the forest fragment later in the same day. We began systematically tracking the troop movements, using a GPS device to record the troop location at 15min intervals from 7am to 5pm over 15±10 days each month, from January to November 2019. We categorised our movement data into two field seasons, January 2019 to May 2019 and August 2019 to December 2019, divided by the monsoon months during which field work could not be conducted, to describe the change in home range of the study troop as they explored the new surroundings. We additionally collected *ad libitum* behavioural data on the troop as it moved over unusual substratum such as roads, tea bushes and swamps, and foraged at the human settlement. A kernel density estimation (Laver & Kelly, 2008) allowed us to determine home range (95% use area) and core use area (50% use area) over the two field seasons, using an optimal bandwidth selection method to delineate kernels from Fotheringham et al., 2000. KDE calculations and visualisation were completed in QGIS (QGis, 2011 version 2.18.3) using the Heatmap plugin.

III. Results

Habitation Visitation Rate

Each of the five troops visited habitation at varied rates (Figure 2), with the BT troop and RT troop visiting habitation most frequently. The overall habitation visitation rate was calculated to be 0.57 times a day.

Fig 2. Habitat visitation rate of the five Puthuthottam troops during October 2018- October 2019



Home range estimation and habitat use

The KDE home range calculations indicated that in the case of each of the five troops, the core use area overlapped with a human settlement (Figure 3).

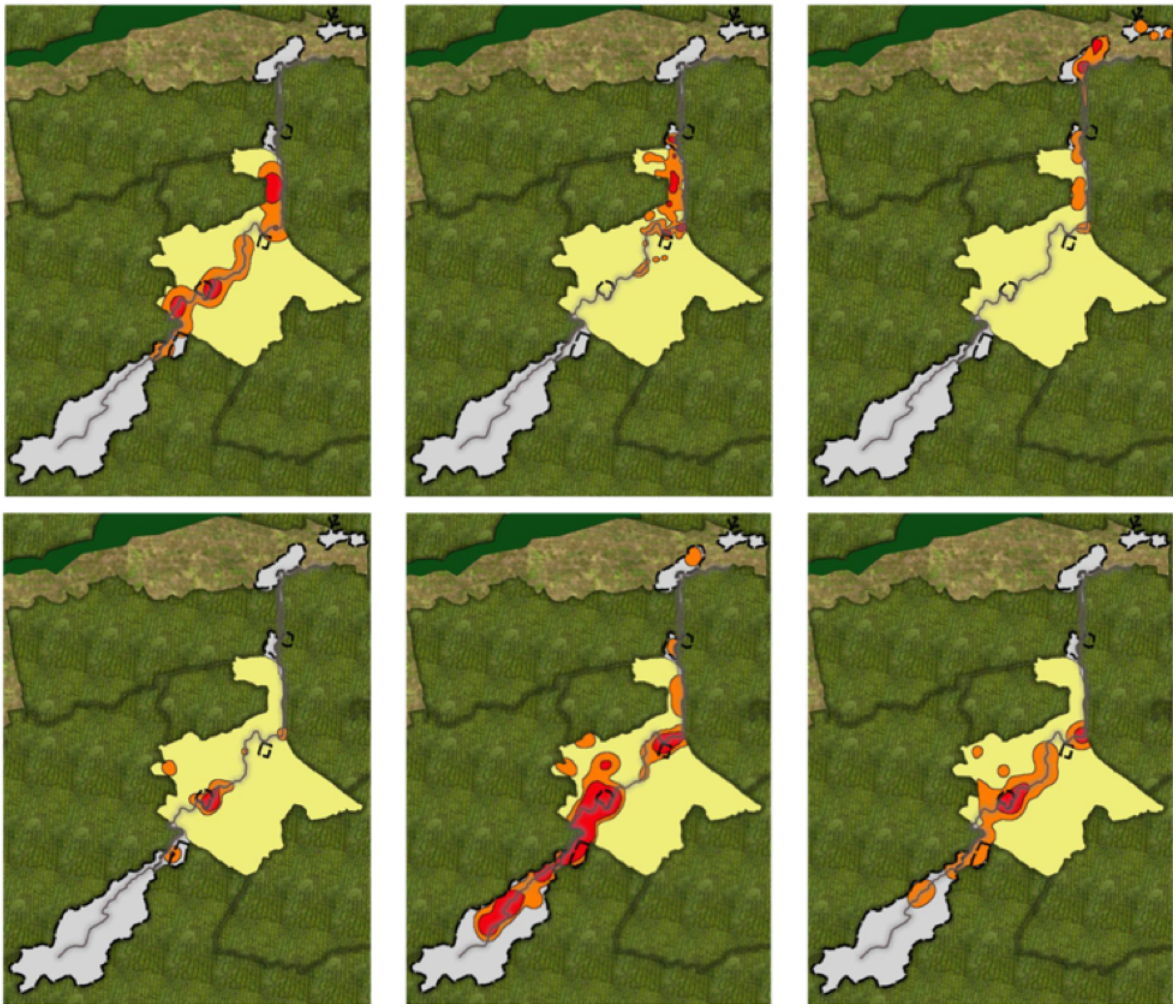


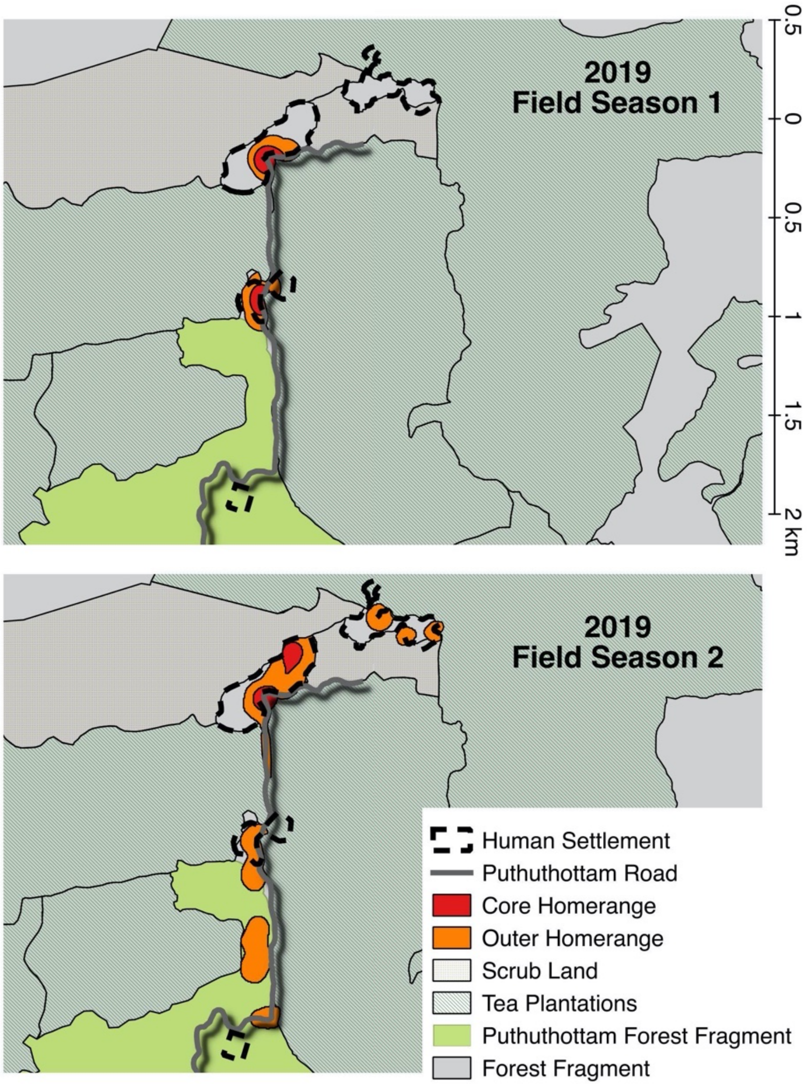
Fig 3. KDE Homerange (orange) and core use area (red) of all lion-tailed macaque troops in Puthuthottam. Left top to right bottom: N36 Troop, IPH Troop, RT Troop, PAP Troop, B Troop, HAN Troop.

