MANIPAL
ACADEMY of HIGHER EDUCATION
(Deemed to be University under Section 3 of the UGC Act, 1956)

Population Status and Resource Utilization of Nicobar long-tailed macaques (*Macaca fascicularis umbrosus*) in Nicobar Islands, India

THESIS TO BE SUBMITTED TO
MANIPAL ACADEMY OF HIGHER EDUCATION

FOR FULFILLMENT OF THE REQUIREMENT FOR THE AWARD OF THE DEGREE OF

DOCTOR OF PHILOSOPHY

BY

AVADHOOT D VELANKAR

Reg. No. 149000036

UNDER THE GUIDANCE OF

H. N. KUMARA

Principal Scientist
Conservation Biology Division, SACON
Anaikatty, Coimbatore - 641108
Tamil Nadu, India

SÁLIM ALI CENTRE FOR ORNITHOLOGY AND NATURAL HISTORY (SACON)

SACON

OCTOBER 2021

MANIPAL
ACADEMY of HIGHER EDUCATION
(Deemed to be University under Section 3 of the UGC Act, 1956)

Declaration of originality of research work and thesis by the student and supervisor

I have not committed plagiarism in any of the forms described in the 'Manipal Academy of Higher Education Plagiarism Policy'. I have documented all methods, data and processes truthfully and

I have not manipulated any data.

I have mentioned all persons who were significant facilitators of the work.

The work has been screened electronically for plagiarism.

Signature
Avadhoot D. Velankar
Reg. No. 149000036

Place : SACON, Coimbatore
Date : 29th September 2021

I, **Dr. H. N. Kumara** certify and attest that the work done by my Ph.D. student **Mr. Avadhoot D. Velankar** is original and vouch that there is no plagiarism.

The work has not been submitted for the award of any other degree/diploma of the same University / Institution where the work was carried out, or to any other University / Institution.

Signature
Dr. H. N. Kumara
Principal Scientist
Conservation Biology Division
Sálim Ali Centre for Ornithology and Natural History

Place : SACON, Coimbatore
Date : 29th September 2021

MANIPAL
ACADEMY of HIGHER EDUCATION
(Deemed to be University under Section 3 of the UGC Act, 1956)

DECLARATION BY THE CANDIDATE

I declare that this thesis, submitted for the degree of Doctor of Philosophy to Manipal Academy of Higher Education, is my original work, conducted under the supervision of my guide **Dr. H. N. Kumara**. I also wish to inform that no part of the research has been submitted for a degree or examination at any university. References, help and material obtained from other sources have been duly acknowledged

Candidate

Signature
Avadhoot Velankar
Reg. No. 146000036
Conservation Biology Division
Sálim Ali Centre for Ornithology and Natural History (SACON)

October 2021

MANIPAL
ACADEMY of HIGHER EDUCATION
(Deemed to be University under Section 3 of the UGC Act, 1956)

CERTIFICATE

This is to certify that the work incorporated in this thesis "**Population Status and Resource Utilization of Nicobar long-tailed macaques (*Macaca fascicularis umbrosus*) in Nicobar Islands, India**" submitted by **Mr. Avadhoot D. Velankar** was carried out under my supervision. No part of this thesis has been submitted for a degree or examination at any university. References, help and material obtained from other sources have been duly acknowledged.

Research Guide

Signature
Dr. H. N. Kumara
Principal Scientist
Conservation Biology Division
Sálim Ali Centre for Ornithology and Natural History (SACON)

October 2021

Acknowledgements

Here begins the end of my journey, which started about 11 years ago when someone told me that Nicobar long-tailed macaques had not been studied much. This journey is not a story of great triumph against all odds as I had hoped it would be, neither this is a tragedy where I lost. However, I cannot help but notice how closely these past 11 years mirror the story of "the old man and the sea" by Ernest Hemingway. Though I may not hold virtues of resilience and resourcefulness like its titular character, I have drifted across the ocean both literally and figuratively in a skiff pulled by an extraordinary force size of which was beyond my imagination. I wish I could have brought it ashore and show it in its full glory. However, this work is a meagre skeleton and snout that remains of what once was a great marlin. It may underwhelm you or leave you in awe, but it is a result of me just holding on to that fishing line. Before I rest and set sails again in the ocean, here I express gratitude to all those who had faith in me and gave me strength to hold on to the line no matter how futile it seemed.

I cannot conjure up the words to reflect the magnitude of influence Dr H. N. Kumara has on me. He has been my teacher and role model even beyond academic life. I could complete this journey only because of his perseverance and belief in me when even I did not. Like young primates learn by imitation, I will keep trying to imitate his ethics and scientific rigour in the future.

This study would not have been possible without the financial assistance provided by the Department of Science and Technology, Government of India (Grant No.SR/SO/AS-49/2011). I am grateful to Andaman and Nicobar Forest Department for their constant support. I sincerely thank the Principal Chief Conservator of Forests, Port Blair, Andaman and Nicobar Islands for granting permission (Permit No. CWLW/WL/134/566) for the study and to the Assistant Commissioner, Andaman and Nicobar Administration for providing the necessary permits to access the tribal areas of Nicobar. A good friend and DFO of Nicobar Division, Shri. Agni Mitra (IFS) helped a lot during the initial stages in setting up the field station and providing human resources in Campbell Bay and Katchal. Further DFO, Mr Jebestin and Mr A. K. Paul, and other forest staff, especially Mr Ajay, Mr. Sajan, Mr. Simon, Mr. Alfans, and Mr Sayeed, were immense help and constant support.

