Intra-specific variation in seed dispersal effectiveness of Lion-tailed Macaques *Macaca silenus*

by

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Under the supervision of

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AcSIR

DECLARATION

I hereby declare that the work conducted under the thesis entitled **“Intra-specific variation in seed dispersal effectiveness of Lion-tailed Macaques *Macaca silenus*”,** is a record of original and independent research work done by me and subsequently submitted for the award of the degree of **Master’s in Wildlife Science** at the **Academy of Scientific and Innovative Research**. This research work has been carried out under the guidance and supervision of **Dr. H. N. Kumara, Principal Scientist, SACON**, and co-supervision of **Dr. Navendu Page**, **Scientist, Thackeray Wildlife Foundation** and **Dr. Rohit Naniwadekar**, **Scientist, Nature Conservation Foundation**. The work has not formed the basis for the award of any other degree, diploma, or any other qualification. I also declare that the thesis embodies my own work, analysis, observation, understanding and the particulars given in it are true to the best of my knowledge.

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CERTIFICATE

This is to certify that the thesis by **Bindu K** entitled **"Intra-specific variation in seed dispersal effectiveness of Lion-tailed Macaques *Macaca silenus*"** is an original and independent research work submitted to the **Academy of Scientific and Innovative Research**, for the award of the degree of **Master's in Wildlife Science**.

Bindu K has put one semester of research work embodied in this thesis under my guidance and supervision. The work presented in this thesis has not been submitted to any other University or Institute for the award of any degree, diploma or distinction.

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EXECUTIVE SUMMARY

1. Tropical forests are one of the most biodiverse ecosystems on Earth. Seed dispersal is one of the important interactions that maintains species richness and ecosystem functions. Vertebrate frugivores, especially birds and mammals, play a crucial role in dispersing seeds. The dispersal effectiveness of these dispersers is influenced by factors such as size, age, sex, dominance hierarchy and behaviour types. Invasive species pose significant threats to tropical ecosystems, rapidly forming mutualistic relations with native dispersers. This study focuses on the lion-tailed macaques *Macaca silenus* in the Western Ghats to explore how age-sex categories influence seed dispersal of native and exotic species in terms of diversity and quantity of fruits consumed, quantity of seeds dispersed, daily distance travelled and seed deposition site.

2. I employed non-invasive behavioural sampling on four troops of the lion-tailed macaques for four months. Focal animal sampling of 375.9 hours was employed on individuals belonging to three age sex categories, including adult males, adult females and subadults. Faecal samples were collected to assess quantity of seeds dispersed, and the substrate at seed deposition site was recorded. The movement of focal individual was tracked for the entire duration of the observation.

3. Subadults consumed higher diversity of fruits than females and males. Subadults also consumed more native fruits, while females consumed more non-native fruits. The pairwise dietary overlap between all age-sex categories was high. The rate of consumption of non-native fruits increased as day progressed. Subadults dispersed significantly less Ficus seeds than the other age-sex categories. Daily movements showed no significant differences across age-sex categories. However, I found weak evidence of males being more likely to disperse seeds on trees, which could be more suitable for *Ficus* germination. The differences in

feeding patterns also highlight the greater importance of subadults in the dispersal of a greater diversity of fruit plant species.

4. The invasives *Coffea* spp. and *Lantana camara* constituted up to 90% of the diet of the three age-sex categories. There was difference in the relative proportions of these two species. Males consumed more *Coffea* spp., whereas subadults and females consumed more *Lantana* fruits. The macaques dispersed *Ficus* seeds in clumps, increasing the risk of predation or microbial infection.

5. This study generates novel information on intra-specific variation in seed dispersal, a relatively understudied topic. It also highlights lion-tailed macaques' significant role in dispersing alien invasive species in degraded rainforests and provides valuable insights into their understudied role as seed dispersers.

Keywords: Intraspecific variation, Age-sex categories, Invasives, Tropical forests, Frugivory.

1. INTRODUCTION

1.1 TROPICAL FORESTS AND SEED DISPERSAL

Tropical forests, covering only 6% of Earth’s land, harbour about two-thirds of the planet's terrestrial biodiversity, making them the most species-rich ecosystems (Gardner et al., 2009; Gentry, 1992). Interspecific interactions play an important role in maintaining this biodiversity. Seed dispersal, a key mutualistic interaction, has impacts on plant richness, distribution, community composition, and fitness in tropical forests (Kakishima et al., 2015; Merritt et al., 2010; Snell et al., 2019; Vellend, 2010). This mutualistic interaction between frugivorous animals and plants has shaped Earth’s biodiversity for over 70 million years (Estrada & Fleming, 1986). A diverse range of animals, from insects to large vertebrates, are involved in the seed dispersal process (Stiles, 2000). Animals disperse seeds on various scales, including local, regional or even transcontinental scales (Farwig & Berens, 2012).

Vertebrate frugivores disperse up to 90% of plant species in tropical communities. More than 75% of the tree species produce fleshy fruits dispersed mainly by birds and mammals (Beckman & Rogers, 2013; Howe & Smallwood, 1982; Wunderle, 1997). Birds and mammals are among the key vertebrate seed dispersers in the tropics (Corlett, 1998; Farwig & Berens, 2012; Jordano et al., 2001). Although most mammals eat some fruit, only a few families play an important role in seed dispersal (Corlett, 1998). Among mammals, bats and primates are important seed dispersers (Stoner et al., 2007). Primates, scansorial-arboreal species and intermediate in size compared to other frugivorous mammals such as bats and mega-herbivores, play a critical role in the dispersal of small to large seeds over long distances (Estrada & Fleming, 1986; Lacher et al., 2019). This signifies the role of primates in the seed dispersal process.

1.2. INTRASPECIFIC VARIATION IN SEED DISPERSERS

Successful animal-mediated seed dispersal is a complex mechanism since it involves removal of ripe fruits (with mature seeds), appropriate seed handling and/or gut treatment by the seed disperser agent that ensures that seeds are not damaged, the dispersal of the seeds away from the mother plant to reduce conspecific competition and predation and provide suitable environmental conditions for the seed to germinate and establish (Howe & Smallwood, 1982). The inter-specific differences in seed dispersal effectiveness across different species, from fishes to mammals, are relatively well-studied (Falcón et al., 2020; Fuzessy et al., 2016; Rogers et al., 2021; Torres et al., 2020). This has demonstrated significant differences among species in seed removal rates, gut treatment, and seed deposition at suitable microhabitats. However, variations in seed dispersal effectiveness within a species may be driven by size, age, sex classes or individual personalities (Zwolak & Sih, 2020). These variations could lead to differences in their seed dispersal effectiveness, including number of seeds dispersed, dispersal distance and the quality of seed deposition site (Snell et al., 2019). For example, males of certain frugivorous birds perch on tall, open branches of trees and display to attract females (Wenny, 2000). During this process, they disperse seeds under the display perches that are suitable for the germination of certain species due to open canopy conditions that reduce fungal infestation. This aspect of intra-specific variation in seed dispersal is relatively less studied than inter-specific variation in seed dispersal.