Home range expansion: a case study

Field Season 1 : During the first field season, the troop had a mean daily range of 0.30 ± SE 0.04 km. Initially, the troop would exit the forest fragment from the northern edge, spending some time at the adjacent Iyerpadi Hospital to forage at open garbage bins before quickly moving along the edge of the road for 1 km to the Rottikadai settlement. In this season, the troop would entirely avoid the swamps and tea bushes, walking only on the single road connecting the two settlements, even as traffic continued to ply. The troop would then spend long periods of time, up to 20 days, at the Rottikadai settlement, foraging almost entirely at a large open garbage pit, and occasionally on the few fruiting trees in the settlement, including ones grown in gardens by the local community. In the evenings, the troop would roost in an *Acacia* stand adjacent to the Rottikadai settlement. The troop returned to the Puthuthottam forest fragment only twice or thrice during this field season, remaining at the northern edge and returning to the Rottikadai settlement within a day. Our home range estimate clearly captured this ranging behaviour with the core use areas overlapping the Iyerpadi Hospital and

Rottikadai settlements, with an area of 25.6 ha, the total home range measuring 48.3 ha (Figure 4).

Field Season 2 : During the second field season, the troop had a mean daily range of 0.59 ± 0.09 km. In this season, the troop returned to the Puthuthottam forest fragment more frequently, while still spending long periods of time in the Rottikadai settlement, and ultimately vising a third human settlement, Iyerpadi, 0.5 km north of Rottikadai. During this time, the tea fields adjacent to the Rottikadai and Iyerpadi settlements were pruned, and members of the troop began to move over the stumps to forage for insects. The adult and subadult males would also explore edges of the swamp, presumably to forage. When visiting the Iyerpadi settlement, the



troop moved along a cable wire linking the Rottikadai settlement, avoiding the surrounding scrub land. While in Rottikadai, the troop began to roost in trees in an unoccupied property within the settlement itself. Our home range estimates indicated that while the core use areas were limited to the Rottikadai settlement and measuring an area of 22.3 ha, the home range extended over an area of 197.43 ha and included parts of the Puthuthottam forest fragment and Iyerpadi settlement (Figure 4).

Fig 4. Home range expansion observed in the RT troop between January 2019-December 2019

IV. **Discussion**

Wild populations are undergoing *synurbisation* at alarming rates, given the unceasing expansion of human activity across the globe. Human-modified habitats pose a serious threat to the long term survival of species, especially those that are unable to quickly adapt to the changing environment. Lion-tailed macaque populations in isolated forest fragments are known to face human-induced threats like collision with vehicles and electrocution, and suffer from inbreeding depression, presumably due to lack of dispersal between fragments (M. S. Ram et al., 2015). While it was previously thought that dispersal across the human-modified landscape of Valparai was entirely impossible, we present first evidence for troop migration over short distances, across tea-plantations.

We observed as one of the five troops present in Puthuthottam began migrating out of the forest fragment in September 2018, culminating in a shift in home range from the forest fragment to an adjacent human settlement almost entirely devoid of natural vegetation by November 2019. The Rottikadai settlement, situated 1 km north of Puthuthottam and immediately adjacent to an *Acacia* stand, contains densely packed houses including grocery shops, residential structures, abandoned lots and a large open garbage pit. While in this settlement, the troop would initially roost at the *Acacia* stand, while roosting in the core of the settlement later in the year.

The Rottikadai settlement is one of the seven human settlements in and around Puthuthottam, the others including the town of Valparai and several smaller labour lines. While multiple lion-tailed macaque troops resident to Puthuthottam frequently visit the immediately adjacent town of Valparai to primarily forage at garbage bins, there is no previous record of a troop moving north of the fragment towards Rottikadai. The northern section of the Puthuthottam forest fragment tapers to form a semi-isolated, highly degraded forest patch, bottlenecked by tea plantations.

Our previous observations of other troops in Puthuthottam indicate that an inter-troop hierarchy prevails in this population with the largest troop, containing ~90 individuals, being the most dominant and frequently engaging in inter-troop aggression, often chasing away other troops in their vicinity (Dhawale, pers obs.). We also observed heightened vigilance in male members of smaller troops in response to the presence of the 'big troop', sometimes leading to pre-emptive movement away from the big troop. When we first observed the study troop moving north of Puthuthottam, the big troop was also recorded at the northern edge. We believe that the initial movement by the study troop in the northern direction was possibly a result of avoiding a direct encounter with the big troop. Once the study troop had discovered a yet uncontested new food resource in Rottikadai, we believe the troop then revisited the settlement more frequently. The presence of the *Acacia* stand near Rottikadai may have allowed the troop to transition between their native habitat and the human settlement. The Iyerpadi settlement, which the troop visited in November 2019, is about 0.5 km from Rottikadai and connected by a narrow mud path. We believe that natural home range expansion from the new core home range led to the study troop ultimately exploring a second human settlement.

Understanding the patterns of behavioural modifications in wild species in response to anthropogenic habitats is becoming a crucial aspect for the management of wildlife in urban settings (Luniak, 2004). Unimpeded dispersal is crucial for the long-term survival of lion-tailed macaques, especially in fragmented landscapes. While the events we have presented pertain to a single troop, we believe that these observations indicate the potential ability of lion-tailed macaque troops to disperse across human-modified habitats over short distances. This may not, however, hold true for the long distance migration, required to maintain natural genetic connectivity. It is, thus, equally important to promote native habitat connectivity to ensure the natural dispersal of the endangered lion-tailed macaque in fragmented landscapes.

V. References

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Changing Ecologies, Shifting Behaviours

Behavioural Adaptations of a lion-tailed macaques in an human-dominated landscape

I. Background

Globally, protected areas designated for the conservation of biodiversity account for a very small percentage of landcover, only about 3.48% [1]. Consequently, wildlife and humans, sharing the same landscape, are often forced to interact with one another and this may lead to conflict situations, wherein one or both species may face tremendous losses. It is, therefore, important to understand the ecology of nonhuman species to explain the persistence of these animals in anthropogenic habitats. It then becomes crucial to examine the behavioural changes displayed by individual animals, as these are often amongst the first responses that a species demonstrates to a changing environment [2].

Habitat-modifications have been shown to favour generalist species [3, 4], and lead to behavioural adaptations across various taxa. Omnivores, such as the black bear Ursus americanus and spotted hyena Crocuta crocuta in urbanized settings, for example, have drastically modified diets and home-ranges, relying heavily on garbage produced by humans [5, 6]. Avian species typically show patterns of homogenisation, leading to high abundance of a few generalist species in response to human-modified habitats [7]. Primates, especially species of the genus Macaca, are known to have adapted to a wide variety of habitats across Asia and Africa [8]. The bonnet macaques of peninsular India, for instance, have traditionally been exposed to human presence and appear to have now behaviourally adapted to anthropogenic habitats and human-provided food [9].