I am deeply indebted to Dr Azeez P.A, and Dr K. Sankar, former Directors and current Director Dr S. Muralidharan, Sálim Ali Centre for Ornithology and Natural History, for their valuable support during the study tenure. I express my sincere gratitude to Dr P. Balasubramaniam and Dr P. A. Arun for easing the process of PhD and related formalities. I am grateful to the faculty of SACON for their constant encouragement and constructive criticism. I am also grateful to the Hostel wardens, administration, and finance, who made my stay on the SACON campus comfortable and instrumental for smooth fieldwork operation in remote islands. It is imperative to say that I would not have been introduced to SACON and Andaman and Nicobar Islands without my friend Dr Shirish Manchi.

I am truly privileged to have amazing peers who helped me during every stage of this study. When going to the islands was just a distant dream, Vardhan, Akshaya, Shirish kept encouraging me to realize it and introduced me to the islands. I was able to make local connections and plan the logistics because of Chetan, Nehru and Zebin. While in the institute, Nishad, Prafull, Jins, Anoop, Anup, Shantanu, Kaushik, Aditi, Milda, Ankit, Ganesh, Nambirajan were the source of inciteful conversations and fun times and breaking bread. I am also grateful to Sayantan, Sheetal for their assistance during fieldwork. Apart from these, my colleagues from UNDP and ATREE also helped me to focus on the path while it seemed lost.

This study would not have been possible without the people of Nicobar. It did not take them more than a couple of days after I arrived to share their homes, food and resources with me. Because of their trust and assimilating nature, I felt at home in remote Nicobar islands in no time. Thinagaran anna, Subramanyam Anna, A. Simachalam, Kiranda and the staff of Suruchi Restaurant all ensured I got food and necessities even during funds were low.

Nicobar belongs to indigenous Nicobarese tribes. Without them, I would not have been able to survey an inch of the dense forests and traversed choppy waters to reach the remote location. I feel deeply honoured that village captains of Pulo Patiya, Pulo Baha, Pulo Ulon, Pulo Panja, Afra Bay, Makachua and Upper katchal shared their food, homes, boat, people and toddy with me to aid in study. Living with them was once a lifetime experience, something akin to what Thoreau must have experienced at ‘Walden pond’. Living with Jerun, Danial, Rahul, Safinia, Safrin, Watson, Taimon, Morris, Subhash and Captain Abraham and their families made me understand the difference in the quality of life and standard of living. I will always remember late Abhioo for his compassion and beaming smile no matter what the odds. I wish we could share one more *jangpop*.

Further, I had terrific lab mates who knew me many times better than I do myself. Aakriti, Aditi, Joydeep, Santosh and Naveen were my compadres who were with me in all ups and downs and provided me with push whenever required. Further, this thesis equally belongs to Partha and Arijit, who were with me during every step of this amazing journey. We have been through a lot, from cooking food to brainstorming research questions to taking care of me during sick days, and I am happy to have found comrades like them.

Finally, my Aai, Baba, Sudhir kaka, Smita kaku, Nandu kaka, Rutuja kaku, Chai, Nikunja, Priyanka and Ashwini were immensely supportive and staying away from them all these years was the hardest of the task.



Contents

Acknowledgements		i-iii
List of tables		iv
List of Figures		v
Chapter		Pages
1	**Introduction**	**1-8**
	1.1 General overview	1
	1.2 Study site	1-5
	1.3 Study species	5-6
	1.4 Objectives	7
	1.5 Methods	7
	1.6 Organisation of the thesis	8
2	**Review of Literature**	**9-12**
	2.1 Overview of genus *Macaca*	9
	2.2 *Macaca fascicularis*; a generalist species	9
	2.3 What makes a species generalist?	10
	2.4 Selecting appropriate methods to understand ranging and habitat use	10-11
3	**Population Status and Distribution of *Macaca fascicularis umbrosus***	**13-24**
	3.1 Introduction	13-15
	3.2 Methods	15-17
	3.3 Results	17-22
	3.4 Discussion	23-24
4	**Activity Budget and Feeding Ecology**	**25-40**
	4.1 Introduction	25-27
	4.2 Methods	27-28
	4.3 Results	28-36
	4.4 Discussion	37-39
5	**Manipulation and Feeding on Coconut**	**41-56**
	5.1 Introduction	41-43
	5.2 Methods	43-48
	5.3 Results	49-54
	5.4 Discussion	54-56
6	**Ranging Pattern and Habitat Use**	**57-66**
	6.1 Introduction	57-58
	6.2 Methods	58-61
	6.3 Results	61-64
	6.4 Discussion	64-65
7	**Summary**	**67-70**
	References	**71-84**
	Publications and Conference Abstracts	**85-91**

List of Tables

Table 1.1 Area and geographical details of the study sites (three islands of Nicobar) 2

Table 3.1. Mean number of *M. f. umbrosus* groups encountered per kilometre in Nicobar Islands 18

Table 3.2. Mean number of *M. f. umbrosus* groups encountered per kilometre in different forest and habitat type in Nicobar Islands 19