Studies examining the consequences of individual variation in seed dispersal on patterns of seed dispersal are relatively few. Differences in the body size of animals can influence fruit-handling behaviour and seed dispersal distances. Similarly, key traits like age group and sex can influence the behaviour of individuals with consequent effects on seed dispersal patterns, an aspect poorly studied in the literature. Benitez-Malvido et. al., 2016 reported that the age and sex of Howler monkeys impact the time spent on foraging and diversity of plant species in their diet, with adults appending more time foraging and consuming a greater diversity of plant species. In primates, dominance rank affects the foraging pattern and seed handling (Dhawale et al., 2020; Tsuji et al., 2020). Studies have shown high-ranking individuals of Japanese macaques get priority access to limited resources, and are not careful in handling fruits, damaging the seeds while eating, thereby reducing the dispersal quality (Tsuji et al., 2020). The study revealed that dominant females monopolised nutritious nuts in resource scarce year. Subordinates resorted to consuming less nutritious berries to avoid conflict, with a reduced mastication rate, thereby serving as high-quality dispersers. Therefore, given the differing ranks, physiological requirements and behaviours, we can expect intra-specific variation in seed dispersal. This aspect has been poorly studied in the literature. Since frugivorous primates have a high representation of fruits in their diets and have well-established hierarchies and morphological differences, they offer a suitable system for studying intra-specific variation in seed dispersal.

1.3. INVASIVES IN TROPICS AND THEIR DISPERSAL

Tropical forests face threats from forest fires, global climate change, deadly pathogens, forest fragmentation and overhunting (Laurance & Peres, 2006). Habitat fragmentation disrupts ecological processes, leading to change in species composition and reduced functional diversity, consequently facilitating the spread of non-native invasive species in tropical forests (Bitani et al., 2020; Joshi et al., 2015). Invasive species pose significant risks to native ecosystems by displacing existing species and integrating into seed dispersal networks (Voigt et al., 2011). Many exotics produce high-energy fruit crops and occur in the early stages of succession, forming mutualistic relationships with dispersers (Cordeiro et al., 2004). Highly invasive plants adapt characteristic morphological traits to favour selection by frugivores. Invasives with fleshy fruits quickly associate with native and non-native dispersers (Ramaswami et al., 2017). Studying intra-specific variation in seed dispersal can help determine the differing roles of different cohorts in the dispersal of alien invasive species.

Lantana camara, one of the ten worst invasives, is dispersed by native frugivorous birds, mainly different species of bulbuls, in many countries (Bitani & Downs, 2022; Chishty et al., 2023; Ramaswami et al., 2017; Taneja et al., 2022). While the dispersal of invasives by birds has been well studied globally, the role of mammals in dispersing exotic species needs to be better understood. In the Western Ghats of southern India, large herbivores, including elephants *Elephas maximus*, gaur *Bos gaurus* and chital *Axis axis* disperse the invasive *Senna spectabilis* (Anoop et al., 2022), while blackbuck *Antilope cervicapra* is known to aid the dispersal of *Neltuma juliflora* (Tahir et al., 2021). However, the dispersal of exotics by primates has been relatively understudied. Similarly, the invasion of coffee in rainforests has been a significant challenge for conservationists. Coffee berries are dispersed primarily by mammals, including civets and primates (Joshi et al., 2015).

1.4. BACKGROUND AND STUDY SYSTEM

Lion-tailed macaque *Macaca silenus* (LTM) is an endemic, habitat specialist, primarily arboreal and frugivorous primate (Dhawale et al., 2020) found in the central and southern portions of the Western Ghats Biodiversity Hotspot of India. Fruits are a significant LTM diet component (Santhosh et al., 2015). Fruit availability affects LTMs' movement and foraging patterns (Krishnadas et al., 2011; Menon & Poirier, 1996). Native fruit species such as *Artocarpus heterophyllus, Cullenia exarillata, Ficus* sp., *Litsea floribunda, Erythrina indica, Syzygium cumini, Moringa oleifera*, among others, are reported in their diet. In severely fragmented rainforests of Anamalai hills, LTMs also feed on exotic species, including *Persea americana, Maesopsis eminii, Coffea arabica, Coffea robusta, Lantana camara, Psidium guajava,* and pods of *Spathodea campanulata* (Dhawale et al., 2020; Menon and Poirier, 1996; Singh et al., 2002a). Although the importance of fruits for these macaques is well documented, there are no studies on the role of macaques in seed dispersal. Intraspecific variations in LTMs such as differences in foraging behaviour, including differences in patterns and time spent on foraging, have been documented (Dhawale et al., 2020). The differences in body size between males and females, with males being much larger, could influence the number of fruits consumed (Correa et al., 2015; Rouff et al., 2005; Zwolak, 2018). Furthermore, males and females have been reported to exhibit different levels and types of curiosity, with females demonstrating a greater propensity to locate food resources (Rouff et al., 2005). These behavioural differences could inadvertently lead to differences in the seed dispersal potential across different age-sex categories of LTMs. Puduthottam is a private and degraded rainforest fragment that has the highest density (>100 individuals/km2) of LTMs among the 45 rainforest fragments in the Anamalai hills of Tamil Nadu (Dhawale & Sinha, 2023; Singh et al., 2002). The severely degraded rainforest fragment has native and exotic invasive fruiting tree species, making it ideal for addressing my study objectives.

1.5. OBJECTIVES AND RESEARCH QUESTIONS

Objective 1. To determine the differences in relative contributions of native and non-native fruits in the diets of different age-sex categories of lion-tailed macaques

1.1. How does the diversity of native and non-native fruits foraged differ across the age-sex categories?

1.2. How do the numbers of native and non-native fruits consumed differ across the age-sex categories?

Objective 2. To determine differences in seed dispersal across age-sex categories of lion-tailed macaques.

2.1. How does daily distance travelled differ across the age-sex categories of lion-tailed macaques?

2.2. How do the number of Ficus seeds deposited by lion-tailed macaques differ across the age-sex categories?

2.3. How do the seed deposition sites differ between the age-sex categories of LTMs?

2. METHODS

2.1. STUDY AREA

Lion-tailed macaque, primarily frugivorous and arboreal primate, is endemic to Western Ghats of southern India. These macaques are distributed across eight locations in Karnataka, Kerala and Tamil Nadu (Dhawale et al., 2020; Kurup & Kumar, 1993; Singh et al., 2002). The Anamalai Hills of Tamil Nadu harbours the largest metapopulation of lion-tailed macaques in its distributional range (Dhawale & Sinha, 2023; Singh, 2019). The primary vegetation type of the area is tropical rainforests, occurring between 600 and 1500 m, above which tropical montane rainforest-grasslands replace them. Once a contiguous stretch of tropical rainforests, these hills have undergone severe degradation over the past two centuries due to land clearing for tea, coffee and cardamom cultivation. Located at the centre of these hills is the Valparai plateau, which spreads over an area of 220 km^2. It is a heterogeneous landscape dominated by tea and coffee plantations interspersed with several rainforest fragments of varying areas, ranging from <10 ha to >100 ha (Dhawale & Sinha, 2022; Umapathy & Kumar, 2000).