Some species, however, still remain, for the large part, isolated from human habitations while others still have only recently begun to come into contact with people. The lion-tailed macaque is a habitat specialist, primarily frugivorous species [10], with very little exposure to humans [11]. In the Valparai region of the Western Ghats mountains of southern India, this species, due to the establishment of commercial plantations and various other encroachments of its rainforest habitats, has recently become exposed to humans and has even begun to frequent their habitations [12]. Given the relatively recent emergence of this phenomenon, however, the ability of such a species to persist in such drastically altered habitats remains largely undocumented.

We thus sought to explore the novel behavioural changes displayed by members of the Valparai subpopulation of lion-tailed macaques as they traversed various anthropogenic habitats. We specifically chose to examine foraging behaviour as it is fundamental to animal survival [13] and it is well established that many taxa show dietary changes in human-altered habitats, often incorporating or even becoming reliant on anthropogenic foods or livestock [3, 14, 15, 16]. We also documented social interactions as macaques are group-living animals displaying complex social behaviours, and social interactions are known to significantly affect foraging behaviours [17, 18]. Additionally, we explored the effects of dominance rank, a feature of social dynamics observed particularly in adult female individuals in many primate species [19, 20, 21], on foraging behaviours. Finally, we examined pairwise allogrooming patterns among the adult females of the troop, as male lion-tailed macaques rarely indulged in such social interactions [22].

Given logistical constraints, we followed only one of the four troops that occupy human-dominated habitats in our study area. We aimed to uncover the changes in behavioural frequencies that occurred when the troop occupied four structurally distinct habitats with varying degrees of human influence. Previous studies have observed consistent patterns of reduction in foraging frequencies and increased resting in response of different primate species to habitats where human-use foods, often easily assessible in large quantities, are present [23, 24, 25]. We thus expected to observe a similar pattern of reduced foraging frequencies displayed by our study individuals in habitats where human-origin foods were present. Likewise, previous studies have observed an increase in affiliation among members within a troop, as a means of reconciliation, when competition over human-use food resources increases in human-dominated habitats [26, 27]. We thus expected to observe a similar pattern of increased intra-troop affiliation amongst the lion-tailed macaques in specific human-dominated habitats where human-origin food was present.

Our study, thus, presents novel insights into the foraging patterns and intra-troop social dynamics of a habitat-specialist primate species in response to habitat-modifications and the presence of humans under drastically changing ecological regimes.

II. Materials and Methods

Study Area

The study was carried out on the Valparai plateau 10° 19' 39.22"N, 76° 57' 18.98"E, located in the Anamalai hill range of the southern Western Ghats mountains, in the southern Indian state of Tamil Nadu. An expanse of around 220 km2, the plateau is a heterogeneous landscape of wet evergreen rainforest fragments interspersed with tea, coffee and Eucalyptus plantations [28]. The Anamalai hills are important for the conservation of the endemic lion-tailed macaque, this being one of the eight remaining locations where the species currently occurs [29].

Since the early 1800s, extensive selective logging has led to the fragmentation and degradation of the native rainforest habitat on the Valparai plateau. One such rainforest fragment, the Puthuthottam forest fragment, with an area of 92 ha and neighbouring the town of Valparai, is of particular importance, as it harbours a subpopulation of macaques with c. 150 individuals (Dhawale, pers. obs). For the purpose of the study, the matrix of habitats present in and around the Puthuthottam forest fragment on the plateau (Figs 1 and 2) were classified as Forest Edge (a 50-m-wide belt around the edge of the forest), Forest Interior (the area of the forest contained within the aforementioned belt), Open Forest Patch (a largely open space within the forest recently planted with coffee saplings) and Human Settlement.

Fig 2. Habitat types present within the Puthuthottam forest fragment: Forest Interior (A), Forest Edge (B), Open Forest patch (C) and Human Settlement (D)

Study Species

The lion-tailed macaque Macaca silenus a species endemic to the Western Ghats and considered highly specialised to the wet evergreen vegetation type, exists today in 49 subpopulations in eight key locations, one of which is the Anamalai hills [29, 30]. This species is known to be arboreal and primarily frugivorous, making it dependent on the native vegetation of the landscape [10]. In recent years, however, fragmentation and degradation have resulted in the species frequently being exposed to human habitations. Unusually, in some areas, including the Puthuthottam forest, the troops have recently begun to move out of the forest fragment and frequent human habitations [12]. Of the four troops present in Puthuthottam, one particular troop, numbering 92 individuals, has been reported to frequent human habitations at rates as high as 0.43 times a day [12].While this particular troop has a high human habitation visitation rate, the other three troops do not exhibit such a pattern (Dhawale, pers obs). It is noteworthy that the members of the local human community have reported sighting lion-tailed macaques near their habitations only over the last ten years [31]. For the purpose of our study, we chose one such troop that spent comparable amounts of time in both anthropogenic habitats as well as relatively undisturbed habitats, thus providing a useful model to study the effects of human presence and anthropogenic habitat modification on the study subjects.

Study Troop and Individuals
The Puthuthottam macaque subpopulation includes four troops, consisting of c. 92, 37, 15 and 26 individuals respectively. One of these four Puthuthottam troops, the individuals of which could be easily identified and which used all the available human-use habitat types, was selected for this study. The troop consisted of 23 individuals, including nine adult females, one adult male, one subadult male and 12 juveniles (one to six years of age) at the start of the study period, with three infants being born subsequently. The troop was habituated for a period of one month at the start of the study period, during which time all the adult members of the troop were also individually identified using their distinctive features, such as facial markings, injuries or other visible abnormalities, including missing body parts or swellings/bulges.

Field Methods
The study primarily involved the non-invasive following of the selected, habituated troop of lion-tailed macaques, with observations being carried out on all the adult members alone. We conducted our observations for over a total of 480 follow-hours during one of two randomly selected sampling periods (from 08:00 to 14:00 h and 14:00 to 18:00 h) on each day, for 14.5 (± SE of 1) days in a month, for four months, from February to May 2016. We collected data using standard behavioural protocols, including instantaneous group scans for a duration of 5 min each at 15 min intervals, during which time the behavioural states of all individuals were noted (S1), and continuous focal animal all-occurrence sampling for foraging and social behaviours, of 10-min duration each conducted on randomly chosen individuals without replacement [32]. Our behavioural sampling effort was 8.80 ± 0.23h per individual, with a total of 96.5 h of focal animal sampling and 217 group scans, consisting totally of 1756 individual scan observations.

All research protocols were reviewed and authorised by the institutional Research Ethics Committee constituted under the Tata Institute for Fundamental Research, Mumbai, India while natural non-invasive observations of the study macaques were conducted with permission from the Tamil Nadu Forest Department (Permit Reference No. WL (A)/ 034559/2015).

Ecological and Behavioural Responses of Lion-tailed Macaques
We defined four different habitats, each of which were qualitatively characterised to include their structural habitats and resource type. The two resource types considered in this study were Human-origin, which included all foods such as commercially grown vegetables for cooking, cooked food items, and packaged food items, and Natural, which included native (e.g Cullenia exarillata) and non-native (e,g Spathodea campanulata) tree species and invertebrates. The four predominant habitat types were identified and characterised during this study, as follows:

Forest Edge: A 50-m-wide belt around the edge of the Puthuthottam forest fragment, containing native and non-native tree species and bordered on one side by a national highway. We chose to demarcate the boundary at 50m from the edge as we observed that the troop spread at any given time was ≤ 50m. This habitat contained Natural food sources, and occasionally Human-origin foods, either dropped along the roadside or in the form of handouts provided by tourists.

Forest Interior: An area of forest contained by the Forest Edge, described above, consisting of native and non-native tree species, all of which constituted Natural food sources.

Open Forest Patch: A relatively open space, largely without canopy cover, present within the Puthuthottam forest and recently planted with coffee saplings. It included only Natural food sources.