Table 3.3. Group Size and age-sex composition of *M. f. umbrosus* groups in Nicobar Islands 19

Table 3.4. Group structure and age-sex ratio of *M. f. umbrosus* in Nicobar Island 20

Table 3.5. Coastline variation after 2004 December tsunami in Nicobar Islands 20

Table 3.6. Number of *M. f. umbrosus* groups encountered per kilometre during 2000, 2006 and 2014 studies in Nicobar Islands 21

Table 4.1. Ethogram of the major behavioural states of the macaques recorded during study period along with brief description. 28

Table 4.2. Number of scans recorded for each activity in each season 29

Table 4.3. Relative frequency and source of major food items consumed by Nicobar long tailed macaques. 32

Table 4.4. Different types of extractive foraging behaviours observed 34

Table 4.5. Review of activity budget studies for genus *Macaca* 38

Table 5.1. Age and sex wise classification of TR group individuals: 45

Table 5.2. Coconut types according to the maturation: 46

Table 5.3. Description of coconut processing behaviours and left-over coconut stages: 47

Table 5.4. Descriptive statistics of coconut choice, and feeding success between different coconut types and age-sex classes. 51

Table 5.5. Variation in coconut choice, pluck pattern and feeding success between different coconut types and age-sex classes 51

Table 6.1. Pearson's product-moment correlation between the intensity of grid use by *M. f. umbrosus* group TR and habitat types available in Campbell Bay, GNI. 62

Table 6.2. Seasonal variation in daily path length (DPL) by TR. 63

Table 6.3. Influence of covariates on the intensity of grid use by *M. f. umbrosus* in Campbell Bay, GNI. 64

List of Figures

Figure 1.1. Study sites: Great Nicobar, Little Nicobar and Katchal of Nicobar group of Islands 3

Figure 1.2. Mean annual rainfall of Great Nicobar Island (data from 2003-2008) 4

Figure 3.1. Map of the Nicobar Islands depicting inundated area due to tsunami and group location of current study with group locations of pre-tsunami study**.** 18

Figure 3.2. Comparison of group structure and age- sex ratios of *M. f. umbrosus* between three study periods. 22

Figure 4.1. Variation in day activity. a. Dry Season, b. Wet Season 29

Figure 4.2. Variation in time activity budget during dry and wet seasons. 30

Figure 4.3. Proportion of food items fed by macaques from plantations in human habitations and forest region 31

Figure 4.4. Proportion of animal, plant or human origin food items fed by macaques 31

Figure 4.5. Proportion of different plant parts eaten by macaques 31

Figure 5.1. Mean proportion of coconut feeding proportion: coconut feeding per respective feeding scans different age-sex macaque individuals. 49

Figure 5.2. Mean proportion of coconut plucking pattern between different age-sex classes 52

Figure 5.3. Ordination plot of nMDS showing age wise segregation in coconut processing behaviours with dots representing adults, triangles representing immature, solid marker showing male and hollow markers as female individuals. 53

Figure 5.4. Markov chain transition diagram showing transitional probabilities between behavioural states used by macaques to process, feed and drink coconuts 54

Figure 6.1. Map of study sites in Campbell Bay region with the home range of study group (TR) 59

Figure 6.2. Proportion of habitat type in the grid cells within the home range of study group Nicobar long-tailed macaque 62

Figure 6.3. Proportion of grid cells used by the study group TR in, a. overall study period, b. the dry season, c. wet season. 63

Abstract :

Long-tailed macaque **(***Macaca fascicularis*) is one of the most widely distributed primates in east Asian countries. The subspecies of long-tailed macaque in India is *M. f. umbrosus*, which is endemic to three Nicobar Islands *viz*. Great Nicobar, Little Nicobar, Katchal. This study arose from the need to create baseline information for the isolated populations of the subspecies. I conducted a study on the ranging pattern, feeding habits, and activity budget of *M. f. umbrosus* for my thesis. For population status and social organization the existing trails used in earlier studies were surveyed. Instantaneous scan sampling was followed for the data collection on activity budgets and feeding ecology. Geo-coordinates of the group were recorded every 30 min while following the group to assess the movement pattern and plot its home-range. The group encounter rate per kilometre in Great Nicobar (0.30) was significantly lower than in Katchal (0.48) with no difference between Little Nicobar (0.35) and the other two islands. The mean group size between Great Nicobar (39.83±17.47, N=6) and Katchal (43.50±26.15, N= 4) did not vary significantly. The population increased at an intrinsic rate (*r*) of 0.12, 0.14 and 0.17 in Great Nicobar, Little Nicobar and Katchal from 2006 to 2014. Throughout the day Resting was the most observed activity and foraging and scouting were the least observed activities. Activities feeding, social and movement occurred at similar proportion to each other through the day-time classes. Study group was observed to feed on 26 major food items of which 12 were introduced by humans and 14 were of native origin. Further seven extractive foraging and tool use behaviors were observed which include food extraction, foraging, food preparation and teeth flossing. females significantly fed on less coconuts compared to males despite showing equal proficiency in manipulation of all coconut types. ANOSIM performed between ages revealed that adults and immature were significantly dissimilar in their behavioral repertoire in processing coconuts. Markov chains for dry, mature and tender coconuts by adult and immature showed differences in behavioural transitions. A total of 830 group locations were collected during the study period, spread over in 66 grid cells of which 6 grids were used most frequently.