I conducted the study in one of the larger fragments, Puduthottam, which covers an area of 92 ha. The fragment adjoins coffee and tea plantations and human settlements, which include labour lines in the plantations and the neighbouring town of Valparai. Additionally, the Pollachi-Valparai National Highway cuts through the fragment. The macaques use all the habitat types, spending significant time in and around human settlements (Dhawale et al., 2020). Puduthottam harbours five troops of LTMs with approximately 200 individuals. Of the five troops, I observed individuals from four troops: BT, NTT, RT and PAP, consisting of ca. 116, 39, 25 and 12 individuals, respectively (Dhawale & Sinha, 2023; Bindu K, Pers. Obs.). Due to its dominance over the other troops, BT often drove other troops into less accessible parts of the fragment, which elephants frequented. Consequently, I collected most of the data

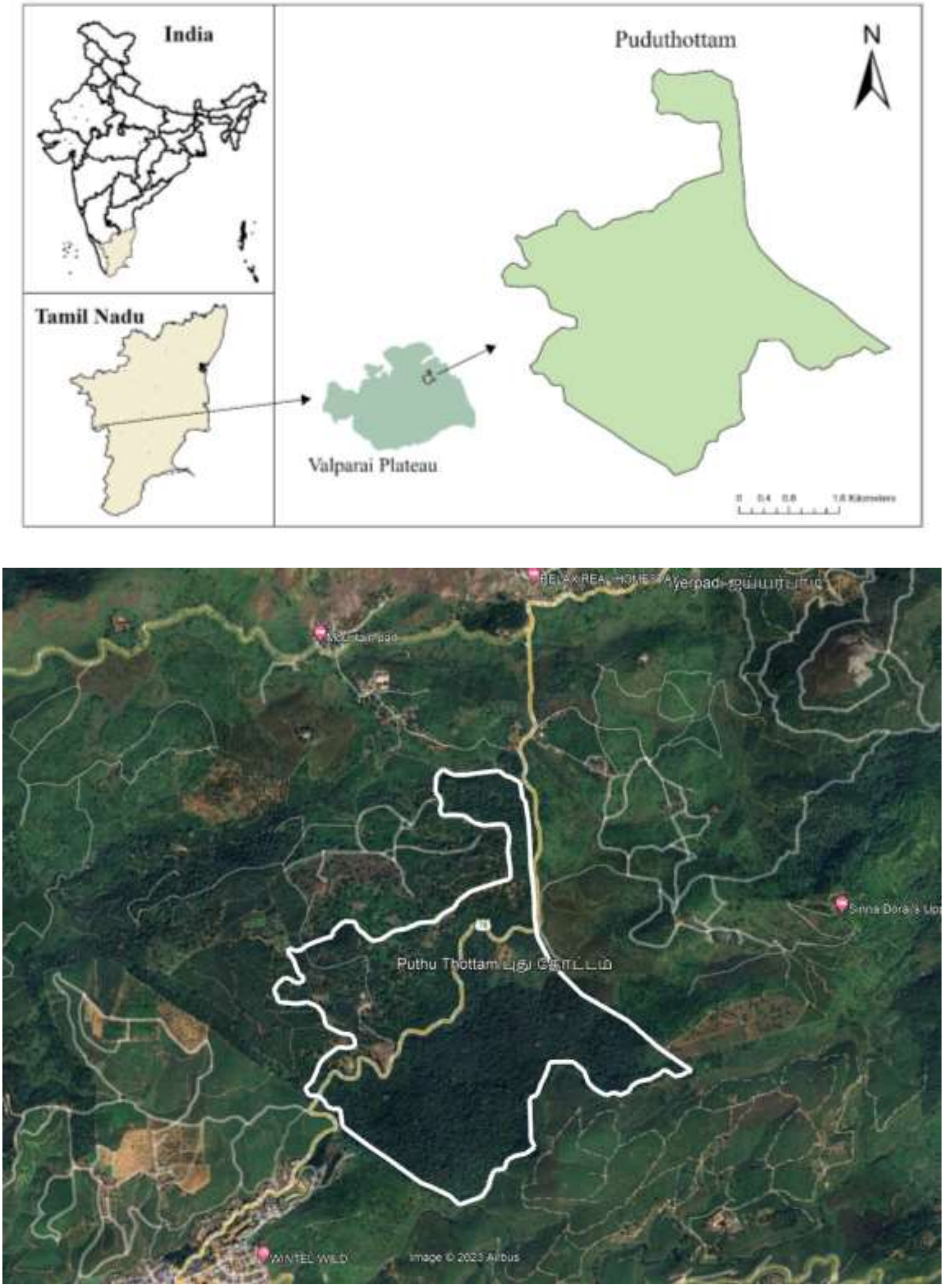

Figure 1. Map of study site, Puduthottam fragment in Valparai Plateau of Anamalai Hills, Tamil Nadu (Adapted from Dhawale et al., 2020)

from the BT troop (Table 1). A single previous study on intra-specific variation in seed dispersal was conducted on a single troop of Japanese macaques (Tsuji et al., 2020)

Table 1. Sampling effort (hours) across four troops distributed across three age-sex categories.

Troop ID	Adult Female	Adult Male	Subadult	Total duration (hr)
BT	66.50	70.71	85.57	222.8
NTT	40.41	27.51	29.67	97.6
PAP	14.57	28.10	7.40	50.1
RT	NA	4.41	0.96	5.4
	121.48	130.72	123.6	375.9

2.2. FIELD METHODS

The study involved non-invasive behavioural observations of LTMs. Observations focused on the feeding bouts, which typically commenced shortly after sunrise, during which the macaques actively searched for and consume a significant quantity of fruits. Therefore, I selected the first troop I saw in the field for observation. I restricted the observations to individuals from three age-sex categories: adult males, adult females, and subadult males (Table 2, adapted from Singh et al., 2002). Data collection spanned over 450 hours of follow observations conducted between January and April 2024.

Focal animal sampling was employed, observing a single individual each day for six hours from 0700 to 1300 hr, across an average of 19.8 (SE: ± 1.84) days per month. The total sampling effort encompassed 375.9 hours of focal observations, distributed among individuals of different age-sex categories: adult males, adult females, and subadult males. I did not observe subadult females due to difficulty in distinguishing them from adult females and juvenile males. I followed the troop in fragments, plantations, and labour lines in the plantations. However, I stopped observations when the troop moved into the adjacent town as they rarely fed on fruits, mainly feeding on human-origin food.

Table 2. Age-sex classification of lion-tailed macaques (adapted from Singh et al., 2002)

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

I categorised the observed activities into moving, resting, grooming, vocalisation, foraging and feeding (modified from Tsuji et al., 2020). When the focal individual engaged in feeding behaviour, I classified the food items into plant, invertebrate, human-origin food, and unidentified material. Specifically, when feeding on fruits, I collected additional details like the fruit species identity, number of fruits consumed, and state of fruit ripeness (ripe/unripe).

I tracked the daily movements of the focal individuals using a Garmin eTrex 20x GPS device. I collected faecal samples upon observing defecation events from individuals of known age-sex category. I recorded the location and micro-habitat characteristics of the deposition sites, including canopy cover, substrate type, and understorey vegetation. The faecal samples were rinsed through a 0.5 mm sieve using fresh water following established methods (Tsuji et al., 2020). The seeds obtained were dried and identified to the species level, except for *Ficus* and *Coffea* seeds, which require microscopic observations for identification. I conducted the analysis for *Ficus* seeds since other seeds appeared infrequently in the samples.