Human Settlement: A particular location containing a hospital building, gardens surrounding the hospital and an Eucalyptus stand adjacent to the hospital. It was also characterised by the presence of both Natural and Human-origin food resources.

We also recorded human proximity to evaluate changes in behaviour in response to human presence in terms of two distance classes, 0-10m and >10m. Behavioural changes in response to human presence has been presented only for the Human Settlement and the Forest Edge, as humans did not occur in the Forest Interior and very rarely used the Open Forest Patch, not captured in the data.

We described the time-activity budget of the study troop in the four habitat types as the proportion of group scans in which each behavioural state was observed. We compared time-activity budgets across habitat types to investigate whether individuals of the study troop varied their behaviour in response to habitat type.

Foraging behaviour was measured in terms of two behavioural components, Active Foraging and Food Search (S1). Active Foraging behaviours included ingesting of food and rummaging through foliage, dry leaves, bark, or other substratum to acquire food during a feeding bout. Food Search behaviour involved sitting alert and looking around for potential food sources, typically before the start of a feeding bout. During each focal sample, we recorded the duration of Active Foraging/or Food Search behaviours, displayed by the focal individual to the nearest 15 seconds. For the purpose of analysis, we extrapolated the foraging durations from seconds per focal sample of 10-min to minutes per hour and then compared the durations of Active Foraging and Food Search across the four habitat types to uncover the response of lion-tailed macaques to habitat type. Additionally, we compared the foraging durations per hour for two habitat types across the two human proximity distance classes to examine the influence of human presence on the macaques.

Diet composition was measured as the proportion of scan records in which individuals were observed to feed on native and non-native plants (plant materials), and other naturally occurring non-plant matter.

Social behaviour was evaluated in terms of all affiliative and aggressive social interactions, consisting of 34 particular behaviours (S1), exhibited by the study individuals and observed during focal animal sampling. These behaviours were grouped into Affiliation and Aggression, in order to characterise the nature of social interactions displayed by the individuals. We recorded the frequencies of Affiliation and Aggression during focal animal sampling and compared the observed frequencies across habitat types to examine the effects of habitat structure and resource type on the social behaviours displayed by individuals of the study troop. Given the inherently rare occurrence of social interactions in lion-tailed macaques, we were unable to test for the effect of human proximity on these behaviours.

We independently investigated a particularly important affiliative behaviour, Allogrooming, which also formed part of Affiliation, defined earlier. Allogrooming was examined in terms of the frequency of initiated allogrooming events per unit time and the duration of allogrooming, as measured by the observed time spent in the behaviour by particular individuals. Another parameter that we calculated was Reciprocity, which was defined as the occurrence of any two study individuals directing allogrooming towards one another. We recorded allogrooming initiation frequencies and durations during focal animal sampling, noting down the time to the nearest five seconds. We examined variation in allogrooming by comparing grooming frequencies and time spent grooming across habitats. We created dyadic matrices containing paired (within an individual) measures of grooming initiation and duration, and compared matrices across habitat types to investigate whether these two measures were correlated. This indicated whether the initiation of an allogrooming event led to an allogrooming bout or was initiated without the intention of beginning a grooming bout, purely as a novel affiliation strategy. We created dyadic matrices containing pairwise allogrooming durations for all females in the study group and compared them across habitats to examine whether Reciprocity was specifically observed in human-modified habitats.

Dominance ranks, particularly among adult females, are known to influence patterns of foraging, where dominant individuals often get first access to food sources and other benefits over subordinate females [20]. We established the dominance ranks of all the females, based on approach-retreat behaviours (S1) collected during focal animal sampling over the whole study period, thus, each adult female was associated with a single dominance rank. We then examined variations in foraging frequencies of the adult females across dominance ranks within all the habitat types.

Statistical Analyses

All statistical analysis was carried out in R, revised version 3.2.4 [33], with all figures and images also created using R as well.

We established non-normality of data by visually inspecting quantile-quantile (Q-Q) plots while the influence of sampling effort on the response patterns observed was ruled out using the Spearman's rank-correlation test.

Time-activity Budgets: We tested for the difference in time-activity budgets across habitat types with the G-test of independence, using the package RVAideMemoire [34].

Foraging and Social Behaviours: We tested for differences in foraging and social behaviours across habitat types using generalised linear mixed-effect models, with individual identity as random effect and the habitat type as fixed effect. We examined differences in foraging behaviour in response to human presence in two human-modified habitats, using a generalised linear mixed-effect model, with an interaction term of habitat type and human proximity as the fixed effect and individual identity as random effect. We also tested for differences in foraging behaviour across dominance ranks for individual females within habitat types using a generalised linear mixed-effect model with dominance rank and habitat type as fixed effects and female identity as random effect. Significance of regression parameters were established using a maximum likelihood ratio test (Laplace Approximation) and models were validated by conducting a visual inspection of residuals using the R package DHARMa [35]. A description of each model with the relevant parameters is presented in Table 1. We added an additional observation-level random effect to each model, in order to account for overdispersion [36]. To investigate individual variation in behaviour within and across habitats, we visually examined the random coefficients from our foraging and social behaviour models. Generalised mixed-effect models were examined using the R package glmmTMB [37].

Table 1. Selected models and model parameters for the generalised linear mixed-effect analysis

Model	*Behaviour of Interest*	*Fixed Effect*	*Random Effect*
1: Habitat effects on Active Foraging	Active Foraging	Habitat Type	Individual ID Observation-level random effect
2: Habitat and human presence effects on Active Foraging	Active Foraging	Habitat Type*Human Proximity	Individual ID Observation-level random effect
3: Habitat effects on Food Search	Food Search	Habitat Type	Individual ID Observation-level random effect
4: Habitat and human presence effects on Food Search	Food Search	Habitat Type*Human Proximity	Individual ID Observation-level random effect
5: Habitat effects on Affiliation	Affiliation	Habitat Type	Individual ID Observation-level random effect
6: Habitat effects on Aggression	Aggression	Habitat Type	Individual ID Observation-level random effect
7: Habitat and dominance rank effects on Active Foraging	Active Foraging	Dominance Rank*Habitat Type	Individual Female ID Observation-level random effect
8: Habitat and dominance rank effects on Food Search	Food Search	Dominance Rank*Habitat Type	Individual Female ID Observation-level random effect

Allogrooming: We used a generalised linear mixed effects model with habitat types as the fixed effect and individual identity as random effect to test for differences in allogrooming frequency and duration across habitat types. We carried out the Mantel test [38] on dyadic matrices of pair-wise measures of allogrooming initiation frequency and duration to test whether allogrooming was being initiated as an affiliative behavioural strategy without the intention of follow-up grooming. We carried out the Mantel test on dyadic matrices of pair-wise allogrooming duration between individuals within each habitat and then compared their correlation across habitats to examine whether Reciprocity was observed in all modified habitats. Mantel tests were carried out using the R package ade4 [39].

Dominance Rank: We determined the positions of all study individual females within the prevailing linear, transitive, social dominance hierarchy through their behavioural responses during pair-wise approach-retreat interactions [40]. We calculated a dominance score, namely the David's Score or DS [41], for each female and then categorised them as being Dominant (the top three females in the hierarchy), Subordinate (the three females with the three lowest ranks in the hierarchy) or Intermediate (the three intermediate females in the hierarchy) individuals.

III. Results

Ecological and Behavioural Responses of Lion-tailed Macaques to Habitat Types
The proportion of time spent by the study lion-tailed macaque troop in different habitat types was variable, with 41% of the observed time being spent in the Forest Interior, 21% in the Forest Edge, 9% in the Open Forest Patch and 29% in the Human Settlement.