Abbreviations

ANOSIM	Analysis of simillarities
ANOVA	Analysis of variance
GIS	Geographical Information System
GLM	Generalized Linear Modelling
GPS	Geographic Positioning System
IUCN	International Union for Conservation of Nature
MCP	Minimum Convex Polygon
MSL	Mean Sea Level
NDWI	Normalized Difference Water Index
nMDS	Non-metric Multi-Dimensional Scaling

1

Introduction



Chapter 1 : Introduction

1.1 General overview

Long-tailed macaque **(***Macaca fascicularis*) is one of the most widely distributed primates in east Asian countries. It has also been introduced in other areas outside its natural range, such as China and Madagascar. Due to its opportunistic behaviour, it is listed among the worst 100 invasive species by IUCN (Lowe et al. 2000). Studies of the wild population of *M. fascicularis* show that it has niche overlap with various other primates like Orangutan (*Pongo pygmaeus*), Müller's Bornean Gibbon (*Hylobates muelleri*), Javan Surili (*Presbytis comata*), Proboscis monkey (*Nasalis larvatus*) and pig-tailed macaque (*M. nemestrina*) (Fittinghoff and Lindburg 1980; Yeager 1996).

Further, *M. fascicularis* is one of the most studied species. Its ranging pattern, feeding habits, and activity budget have been well studied from Kalimantan, East Borneo, Singapore and Thailand (Boer 1989; Yeager 1996, Brotcorne et al. 2014; Corlett and Lucas 1990; Eudey 2008; Fittinghoff and Lindburg 1980; Hambali et al. 2012; Wheatley 1988). However, such information was not available on the Indian population. Prior to this study, there were only two studies from India, which comprised short surveys to assess the population status (Sivakumar 2010a; Umapathy et al. 2003). This study arose from the need to create baseline information for the isolated populations of the subspecies found in India. I conducted a study on the ranging pattern, feeding habits, and activity budget of *M. f. umbrosus* for my thesis, which helps in understanding the species by comparing similar studies conducted elsewhere.

1.2 Study site

The study site comprises three islands of the Nicobar group in the Andaman and Nicobar archipelago, where Nicobar long-tailed macaques are found (Fig. 1.1). These islands are southern extensions of the Arakan Yoma mountain ranges (Sankaran 2005). Although these islands are part of the Indian Territory, they resemble their closest counterparts in Sumatra and Indonesia bio-geographically. The Nicobar group of islands are also part of The Sundaland Global Biodiversity Hotspot (Chitale et al. 2015). Great Nicobar is the southernmost island in this group is about 176 km away from the northernmost tip of Sumatra and Indonesia. The Nicobar group comprises 24 islands, of which 12 are inhabited by people. These islands can be divided into three distinct groups, *viz*. Northern Car Nicobar Group, Central Nancowry Group

and Southern Great Nicobar Group (Sankaran 2005). Nicobar long-tailed macaques (*M. f. umbrosus*) are distributed over three islands of the Nicobar group of islands that include Great Nicobar, Little Nicobar and Katchal (Umapathy et al., 2003 see Fig. 1.1). Great Nicobar and Little Nicobar Islands belong to the southern group of islands, and Katchal lies in the central group of islands. Great Nicobar is the largest island in the Nicobar group (895.48 km^2). The geographical details of these islands are provided in Table 1.1. The primary forest type of these islands is tropical evergreen, and all islands have more than 98% forest cover (Balakrishnan 1989). These islands flaunt a high degree of endemism in their flora and fauna (Rao 1986; Balakrishnan 1989). The remoteness of these islands, coupled with high biodiversity occurring in small pockets, makes the archipelago vulnerable to natural disasters and exploitation. Hence these islands are of great importance for conservation.

Table 1.1 Area and geographical details of the study sites (three islands of Nicobar)

	Great Nicobar	Little Nicobar	Katchal
Geocoordinates	93° 38′ 05.6″- 93° 57′ 13.7″ E and 6° 44′ 7.8″- 7° 13′ 46.6″ N	93° 36′ 14.0″-93° 46′ 17.4″ E and 7° 14′ 45.2″- 7° 26′ 33.7″ N	93° 28′ 32.9″-93° 18′ 06.8″ E and 7° 52′ 24.2″-8° 1′ 33.6″ N
Area in km^2	895.48	138.25	139.39
Highest altitude(m ASL)	642	470	230

Apart from indigenous Nicobarese and Shompen (endemic to Great Nicobar Island) tribes, mainlanders have colonised these islands since the 17th century (Sankaran 2005). After 1947, these islands became part of the Republic of India. Since then, many colonies have been established on these islands by people from mainland India. Fishing, coconut and areca nut cultivation are the primary source of livelihood of these people. Being in close proximity with forests, there is a high risk of human-wildlife conflict, especially due to macaques (Umapathy et al. 2003) and wild pigs. The importance of biodiversity conservation on these islands juxtaposed with increasing anthropogenic conflicts makes the detailed conservation studies of these islands essential.