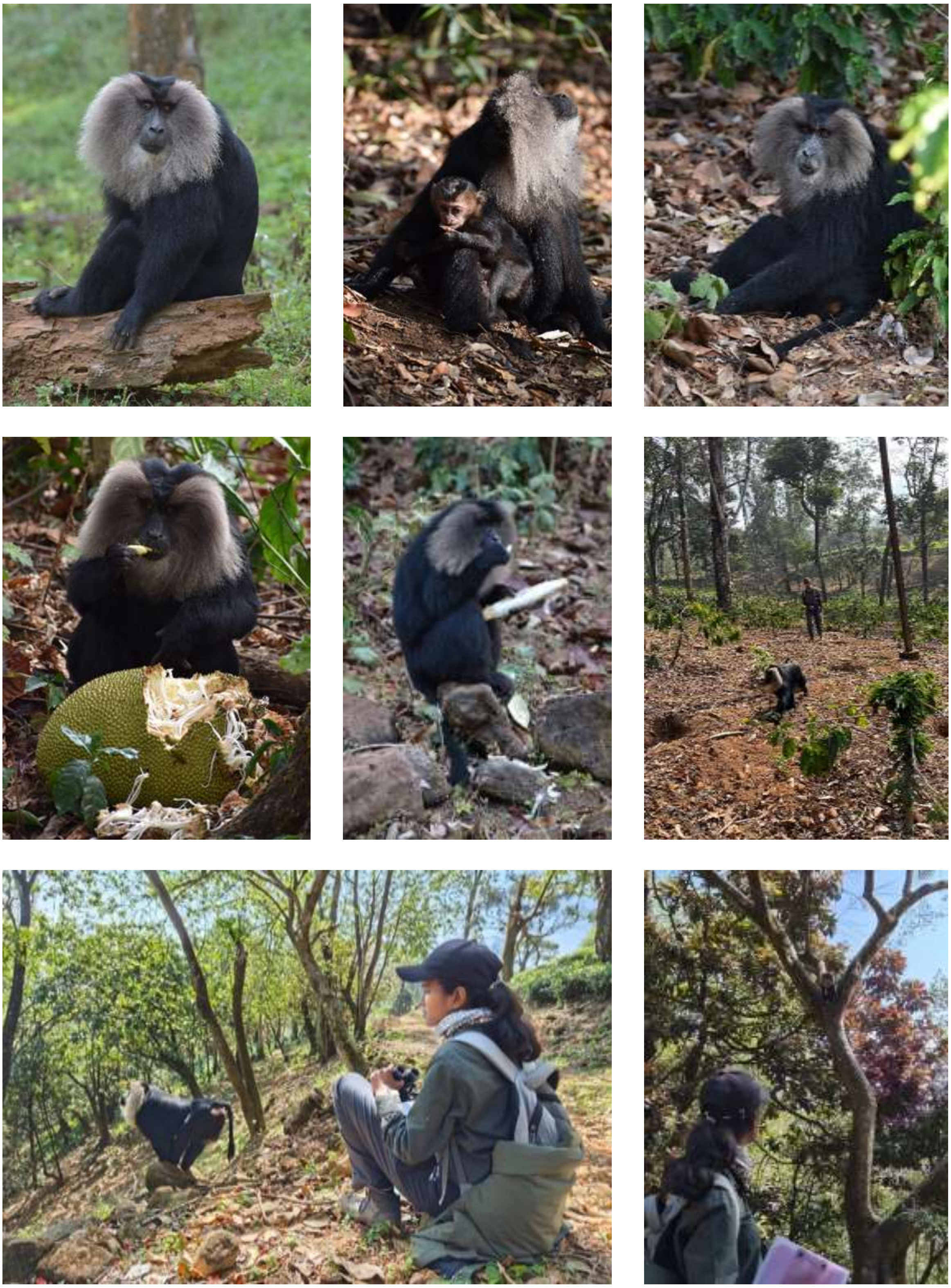

Plate 1. Adult male, female and subadult (top row, L-R). LTM male feeding on *Artocarpus heterophyllus* (middle row-left). LTM female feeding on *Spathodea campanulata* (middle row-right) and me collecting data (middle row-left, bottom row)

2.3. STATISTICAL METHODS

All statistical analysis was performed in R, version 4.2.1 and visualised using ggplot2 (R Core Team, 2022). To determine the evenness in the diet of the different age-sex categories, I used the Shannon-Wiener Diversity index where higher values indicate greater evenness. To determine the diversity of fruits in the diet of the macaques, I calculated Hill-Shannon diversity. I evaluated the sampling completeness for each age-sex category using sample coverage, which estimates the proportion of the total community represented in the sample (Roswell et al., 2021). The coverage for all three cohort categories (adult male, adult female and subadults) was >99%, indicating sampling adequacy. I computed Hill-Shannon diversity for native and non-native fruits consumed by each age-sex category using the R package 'iNEXT' (Hsieh et. al., 2024). The data was bootstrapped 50 times to obtain the 95% confidence interval. I compared the diversity metric across three age-sex categories, and I inferred statistically significant differences if the confidence intervals didn't overlap (Cumming et al., 2007). I computed Pianka's niche overlap indexes to determine pair-wise dietary overlap in fruits between different age-sex categories using the R package 'spaa'. The data was bootstrapped 999 times.

I performed Chi-squared test to examine differences in the proportions of native and non-native fruits across age-sex categories. I performed Chi-squared test to examine the differences in proportions of different non-native species across age-sex categories. The sampling effort for each focal observation was different. To standardise the effort, I calculated the rate of fruit consumed, i.e., fruit consumed per hour. I used general linear models (with Gaussian error structure) to determine the effect of age-sex category on the number of fruits fed upon, using R package 'stats'. I analysed native and non-native fruit data separately. I used the age-sex category and time since sunrise (min) as the predictor variables. I included time since sunrise as one of the predictors, as the start time of behavioural observations differed depending on when I was able to locate the troop and start the focal observations. Since time of the day could influence their fruit consumption, I included time since sunrise in the analysis. I only considered ripe fruits for the analysis, as unripe fruits had very little representation.

I used general linear models to determine if the daily movement (per hour) differed across the age-sex categories. The data was log-transformed to approximate normality. I used generalised linear model to determine if the number of *Ficus* seeds dispersed differed across the age-sex categories. I fitted negative binomial regression model since the data was overdispersed. I plotted violin plots with box plots inside to compare the daily distance travelled across age-sex categories. I performed Chi-squared test to determine the association between age-sex cohorts and different kinds of substrates (bare rock, leaf litter, rock and tree trunk) where the faecal samples were found.