The time-activity budget of the troop differed significantly between the Forest Interior and the Human Settlement (G-test of independence, $G = 84.041$, $df = 4$, $p < 0.001$)but there were no significant differences between that in the Forest Interior and in the other two habitats.

Active Foraging displayed by macaques in the Forest Interior (GLMM, $\beta 0 = 0.95 \pm 0.13$, $z = 7.30$, $p < 0.001$) increased in the Open Forest Patch ($\beta 1 = 0.66 \pm 0.28$, $z = 2.39$, $p = 0.01$) and Forest Edge ($\beta 2 = 0.63 \pm 0.21$, $z = 2.95$, $p = 0.004$) but decreased in the Human Settlement ($\beta 3 = -0.87 \pm 0.23$, $z = -3.70$, $p < 0.001$; Fig 3). In the Forest Edge, Active Foraging was not significantly higher when humans were >10 m away (GLMM, $\beta 0 = 1.66 \pm 0.17$, $z = 9.60$, $p < 0.001$), as compared to when they were within a distance of 10 m ($\beta 1 = -0.86 \pm 1.10$, $z = -0.80$, $p = 0.43$). In the Human Settlement, however, Active Foraging was lower when humans were >10 m away (GLMM, $\beta 0 = 0.08 \pm 0.21$, $z = 0.30$, $p = 0.60$) but significantly higher when they were within 10 m ($\beta 1 = 1.77 \pm 0.75$, $z = 2.4$, $p = 0.01$; Fig 4).

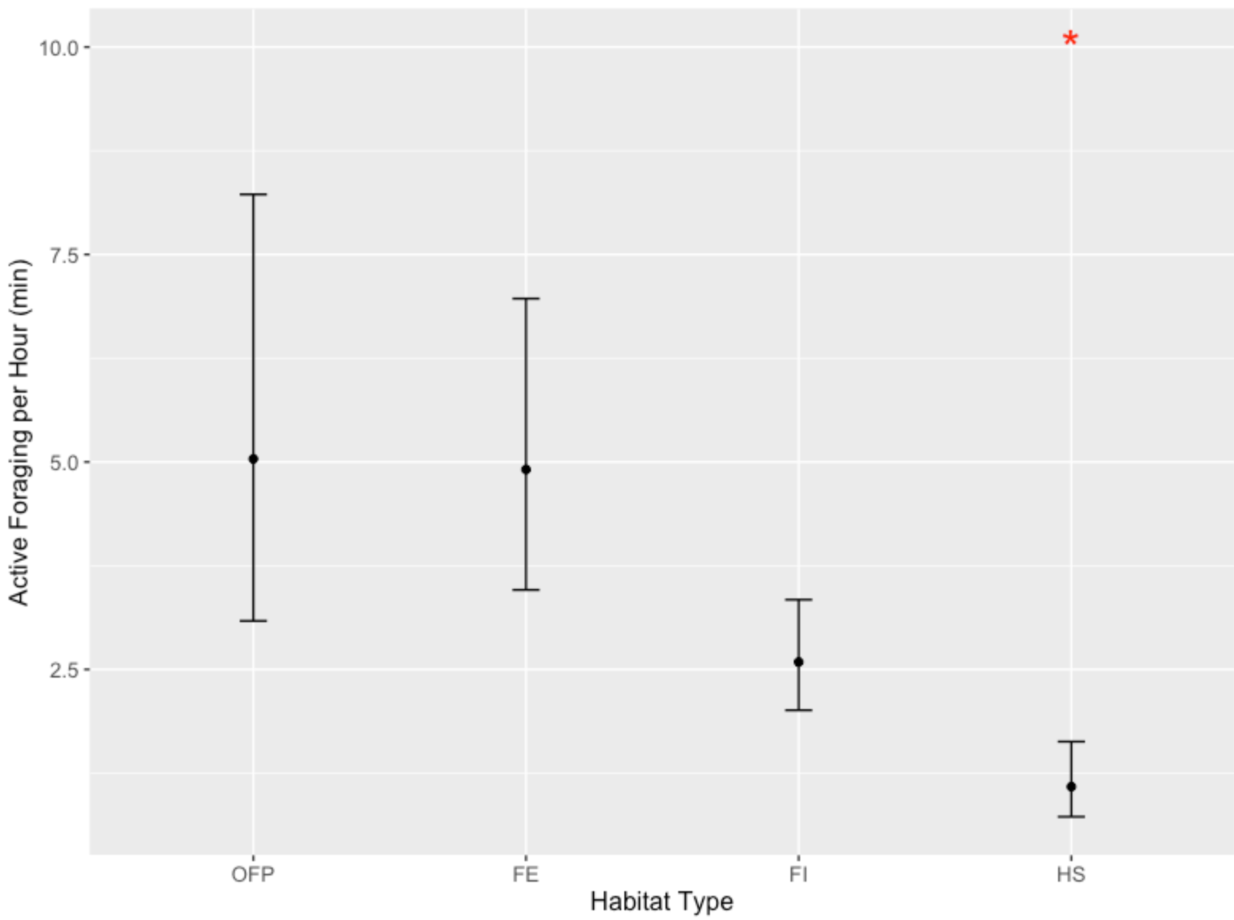

Fig 3. Predicted mean Active Foraging per hour across habitat types, with 95% confidence intervals. *Statistically significant at $p \leq 0.05$. FE = Forest Edge, FI = Forest Interior, OFP = Open Forest Patch, HS = Human Settlement