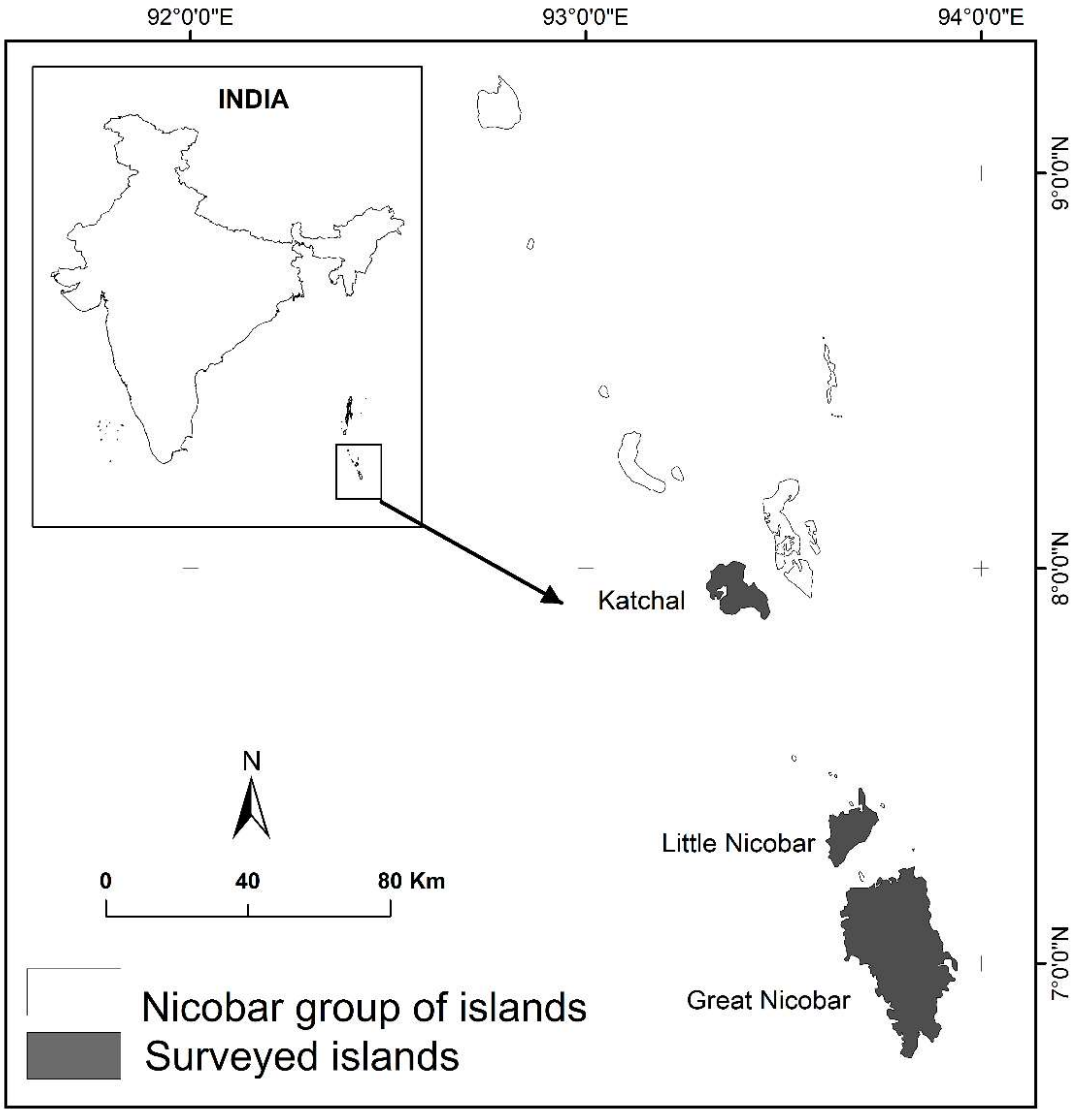


Figure 1.1. Study sites: Great Nicobar, Little Nicobar and Katchal of Nicobar group of Islands

Rainfall: The Islands of Nicobar receives rainfall throughout the year. Monsoon sets in May and receives 300 to 500 mm of rain every month till November. Other months receives < 100 mm. The data from 2003-08 shows the mean annual rainfall of Great Nicobar was 3200 mm. May to November was considered as the wet season and December to April as the dry season (Fig. 1.2).