3. RESULTS

3.1. FRUIT DIVERSITY IN DIET

I observed the LTMs feeding on 24 species of plants (Table 3). The species richness of fruits consumed by subadults, females and males was 19, 17 and 17, respectively. However, the Shannon-Wiener diversity index for females, males and subadults was 1.9, 1.4 and 2.1, respectively, indicating that the diets of the subadults were relatively most even and of the adult males were the least even among the three groups. The Hill-Shannon diversity of fruits in the diet of females, males and subadults was 6.4, 3.9 and 8.2 species, respectively. The diversity differed significantly between all three age-sex categories (Fig. 2a, b and c). A similar trend was observed for the diversity of native fruits, with subadults feeding on the most diverse fruits (6.3 species), followed by females (4.2 species) and then males (2.8 species). The diversity of non-native fruits consumed by males (3.1 species) was lower than that consumed by females (3.9 species) and subadults (3.7 species), as inferred from non-overlapping 95% CI

Despite the differences in species richness of native and non-native fruits in the diet of females, males and sub-adult LTMS, Pianka's niche overlap index indicated high dietary overlap between female-male (0.75), female-subadult (0.94) and male-subadult (0.83) (Fig. 2d). The 95% CI for the three combinations overlapped.

3.2. QUANTITY OF FRUITS IN DIET

I found that subadults consumed a higher proportion of native fruits and females consumed a higher proportion of non-native fruits than the other age-sex categories (χ^2 = 306.31, df = 2, $p < 0.001$). The analysis was conducted separately for native and non-native species in the diet (Fig. 3a).

There was no significant effect of age-sex category on the rate of native (*F* = 1.65, df = 2, 148, *p* = 0.18; Table 4) and non-native fruits (*F* = 0.7, df = 2, 95, *p* = 0.5; Table 5) consumed. However, time since sunrise (min) has a significant effect on the rate of non-native fruits eaten per hour (Table 5). I found that males consumed a higher proportion of *Coffea robusta* and a lower proportion of *Lantana camara* than females and subadults (χ^2 =70.86, df = 14, $p < 0.001$; Fig. 3b).

3.3. DAILY MOVEMENT

I recorded a total of 107 tracks of varying lengths during the study. There was no significant effect of age-sex category on daily movement ($F_{2,104}$ = 0.8787, p = 0.42; Table 6; Fig. 6).

3.4. SEED DISPERSAL QUANTITY

During the study, a total of 51 fresh faecal samples were collected, from which 121,375 seeds were identified, belonging to six plant species, including *Ficus sp., Coffea sp., Maesopsis eminii, Spathodea campanulata, Scurrula parasitica* and *Lantana camara*. Only *Ficus* seeds were considered for further analysis, since other seeds appeared infrequently in the samples. Subadults dispersed significantly less *Ficus* seeds when compared to the other age-sex categories (Table 7).

3.5. SEED DEPOSITION SITE

I found a total of 51 faecal samples (females: 20, males: 18, subadults: 13). The relative proportion of faecal samples across different substrates differed marginally across cohorts (χ^2 = 11.63, df = 6, p = 0.07; Fig. 7b). Male LTMs were more likely to disperse seeds of Ficus on trees, which are more likely to be suitable habitats for the germination of Ficus seeds.

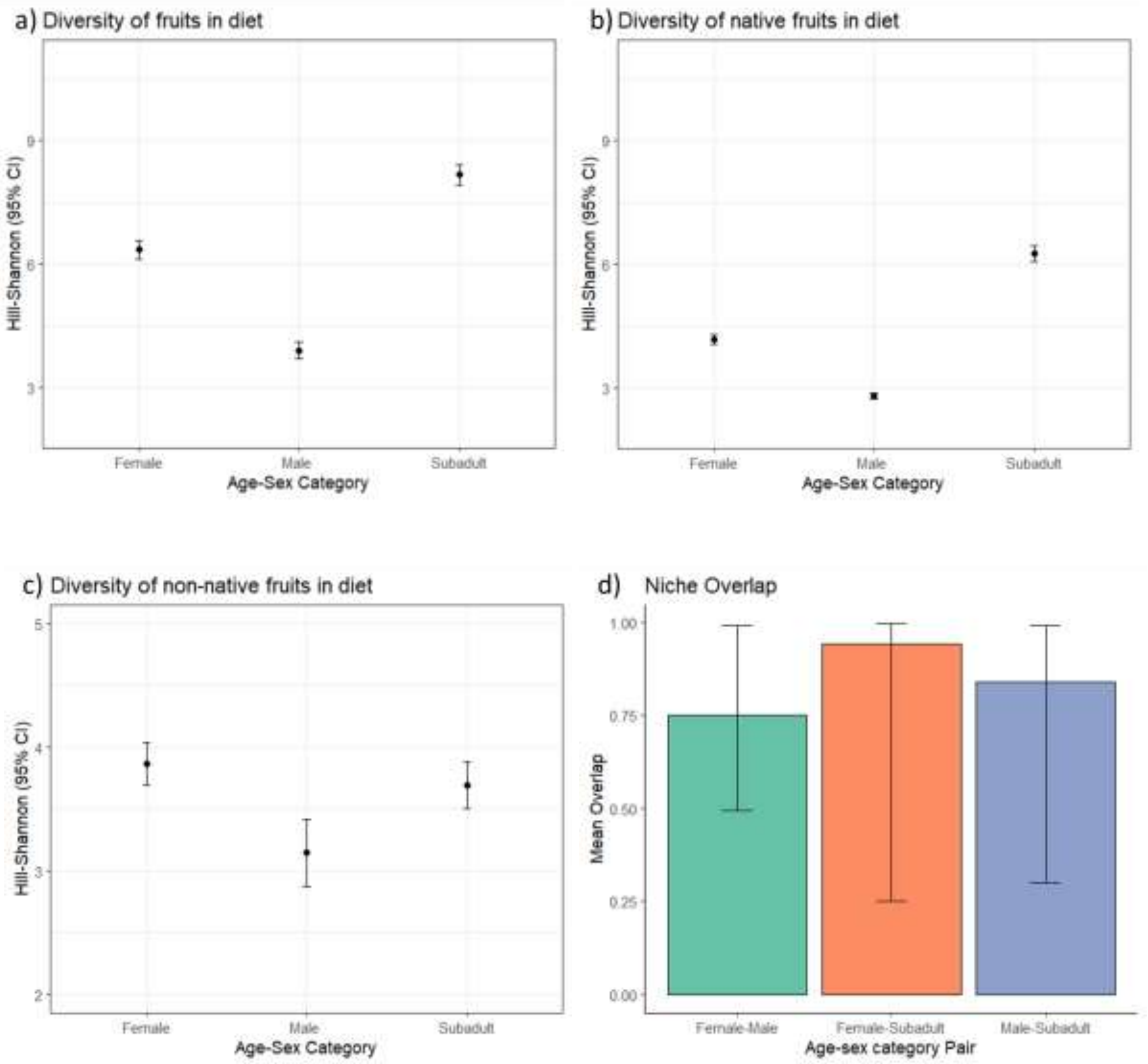

Figure 2. Taxonomic diversity (Hill-Shannon Diversity Measure) of a) all fruits (native and non-native), b) native fruits, and c) non-native fruits consumed across age-sex categories, compared using Hill-Shannon measure. Bars indicate bootstrapped 95% confidence intervals. d) Pairwise niche overlap (95% CI) indicates the compositional similarity of fruits consumed between different cohorts.

Table 3. Number of fruits of different plant species that I observed the different cohorts of Lion-tailed macaques feeding on during the study period.