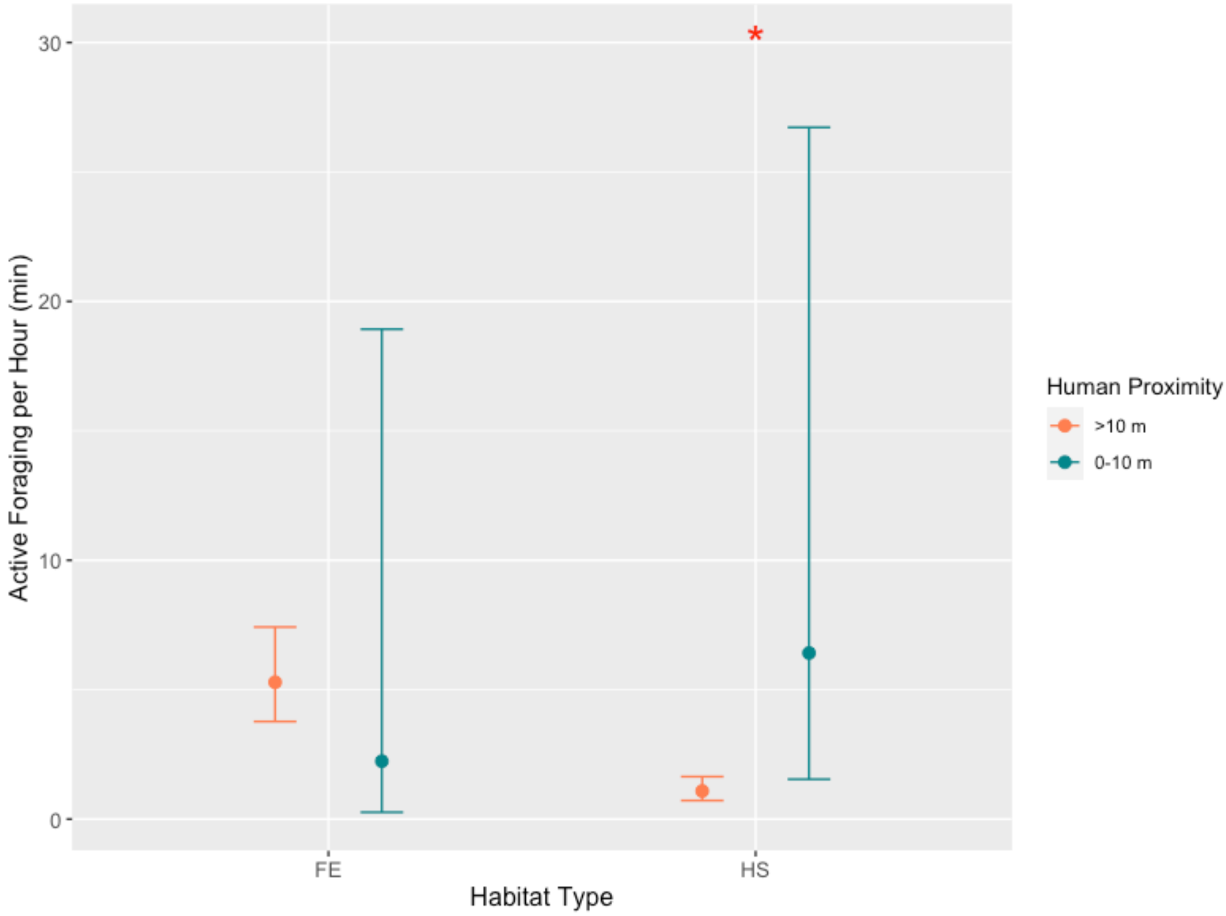

Fig 4. Predicted mean Active Foraging per hour across human proximity distance classes in two modified habitats types, with 95% confidence intervals. *Statistically significant at $p \leq 0.05$. FE = Forest Edge, FI = Forest Interior, OFP = Open Forest Patch, HS = Human Settlement

As observed for Active Foraging, Food Search in the Forest Interior (GLMM, $\beta 0 = 0.59 \pm 0.10$, $z = 5.48$, $p < 0.001$) was comparable to that in the Open Forest Patch ($\beta 1 = 0.34 \pm 0.20$, $z = 1.64$, $p = 0.10$) but significantly lower than that in the Forest Edge ($\beta 2 = 0.58 \pm 0.15$, $z = 3.60$, $p < 0.001$) and significantly higher than in the Human Settlement ($\beta 3 = -0.86 \pm 0.18$, $z = -4.80$, $p < 0.001$). In the Forest Edge, Food Search did not vary significantly between when humans were >10 m away (GLMM, $\beta 0 = 1.21 \pm 0.12$, $z = 9.73$, $p < 0.001$) and when they were within 10 m ($\beta 1 = -0.32 \pm 0.79$, $z = -0.4$, $p = 0.06$). In the Human Settlement too, Food Search did not differ significantly when humans were >10 m away (GLMM, $\beta 0 = -0.16, \pm 0.16$, $z = -0.97$, $p = 0.33$) or within a distance of 10 m ($\beta 1 = -0.23 \pm 1.05$, $z = -0.07$, $p = 0.90$).

A close investigation of the dietary composition during foraging indicated that the study troop consumed plant parts from a total of 19 species, as well as other non-plant matter (Table 2). The proportion of plant matter in the diet varied significantly between the Forest Interior and the Open Forest Patch (G-test of independence = 60.80, df = 1, $p < 0.001$) and between the Forest Interior and Forest Edge (G = 16.139, df = 1, $p < 0.001$) but not between the Forest Interior and the Human Settlement. The troop was thus observed to feed on plant matter significantly more in the Forest Interior than in the Forest Edge and more on invertebrates in the Open Forest Patch than in the Forest Interior.

Table 2. Percentage of food species and their parts consumed by the study lion-tailed macaque troop during the study period

Family	Species	Parts	Percentage
Lauraceae	Litsea floribunda	Fruits	12.6
Moraceae	Ficus exasperata	Fruits	11.5
Moraceae	Artocarpus heterophyllus	Fruits	10.1
Moraceae	Ficus tinctoria	Fruits	9.5
Moraceae	Ficus racemosa	Fruits	5.3
Rubiaceae	Coffea liberica	Fruits	2.9
Bignoniaceae	Spathodea campanulata	Pods	2.6
Fabaceae	Erythrina indica	Buds/Pods	2.4
Moraceae	Ficus tsjahela	Fruits	2.2
Moraceae	Ficus hispida	Fruits	1.8
Myrtaceae	Syzygium cumini	Fruits	1.5
Verbenaceae	Lantana camara	Fruits	1.3
Myrtaceae	Psidium guajava	Fruits	0.6
Lauraceae	Persea americana	Fruits	0.3
Moringaceae	Moringa oleifera	Flower/Buds	0.3
Rubiaceae	Coffea canephora	Fruits	0.2
Bombacaceae	Cullenia exarillata	Fruits	0.1
Passifloraceae	Passiflora edulis	Raw Fruits	0.1
Others: Natural food (bark, lichens, fungi, invertebrates) and Provisioned food			34.7

The frequency of Affiliation in the Forest Interior (GLMM, $\beta0 = -8.89 \pm 0.95$, $z = -9.30$, $p < 0.001$) was significantly lower when compared to that in the Open Forest Patch ($\beta1 = 1.18 \pm 1.26$, $z = 0.93$, $p = 0.30$), Forest Edge ($\beta2 = -0.65 \pm 1.73$, $z = -3.80$, $p = 0.70$) and the Human Settlement ($\beta3 = 0.59 \pm 1.19$, $z = 0.50$, $p = 0.60$).

The frequencies of Aggression, as observed in the Forest Interior (GLMM, $\beta0= -10.23 \pm 1,2$, $z = -8.5$, $p < 0.001$) was significantly lower when compared to the Open Forest Patch ($\beta1= 1.98 \pm 1.47$, $z = 1.34$, $p = 0.18$), Forest Edge ($\beta2= 1.75 \pm 0.94$, $z = 1.86$, $p = 0.06$) and Human Settlement ($\beta3= 0.58 \pm 1.76$, $z = 0.33$, $p = 0.74$; Fig 5).