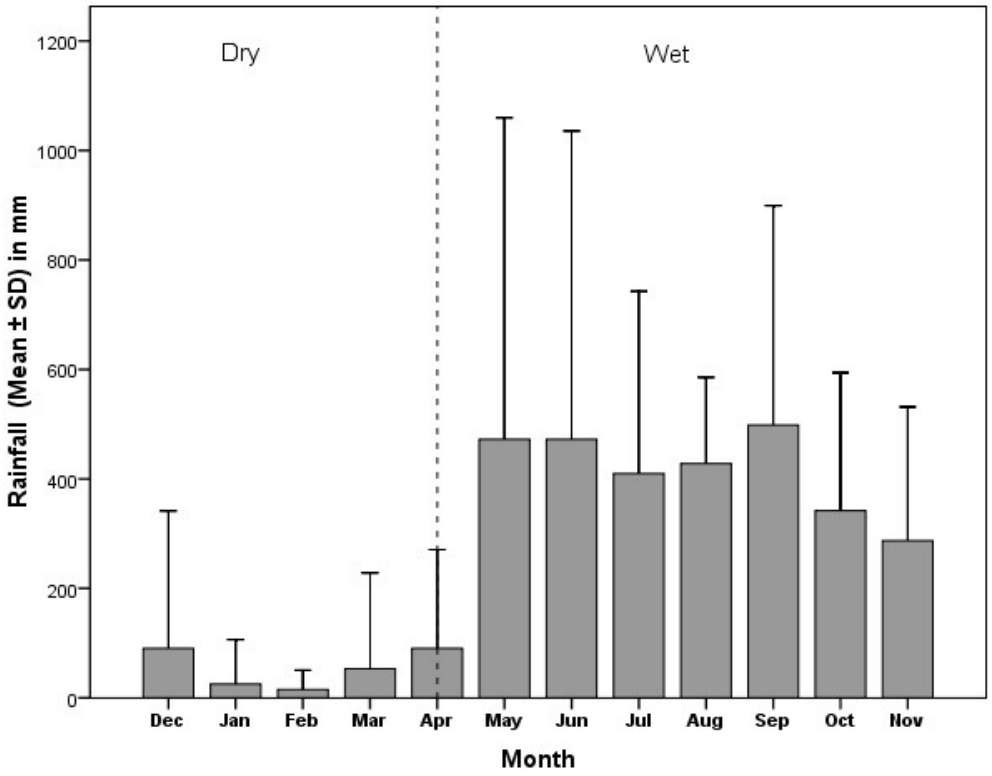


Figure 1.2. Mean annual rainfall of Great Nicobar Island (data from 2003-2008)



(View of Mt. Thullier, highest point in Great Nicobar Island from the Laful Bay)

In December 2004, the islands were hit by a devastating tsunami, which destroyed much of the coastal habitat and even the inland forests in some islands. Reports reveal that on some islands like Katchal, the destruction to coastal forests was total and moderate to severe destruction on Great and Little Nicobar (Ramachandran et al. 2005). The *M. f. umbrosus* is known to associate with swamp, riverine and mangrove forests along the coasts of these Islands. The later survey immediately after the tsunami by Sivakumar (2010a) revealed a sharp decline in the population size and skewed age-sex ratios in the *M. f. umbrosus* population.

1.3 Study species

The long-tailed macaque (*M. fascicularis*), also known as the crab-eating macaque, has a wide distribution range across many South-East Asian countries includes Bangladesh, Brunei, Cambodia, India, Indonesia, Lao PDR, Malaysia, Myanmar, Philippines, Singapore, Thailand, Timor-Leste and Vietnam. Groves (2001) recognised ten subspecies based on morphological characters (Fig. 1.1). Most of the subspecies are geographically isolated. The species has been categorised as 'Vulnerable' in the IUCN Red List (2021) due to its declining population trend.

The subspecies of long-tailed macaque in India is *M. f. umbrosus*, which is endemic to three Nicobar Islands *viz*. Great Nicobar, Little Nicobar, Katchal (Umapathy et al. 2003). It has also been categorised as 'Vulnerable' in IUCN (2021) Red List. Even though the Nicobar population is showing increasing trend, it is still deemed vulnerable due to its restricted distribution and susceptibility of its habitat to natural calamities. The subspecies is accorded the highest protection under 'Schedule-I' of the Indian Wildlife Protection Act (Anonymous 1972). In these three islands, about 4800 individuals were estimated before the 2004 tsunami (IUCN 2011). As a species, long-tailed macaques are commonly found along the seashore, mangrove forests and swamps (Fooden 1995). However, since the range of each subspecies is highly restricted to the isolated islands, their habitat is potentially susceptible to degradation on account of global warming and anthropogenic pressures (Carew-Reid 1990; Nelleman 2007). In many countries, shrimp farming, shipbuilding, agriculture and logging, among other activities, have significantly reduced the extent of their habitats (Nelleman 2007). Consequently, a decline in the population has been reported from several countries (Molur et al. 2003; Eudey 2008). It was considered as a widespread but rapidly declining species during the 2008 International Primatological Society conference. In later discussions, issues

concerning the need of monitoring populations of this species, especially in areas from where they are often captured for laboratories and at vulnerable habitats, were discussed.



(Nicobar long-tailed macaque adult female with juvenile)

1.4 Objectives:

Objective I: To assess the current population status and distribution of *M. fascicularis* in Great Nicobar, Little Nicobar and Katchal islands.

Objective II: To evaluate resource availability and resource use by *M. f. umbrosus*

Food, time and space are the major resources used by macaques. To Evaluate each of these in-depth, objective II was divided into three research questions which were addressed separately.

A. How is the time-activity budget of *M. f. umbrosus,* and what is their feeding ecology?
B. How does *M. f. umbrosus* acquire food from one of its major food resources, such as coconut?
C. What is the ranging pattern and the habitat use by *M. f. umbrosus*?

1.5 Methods

The study was conducted between January 2013 and January 2016. *Population status and social organisation*: The macaques in these islands were assessed using the existing trails used in earlier surveys by Umapathy et al. (2003) and Sivakumar (2010a). Location, group size and age-sex of the individuals were recorded for all macaque groups sighted. The distance was recorded using the handheld global position system (GPS).