Species	Family	Type	Female	Male	Subadult
Artocarpus heterophyllus	Moracea	Native	13	28	37
Coffea arabica	Rubiacea	Non-native	154	350	146
Coffea robusta	Rubiacea	Non-native	261	47	110
Cullenia exarillata	Malvaceae	Native	0	0	1
Eugenia uniflora	Myrtaceae	Non-native	0	38	0
Ficus amplissima	Moraceae	Native	16	556	356
Ficus exasperata	Moraceae	Native	96	92	108
Ficus microcarpa	Moraceae	Native	1001	259	705
Ficus nervosa	Moraceae	Native	33	2	0
Ficus racemosa	Moraceae	Native	91	102	65
Ficus religiosa	Moraceae	Native	15	0	0
Ficus superba	Moraceae	Native	0	0	68
Ficus tinctoria	Moraceae	Native	1974	3647	1554
Ficus tsjahela	Moraceae	Native	165	240	317
Lantana camara	Verbenaceae	Non-native	284	79	133
Litsea nigrescens	Lauraceae	Native	24	28	35
Litsea floribunda	Lauraceae	Native	0	0	57
Maesa indica	Primulaceae	Native	0	0	65
Persea americana	Lauraceae	Non-native	0	1	0
Psidium guajava	Myrtaceae	Non-native	13	13	7
Scurrula parasitica	Loranthaceae	Native	771	50	600
Spathodea campanulata	Bignoniaceae	Non-native	36	11	21
Syzygium aqueum	Myrtaceae	Non-native	16	0	0
Syzygium rubicundum	Myrtaceae	Native	0	0	3

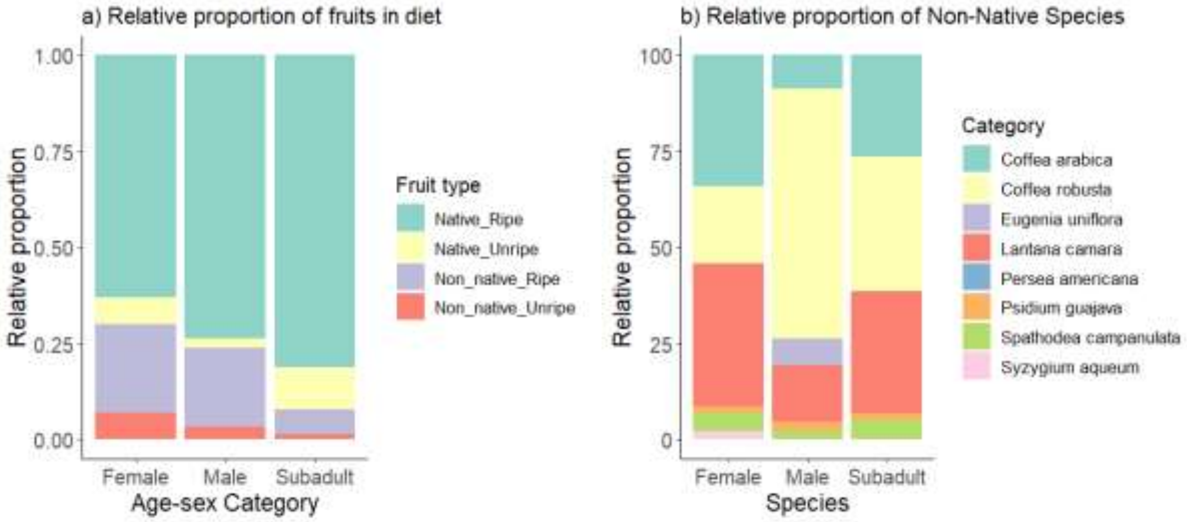

Figure 3. Relative proportions of fruits in the diet. a) There is low representation of unripe fruits, and a higher proportion of non-native and native fruits in the diet of females and subadults, respectively. b) Relative proportions of different non-native species in diet. Adult male consumed more coffee compared to other alien fruit species, while Lantana camara formed a significant part of the diet of females and subadults.

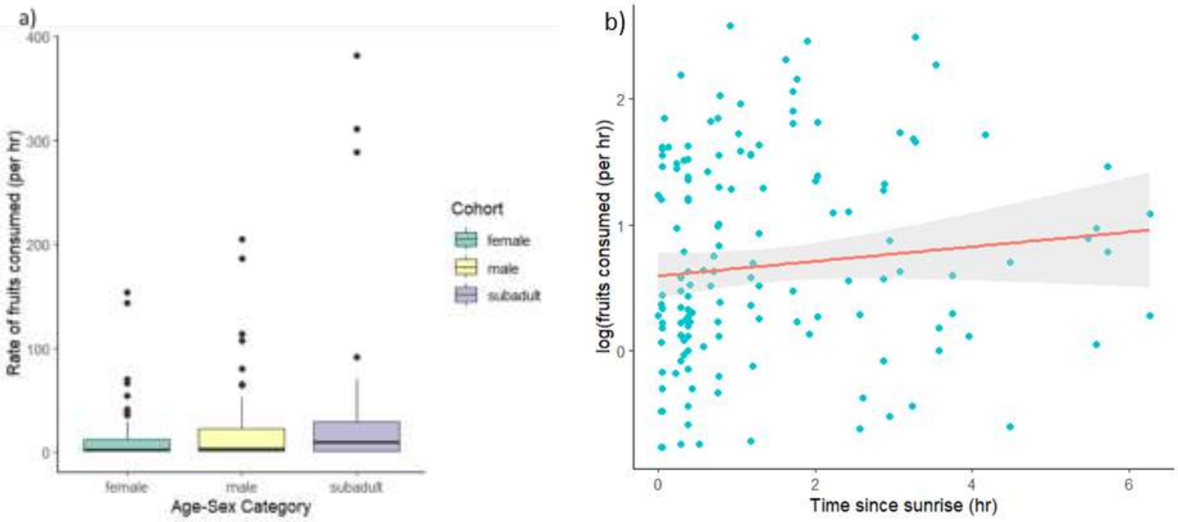

Figure 4. a) The rate of native fruits consumed (per hr) by each age-sex category. b) The rate of native fruits eaten (per hr) did not vary as the day progressed.

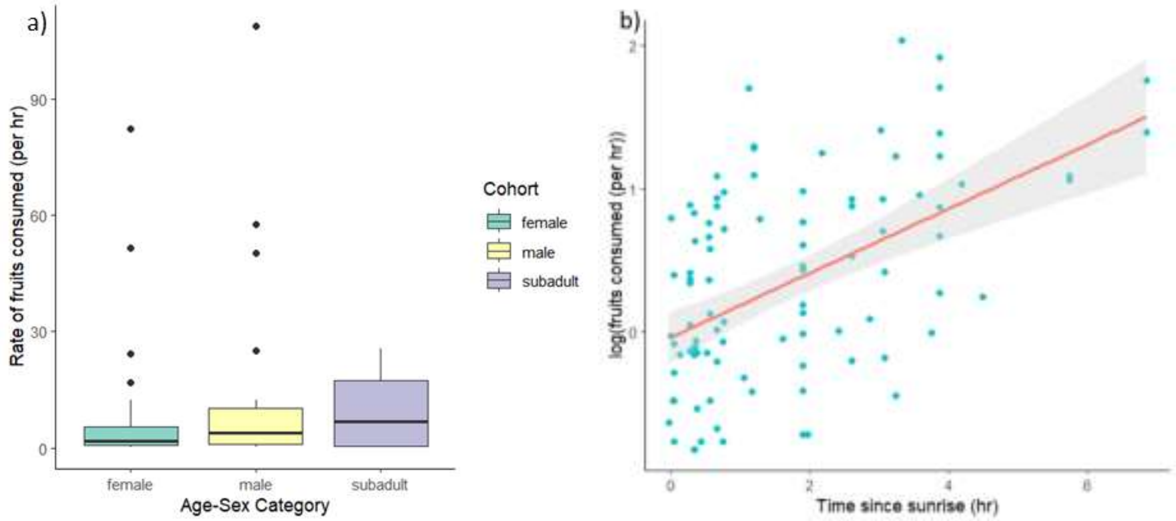

Figure 5. a) The rate of non-native fruits consumed (per hr) by each age-sex category. b) The rate of non-native fruits eaten (per hr) increased significantly as the day progressed.