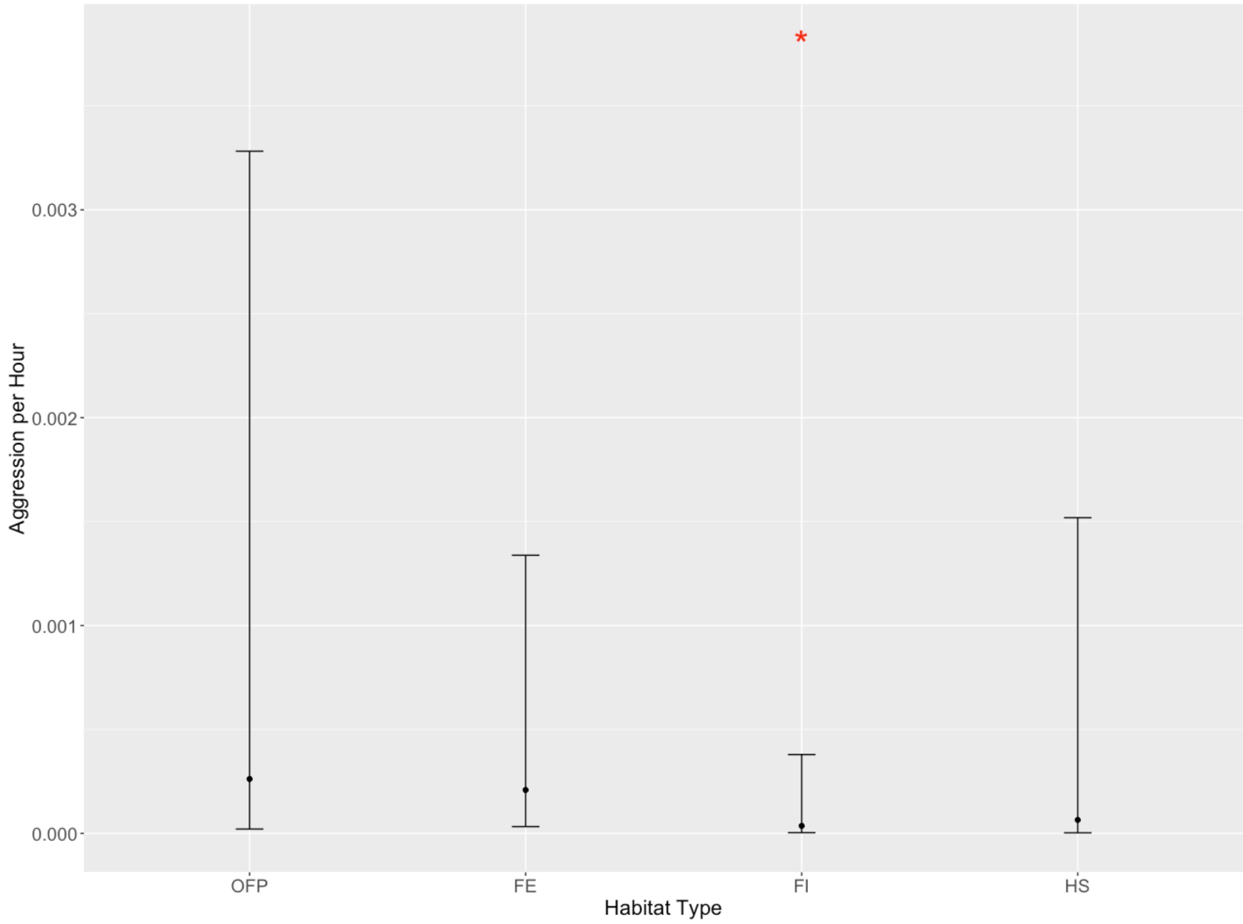

Fig 5. Predicted mean frequency of Aggression per hour, across habitats types, with 95% confidence intervals.. *Statistically significant at $p \leq 0.05$. FI = Forest Interior, FE = Forest Edge, OFP=Open Forest Patch , HS=Human Settlement

The observed allogrooming frequencies and durations were comparable across all habitat types (S4). The correlation between frequency of initiated allogrooming and allogrooming duration was significantly high in the Forest Interior (Mantel test, correlation coefficient = 0.97, $p < 0.001$), Forest Edge (0.95, $p < 0.001$), and Open Forest Patch (0.85, $p = 0.0018$) but relatively low in the Human Settlement (0.50, $p = 0.003$).

Reciprocity in allogrooming was observed to be significantly high in the Forest Interior (0.63, $p < 0.001$), and relatively less so in the Open Forest Patch (0.28, $p = 0.04$). There was, however, no Reciprocity in allogrooming in the Forest Edge (0.23, $p = 0.08$) or in the Human Settlement (0.24, $p = 0.08$).

Influence of Dominance Hierarchy on Foraging Behaviour of Female Macaques

In the Forest Interior, Active Foraging displayed by Dominant females (GLMM, $\beta 0 = 2.30 \pm 0.09$, $z = 24.90$, $p < 0.001$) was comparable to that by Intermediate females ($\beta 1 = -0.02 \pm 0.13$, $z = -0.20$, $p = 0.83$), but significantly higher than that shown by Subordinate females ($\beta 2 = -0.45 \pm 0.13$, $z = -3.38$, $p < 0.001$). In the Open Forest Patch, in contrast, Dominant females (GLMM, $\beta 0 = 1.57 \pm 0.16$, $z = 9.90$, $p < 0.001$) Actively Foraged for significantly less time than did Intermediate females ($\beta 1 = 1.19 \pm 019$, $z = 6.22$, $p < 0.001$) or Subordinate females ($\beta 2 = 0.98 \pm 0.18$, $z = 5.23$, $p < 0.001$). In the Forest Edge, Dominant females Actively Foraged for less time (GLMM, $\beta 0 = 2.22 \pm 0.10$, $z = 21.60$, $p < 0.001$), as compared to Intermediate ($\beta1 = 0.39 \pm 0.14$, $z = 2.74$, $p = 0.006$) or Subordinate females ($\beta2 = 0.41 \pm 0.14$, $z = 2.91$, $p < 0.001$). In the Human Settlement, however, Active Foraging displayed by individuals of Subordinate rank, when compared to that by females of Dominant rank (GLMM, $\beta0 = 1.13 \pm 0.14$, $z = 7.98$, $p < 0.001$) or of Intermediate rank ($\beta1 = -0.06 \pm 0.19$, $z = -0.31$, $p = 0.75$), was significantly higher ($\beta2 = 0.67 \pm 0.18$, $z = 3.66$, $p < 0.001$). It is noteworthy that there was no significant influence of dominance rank on Food Search in any of the four habitats. A closer investigation of individual variation revealed that none of these behaviours appear to be influenced by the Dominance status or the Sex of the individual (S4).

Individual-level Behavioural Variation in Lion-tailed Macaques

An examination of the random slopes for Individual identity, a random coefficient in our generalised linear mixed-effects analysis of Active Forage, Food Search, Affiliation and Aggression indicated that neither Dominance Rank nor Sex appeared to explain the variation in the behavioural profiles across the study individuals (S4).

IV. Discussion

With the dramatic, unceasing increase in the expansion of human-dominated landscapes, globally, human-wildlife interactions, which are usually detrimental to all the species involved, are on the rise. In the face of such rapidly changing ecological conditions, behavioural shifts displayed by individual animals are often the first response to environmental change [2] and documenting these responses have become crucial for our understanding of the persistence and management of nonhuman species in these often drastically altered habitats. Habitat-modifications, while occasionally providing new and easily accessible food resources of human origin, have severe detrimental effects, such as increased mortality, even for generalist animal species [42]. Primates, especially macaques, present interesting case studies, as they are extremely ecologically adaptable and capable of co-existing and interacting with humans at rather close quarters. What is often not recognised, however, is that some of these so-called adaptable macaques are now becoming locally extinct [43, 44] and even the common species may have begun to slowly disappear from their well-known, and thus often neglected, habitats [9, 45, 46]. Changes in the demography and behavioural ecology of newly threatened populations of these species, therefore, can be overlooked and fail to garner crucial conservation attention [46, 47].

The lion-tailed macaque is, in many ways, a unique primate, as it is a species that is evolutionarily adapted to the wet evergreen rainforests of the Western Ghats mountains of southern India, a global biodiversity hotspot but, in recent years, some troops of a particular subpopulation of the species has begun to frequent human-dominated areas adjacent to its now-fragmented forest habitats. Consequently, they now interact closely with humans and feed quite often on human-origin resources. This study has, accordingly, documented in some detail the ecological and behavioural patterns exhibited by possibly the most exploratory of these lion-tailed macaque troops as it increasingly explored an anthropogenic landscape over the day and regularly across the months of the year.