Instantaneous scan sampling was followed for the data collection on activity budgets and feeding ecology. The focal group was followed from 0700 to 1800 hr, and each individual's food items and the group's behavioural states were recorded as per the developed ethogram. Continuous focal animal sampling with a structured data sheet was used to collect coconut processing data (Altmann 1974). All coconut approaching activity *viz.* processing, drinking and feeding were collected in time bout (seconds), where activities were recorded separately as one count until it was replaced by another. A handheld GPS unit was used to record the geo-coordinates of the group every 30 min while following the group to assess the movement pattern and plot the home ranges. Any interaction with other groups has been recorded *ad libitum*.

1.6 Organisation of the thesis

The thesis illustrates the nature of a complex social species through observations carried at the population, group, and individual levels. Chapter-1 of the thesis provides a general overview and rationale behind the study and a detailed description of the study area and study species. It is followed by objectives and research questions, and specific methods employed to achieve them. Chapter-2 is a compilation of existing knowledge available in published peer-reviewed literature. It sheds light on the current scientific consensus on the aspects of the species discussed in the objectives. It also examines the adequacy of methods used to address the set objectives. Chapters 3, 4, 5 and 6 are technical chapters addressing each objective and research question. Chapter-3 is an exploration of the current population status of the species. It compares the earlier population status to understand the species' response after a sharp decline in the population due to natural disasters. Chapter-4 is a group level assessment of the activity budget and feeding ecology of *M. f. umbrosus*. Chapter-5 delves into understanding behavioural plasticity and efficacy demonstrated by the individual for extractive foraging on one of the major food sources, i.e., coconut. Chapter-6 explores the focal group's cognitive map of their surroundings by studying grid cell use and daily path length. It also focuses on determinants of variation in the intensity of grid cell use and daily path length. I summarise the findings and how objectives contribute to the existing knowledge of the species in Chapter-7.

2

Review of Literature



Chapter 2 :
Review of Literature

2.1 Overview of genus *Macaca*

Macaques are one of the most widespread genus of the Cercopithecidae family, which besides great apes and gibbons, are the closest relatives of humans (Groves 2001). Gular pouches and high crowned molar teeth are some of the morphological traits separating them from folivorous colobines. Though they originated in Africa, macaques are the only cercopithecines to have migrated to Asia (Zinner et al. 2013). Macaques even habituated the Sundaic region and crossed the Wallace line to populate the Sulawesi islands and Timor (Abegg and Thierry 2002; Fooden 1982). Among macaques, *Macaca fascicularis* is one of the most widespread species with ten distinct sub-species.

2.2 *Macaca fascicularis*; a generalist species

M. fascicularis live in large groups with a group size varying from 25 on the Nicobar Islands (Umapathy et al. 2003) to 150 individuals in Thailand (Malaivijitnond and Hamada 2008). They show high ecological plasticity and have adapted to survive from mangrove swamp forests to dense tropical forests, sub-alpine forests, and human-dominated landscapes with a wide range of dietary habits, reproductive parameters and home-range sizes (Hock and Sasekumar 1979; Wheatley 1989). *M. fascicularis* are omnivorous and feed on fruits, seeds, insects, tubers and handouts from humans (Wheatley 1989). The monkeys that live in forests tend to become more frugivorous (Yeager 1996), whereas, in human-dominated landscapes, they exploit any available food resources and tend to become omnivorous (Wheatley, 1989). Further, in disturbed forests and human-dominated landscapes, they tend to have larger group sizes, smaller home ranges and higher reproductive index (Wheatley 1989, Aggimarangsee 1992). A classic study by van Schaik et al. (1983) showed that the day range length and the time spent travelling and searching for dispersed food items show a monotonic increase with group size. Likewise, social tension increases with group size. In larger groups, more vigorous competition for food leads to a reduction in the rates at which females give birth. Due to its ability to utilize altered landscapes effectively and its behaviour plasticity to seek novel food sources has enabled *M. fascicularis* to be resilient to population decline due to natural disasters, forest fires and habitat loss.

2.3 What makes a species generalist?

Primates possess prehensile limbs and sensory-motor skills, which enables them to develop complex object manipulation (Macfarlane and Graziano 2009; Pouydebat et al. 2011). This ability to manipulate objects manifests as extractive foraging and tool use. Environmental constraints such as resource distribution and competition further induce primates to use their physical abilities in innovative ways (Chappell et al. 2015). *Cebus capucinus* was observed to utilize embedded or mechanically protected insects during the period of food scarcity (Melin et al. 2014). Similarly, *M. fascicularis* was observed to shift to an insect-based diet after a period of drought, and forest fire had altered the landscape (Berenstain 1986). This ability to switch to a high-cost food source in the absence of preferred low-cost food makes primate individuals resilient. However, whether species or population is resilient depends upon how such behaviours are diffused. Social tolerance and more co-feeding and play between age, sex and dominance rank influence how these behaviours propagate through population (King 1994; Fagen 2002; Rapaport and Brown 2008; Tan 2017).

In the wild, *M. fuscata*, *M. fascicularis*, *M. silenus, M. radiata, and M. tonkeana* have been observed to perform tool-aided and complex foraging such as the use of stone tools to break open gastropod shells, cleaning food with water or leaves, using leaves to clean caterpillar hairs, etc. (Malaivijitnond et al. 2007). This enables macaque species to have a broad food spectrum.