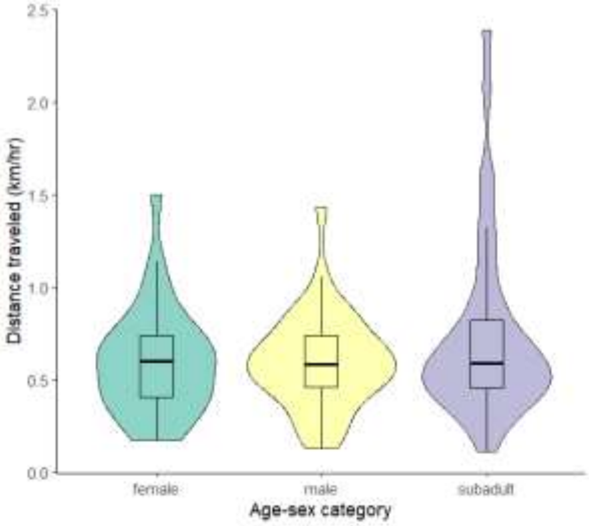

Figure 6. The daily distance travelled (km per hr) across age-sex categories is not significantly different.

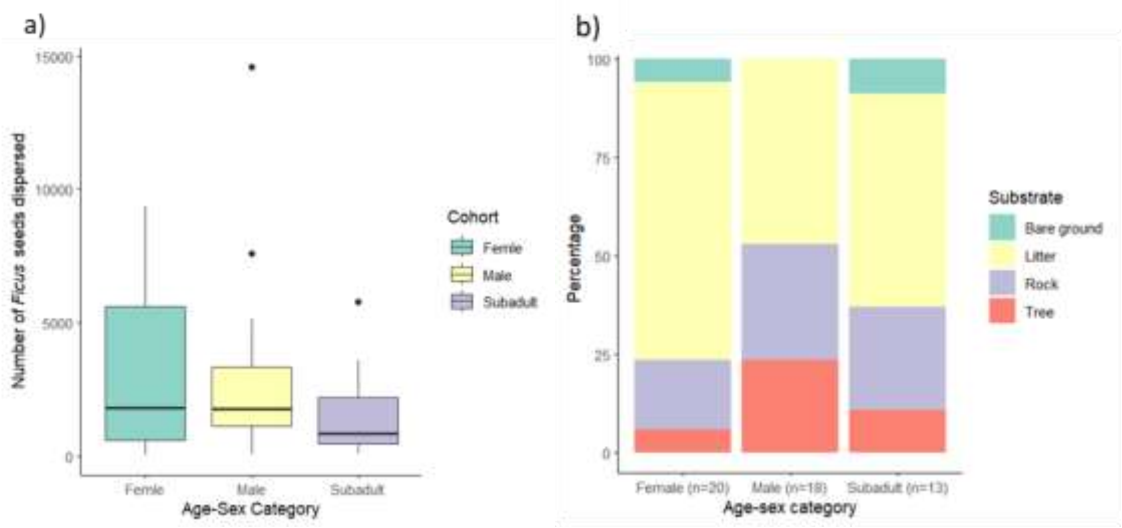

Figure 7. a) Number of Ficus seeds dispersed per scat by each age-sex category. b) Proportion of substrate at seed deposition sites across age-sex categories.

Table 4. Output of the General Linear Model to determine differences in the number of native fruits consumed per hour by different age-sex categories.

Formula = log (Fruits consumed per hr) ~ Age-sex category + Time since sunrise (min)				
$R^2 = 0.033$, Adjusted $R^2 = 0.013$				
$F_{3,147} = 1.65$, $p = 0.18$				
Coefficients:				
	Estimate	SE	t value	*p*
Intercept: Female	0.494	0.124	3.995	**<0.001**
Male	0.058	0.169	0.344	0.732
Subadult	0.294	0.171	1.723	0.087
Time_since_sunrise_min	0.001	0.001	1.080	0.282

Table 5. Output of the General Linear Model to determine differences in the number of non-native fruits consumed per hour by different the effect of age-sex categories.

Formula = log (Fruits consumed per hr) ~ Age-sex category + Time since sunrise (min)				
$R^2 = 0.267$, Adjusted $R^2 = 0.243$				
$F_{3,94} = 11.4$, $p = <0.001$				
Coefficients:				
	Estimate	SE	t value	*p*
Intercept: Female	-0.046	0.101	-0.461	0.646
Male	-0.014	0.151	-0.092	0.927
Subadult	0.062	0.182	0.339	0.735
Time_since_sunrise_min	0.004	0.001	5.686	**<0.001**

Table 6. Output of General Linear Model to determine differences in the distance travelled by different age-sex categories

Formula = log (Distance travelled (km/hr)) ~ Age-sex categories				
R = 0.017, Adjusted R = -0.002				
F = 0.879, p = 0.418				
Coefficients:				
	Estimate	SE	t value	*p*
Intercept: Female	-0.2766	0.04223	-6.551	**<0.001**
Male	0.00764	0.05761	0.133	0.895
Subadult	0.06607	0.05626	1.174	0.243

Table 7. Output of the Generalised Linear Model to determine differences in the number of Ficus seeds dispersed by different age-sex categories.

Formula = Number of *Ficus* seeds ~ Age-sex category				
Family = Negative Binomial				
AIC = 891.5, Ɵ = 0.903, Residual deviance: 58.40 on 47 df				
Coefficients:				
	Estimate	SE	t value	*p*
Intercept: Female	8.064	0.241	33.403	**<0.001**
Male	-0.074	0.346	-0.214	0.830
Subadult	-0.766	0.379	-2.021	**0.043**

4. DISCUSSION

This study addresses a topical issue of intra-specific variation in seed dispersal, that has been relatively underexplored in the seed dispersal literature. It demonstrates that differences in cohorts results in differences in diversity and relative proportions of native and non-native fruits being consumed by Lion-tailed Macaques. I demonstrate that male LTMs consume a lower diversity of native and non-native fruits compared to subadults and females. I also found that male LTMs had higher representation of *Coffea* in their diets than females and subadults. However, I did not find any differences in the consumption rate of native and non-native fruits and distances covered. Subadult LTMs dispersed less *Ficus* seeds than males and females. There were marginal differences in the substrates where the seeds were dispersed. Male LTMs were more likely to disperse *Ficus* seeds on trees which are likely more suitable microhabitats for *Ficus* seeds to germinate. Although several studies have highlighted the importance of fruits as the primary diet of LTMs (Krishnadas et al., 2011; Krishnamani & Kumar, 2018; Santhosh et al., 2015; Singh, Kumara, et al., 2002), this study has generated valuable information on the role of LTMs, a rainforest specialist endemic primate, in seed dispersal of native and non-native plants.