A consistent pattern of a drastic decrease in time spent foraging under provisioning regimes, along with an increase in resting behaviour, has been displayed by populations of different species of primates, such as the white-faced capuchin, savanna baboon, rhesus macaque and the barbary macaque [23, 24, 25, 48]. A similar pattern was displayed by our study troop when it had access to human-origin resources it reduced foraging significantly and spent an increased amount of time resting. Additionally, the troop would raid the hospital building from anywhere between 20 min to an hour (Dhawale, pers. obs.), following which they would rest in the adjacent Eucalyptus stand. Human-origin food, often considered to be of high quality, may occasionally be included by primates in their diet as a strategy to substitute the loss of natural food sources [23]. Consequently, this may result in a troop ultimately becoming dependent on human-origin foods for survival [25], even preferentially gravitating towards areas where human-origin food is regularly available [27, 40]. As it was not possible to collect data during macaque raids on human habitations during this study, a clear estimate of how much of the diet of the study troop consisted of human-origin food could not be established. Evidence from the dietary composition of the troop, however, suggested that such foods was indeed incorporated by individuals as part of their diet. Additionally, in the Open Forest Patch, where much of the under- and mid-storey vegetation has been cleared to plant coffee saplings, the troop consumed a higher amount of invertebrates than they did plant matter, as compared to the other three habitats. Individuals would thus actively forage at high frequencies in this habitat, spending extended periods of time rummaging through dry leaves and bark to acquire insects.

In several studies, the inclusion of provisioned food in the diet of primates have been shown to increase individual fitness, leading to increased reproductive output [49, 50]. Several other studies, however, report detrimental effects of provisioning on the social dynamics, physiological health and survival of nonhuman primates [51, 52, 53, 54]. Additionally, when primates are considered pests by humans, especially in the context of home- or garden-raiding, there is increased direct conflict between the two species. Human-nonhuman primate conflict can result in heavy costs to both parties, even, in certain cases, threatening the persistence of the species in a human-dominated landscape [55]. Troops of certain primate species can quickly learn to recognise humans as a potential source of food, even without the actual presence of provisioned foods [25, 56]. In the Forest Edge, during our study, for example, tourists would often stop their vehicles to observe the lion-tailed macaques, subsequently, the macaques learnt to reduced their Active Foraging and Food Search when tourists were within a distance of 10m. Instead, the macaques directed their attention to the vehicles or the tourists, several members moved closer, some even descending onto the road to bipedally survey the vehicles. The adult male particularly approached the vehicles on multiple occasions, this approach almost invariably being followed by tourists attempting to provide food handouts (Dhawale, pers. obs.). Such behavioural associations are known to occasionally lead to individuals running onto roads, putting them at potential risk of accidents [57, 58, 59]. In the Human Settlement, humans would often be present within or around the hospital building and the macaques occasionally within 10 m of them. Active Foraging increased under these circumstances, indicating that the macaques were primarily utilising the hospital building, and human presence as indicators, to search for human-origin foods. Long-term studies are, however, needed to provide further information on the degree of qualitative and quantitative dependence on and the patterns of exploitation of human-origin food sources by this population of lion-tailed macaques.

In addition to provisioned food releasing macaque troops from the pressures of intensive foraging, certain studies have reported significant increase in social interactions, with individuals modifying their social strategies under these conditions, bonnet macaques being a notable example [26, 27]. In the case of the study lion-tailed macaques, there was only a marginal increase in frequencies of Affiliation in the Human Settlement. There appeared to be an increase in rates of Aggression in certain habitats, the Open Forest Patch, for example, primarily directed by the adult male towards the subadult male when he attempted to mate with females, a possible manifestation of reproductive competition. The increased aggression in this habitat may have been partly driven by the increased visibility of the troop individuals to one another, a situation not typical in the natural habitat – the rainforest canopy – of the species, allowing the dominant male to detect and react to attempts made by the subadult male to mate with the females. There also appeared to be no increase in the frequency of aggression in the Human Settlement. This was a surprising finding, given that competition over provisioned food is often severe among macaques [26, 27] but it could be argued that these resources were possibly not limiting. This is supported by our observation of a significant increase in the proportion of time spent Resting by the study troop in this particular habitat over the entire study period.

Allogrooming in macaques has been shown to vary as a direct result of human presence, where grooming bouts are shorter and infrequently reciprocated, with individuals also spending less time in grooming under these circumstances [26, 27, 60, 61]. In our study area, the intensity of human activity was relatively low and the troop would usually feed near the buildings before quickly moving on to the adjacent Eucalyptus stand, where they would proceed to rest or groom. In lion-tailed macaques, grooming is known to be generally directed up the hierarchy [22]. Our analysis of the patterns of allogrooming in the study troop also revealed that reciprocity in allogrooming, strongly displayed by the study females in forested habitats, broke down significantly in human-dominated habitats. This may have occurred as grooming could have conceivably become a strategy not only to maintain social relationships with other members in the troop but also one to be manipulated in order to reap the benefits of escaping aggression from the most dominant individuals in the troop, as has also been shown earlier in bonnet macaques [26]. Moreover, the observed positive correlation between frequency of initiated allogrooming and the duration of time subsequently spent in it, displayed by the study female lion-tailed macaques in the Forest Interior, Forest Edge and the Open Forest Patch, dissipated in the Human Settlement. This raises the possibility that the macaques initiated grooming more frequently, while reducing time spent in grooming, as a potentially novel social strategy to escape aggression and effect reconciliation under scenarios of increased competition, as prevailed in the anthropogenic habitat, an observation also made earlier in bonnet macaques [26].

Dominance rank is a crucial aspect of the life of social animals, even being shown to affect lifetime reproductive success [21]. Patterns of dominance, especially among the female members of primate troops, become further intensified when food resources occur in a clumped distribution, which is often the case for human-origin foods [27, 62]. In the case of our study troop, subordinate individuals foraged at higher frequencies when compared to dominant individuals in habitats where human-origin foods were present, perhaps as compensation for delayed access to food, privileged first access being reserved for dominant members of the troop.

It is important to note here that our generalised linear mixed-effect analysis of the inter-individual variation in behavioural profiles displayed by the adult individuals in the study troop in certain habitats, including the Forest Edge or Open Forest Patch could not be explained by either sex or dominance rank, the two biological variables that we examined. These variations in behaviour could, however, conceivably be explained by other aspects of the biology of the individual that we did not examine, including, for example, personality or temperament [63]. Such variation, even if not understood completely, could contribute significantly to the ability of individuals to cope with a changing environment. Several questions then beg answers: Are certain individual lion-tailed macaques more likely to initiate novel behavioural strategies and if so, what drives this likelihood? Are these behaviours then learnt by other members of the troop and does such learning lead to the establishment of adaptive behavioural traditions, as has been observed earlier in a population of occasionally provisioned bonnet macaques [64]?

Drivers of primate behavioural ecology, such as human-origin foods and physical human presence, are only some of the factors considered in this study. There are, however, other crucial factors that have not been accounted for in the present investigation.. Quantifying the underlying vegetation, for example, may provide a better understanding of the decisions made by the study troop, those that have a clear bearing on the management of potential human-primate conflict and the conservation of this endangered primate species. Additionally, our data represent only the dry season of the year [65] and these behaviours may further vary as availability of resources within the forest change across seasons.

It is widely acknowledged that habitat-modifications affect wildlife of all taxa [66]. Altered habitats tend to favour generalist species, leaving specialist species especially vulnerable to habitat disturbances [67] and this makes it all the more important to investigate the persistence of such species in response to anthropogenic influences. The insights obtained from this study provide a crucial first step in understanding the potential long-term effects that a relatively recent phenomenon, an evolutionarily rainforest-adapted species gradually undergoing a paradigm shift in ecological regimes, through its discovery of an alien, anthropogenic environment may have on the long-term survival of species populations, particularly under conditions of increasing human influence. It may also be strongly suggested that species like the lion-tailed macaque, while being classified as specialist species, seem to have the inherent ability, as do perhaps all macaque species, to adapt to and thrive in human-modified habitats, and this discovery, by itself, may have important implications for the management.

V. References

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