4.1. DIFFERENCES IN FRUGIVORY AMONG AGE-SEX CATEGORIES

My study was based on the premise that differences in body size, behavioural traits and nutritional needs vary across age-sex categories (Zwolak, 2018), which resulting in differential feeding habits and dispersal services provided by them. Among the multiple aspects of frugivory I examined, I found clear differences in the diversity of native and non-native fruits consumed and relative proportions of native and non-native fruits consumed. Sub-adult LTMs fed on a greater diversity of native fruits, while males fed on fewer species of non-native fruits. Hill-Shannon Diversity measure provides information on species commonly represented in the diets of the different age-sex categories. Macaques are likely to play a less important role for rarely consumed species. Subadults were found to consume a significantly higher diversity of native fruits, highlighting their role as important consumers and potential seed dispersers of a greater diversity of plants. Adult males on the other hand, consumed the least diversity of fruits. This might be explained by the differences in the behaviour of the adult males, females and subadults. Adult males usually are in the centre of the troop, feeding on many fruits at once, followed by long resting periods. Females spend more time foraging and feeding to meet their high nutritional requirements for lactation, followed by long allogrooming sessions with other females and sometimes males. However, subadults are constantly foraging, searching for food resources and travel more than the other two age-sex categories (Bindu K – unpublished data). Thus, greater exploration time of sub-adults may also result in them feeding on greater richness and evenness of fruits consumed by them. Adult males may also feed on fewer species but might be feeding on the choicest of fruits, as is evident from the Shannon-Wiener index, which suggests that the diets of males were the least even and dominated by fewer species. Future studies need to examine the nutrient content of fruits eaten by the different groups and determine qualitative and quantitative differences in nutrients and energy content consumed by them. These differences in frugivory patterns also highlight the greater importance of subadults in the dispersal of a greater diversity of fruit plant species.

The fruit diet showed high overlap between pairs of different age-sex categories. The overlap was highest between female and subadult. The high overlap indicates higher compositional similarity between fruits consumed by females and subadults, possibly due to similar behaviour patterns between them compared to males. Despite the differences in the diversity of fruits consumed, the high dietary overlap is likely observed since Pianka’s niche overlap index takes into account all species, irrespective of their rarity, whereas the Hill-Shannon diversity metric gives emphasis to relatively common species.

4.2. INTRASPECIFIC DIFFERENCES IN SEED DISPERSAL OF ALIEN INVASIVE SPECIES

There is limited literature on intraspecific variation in seed dispersal of alien invasive species. I found that up to 25% of the diet of the female and male LTMs is non-native species. This suggests that LTMs are important agents for the spread of alien invasive species in the landscape. The high representation of alien species in their diets is a likely consequence of the high prevalence of these alien species in the study site and the lowered availability of native fruits due to past disturbances. Comparative studies are required to determine if the relative proportion of alien species decreases with increasing availability of native fruit species. Given that the study site has the highest density of LTMs in the region, alien species are likely playing an important role in sustaining these populations, an aspect that needs further exploration.

I found that the roles of different age-sex categories of LTMs in the dispersal of invasive alien species may differ. Given the long history of human use of the landscape, particularly by the British, the area has a significant presence of non-native species, including alien invasives like *Coffea* and *Lantana*. These two species are among the worst invasives in the landscape (Joshi et al., 2015). While *Lantana* is spreading in relatively more open areas, *Coffea* is prevalent even in rainforests, raising significant conservation concern. These two alien species collectively contributed to up to 90% of the diets of three age-sex categories. However, interestingly, the relative proportions of *Coffea* and *Lantana* differed. Males mostly consumed *Coffea*,

Picture 1 LTM spitting *Coffea* seeds ©Wikimedia Commons

while females and subadults consumed a significant proportion of *Lantana* seeds. While *Coffea* seeds are spat undamaged (pers. obs.), the tiny *Lantana* seeds are dispersed undamaged through the scats. Thus, the different groups are likely playing a differential role in the seed dispersal of these invasive species in the landscape. Interestingly, the relative proportion of ripe non-native fruits in diets of subadults was the least, while female was the highest. This in conjunction with differences in relative abundances of males, females and subadults in the troops will imply that the number of seeds dispersed of the different alien invasives are likely to differ among the age-sex categories.

4.3. VARIATION IN QUALITY OF SEED DISPERSAL

The quality of seed dispersal service is determined by seed handling behaviour and microhabitats where the seeds are dispersed (Schupp et al., 2010). The number of seeds dispersed is known to differ with sex, body size of the frugivore. Larger individuals of *Deinacrida connectens*, a flightless insect, consume and disperse large number of seeds (Larsen & Burns, 2012). Females of Agile opossum, *Gracilinanus agilis*, are known to disperse more seeds than the males (Camargo et al., 2011). Generally, members of all the three age-sex categories had a low representation of unripe fruits. Therefore, they mostly disperse mature seeds. For some species (e.g., *Artocarpus heterophyllus*), the LTMs also feed on the seeds (pers. obs.), offering poor seed dispersal service. For most species, however, I found that they were dispersing the seeds. When seeds are spat by macaques (e.g., seeds of *Coffea*), the dispersal distances are generally short (~20 m), but defecated seeds may be dispersed up to 250 m from parent tree (Tsuji & Su, 2018). Thus, macaques are mostly dispersing the seeds away from the parent tree. I did not find differences in movement patterns across the three categories. Therefore, the individuals across age-sex categories, are likely to disperse seeds at similar distances, unless there are systematic differences in seed retention times across males, females and subadults, an aspect that is currently unknown. I was able to successfully identify *Ficus* seeds in the faeces. Subadults dispersed lower number of *Ficus* seeds than males and females. Though subadults are eating higher proportion of native fruits, they are dispersing very less seeds of native species per scat. There were typically up to 2000 *Ficus* seeds in one LTM scat. Thus, LTMs are mostly doing clumped dispersal of *Ficus* seeds (as is also being done by other animals that feed on *Ficus*) making them vulnerable to pathogen infestation and predation (Anderson et al., 2009; Howe, 1989; Nishikawa & Mochida, 2010; Tsuji & Su, 2018). However, I found weak evidence for the tendency of the male macaques to defecate on trees, which may result in scattering of seeds (thereby reduced predation and competition) and certain *Ficus* seeds landing in favourable microsites for germination on trees. This aspect needs to be examined in greater detail in future.

4.4. CONCLUSIONS

This study demonstrates differences in the frugivory of native and non-native fruits among adult males, adult females and subadult LTMs with implications for seed dispersal and spread of alien invasive species in this human-impacted rainforest site in the Western Ghats. This study also demonstrates the significant contribution of alien species in the diets of adult LTMs, and consequently, their role in the spread of these alien invasive species in a degraded rainforest patch. This study has also generated valuable information on the role of endemic and forest specialist LTM as seed dispersers, which has been poorly studied in the literature.

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