2.4 Selecting appropriate methods to understand ranging and habitat use.

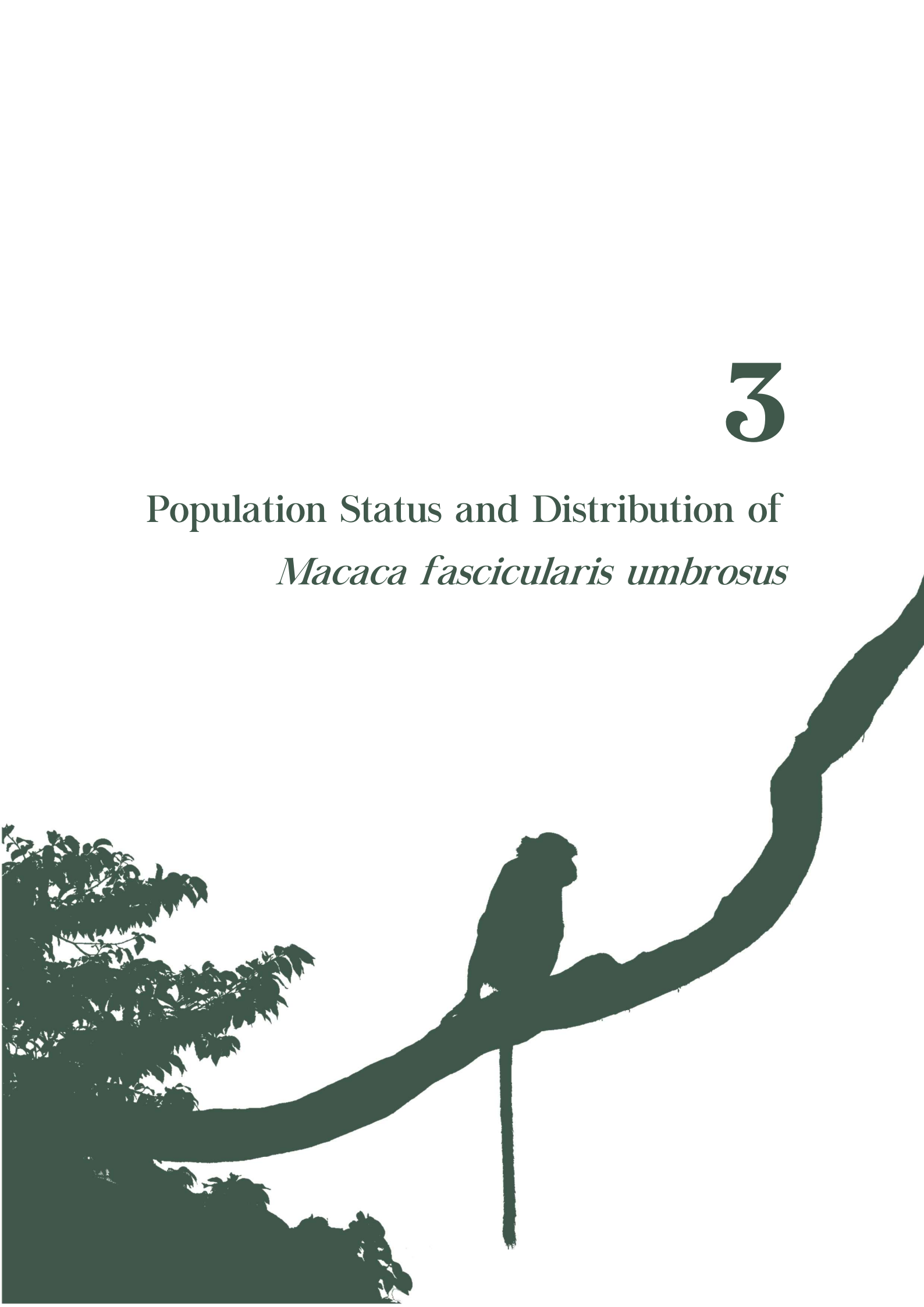
The ability of locomotion is a crucial distinguishing property of the animal kingdom. It has been historically observed that animals do not roam at random and display distinct territoriality. These territories or home ranges were defined as 'that area traversed by the individual in its normal activities of food gathering, mating and caring for young' (Burt 1943). Apart from this traditional approach, Powell (2000) defined home range as a cognitive map of an area animal maintains because of its perceived value by the animal. Kie et al. (2010) demonstrate how these definitions affect the estimations of home ranges by various techniques and state that the choice of home range estimator should be based on insights into animal's behaviour and ecology.

Home range estimation is an essential part of primate studies, without which understanding the population size, resource utilization and territoriality is difficult. Most commonly used methods

in primate studies include Minimum Convex Polygon (MCP) (Rodgers and Carr 1998), Kernel methods (Pimley et al. 2005; Seaman and Powell 1996; Worton 1989), grid count and Adjusted MCP (Grueter et al., 2008). Various research articles have differing opinions for home range estimates using Kernel Methods. (Seaman and Powell 1996) and (Pimley et al. 2005) found kernel estimators to be more reliable than other techniques. Seaman and Powell also state that Fixed Kernel (FK) Method with least square cross-validation (LSCV) chosen as a smoothing factor provides reliable estimates with least errors than the Adaptive Kernel (AK) and ad-hoc smoothing parameter. While (Boyle et al. 2009) show how AK and FK are not suitable for continuous forest fragments, and MCP gives more reliable estimates. Boyle also states that using LSCV as a smoothing factor underestimated area for some forest fragments. The majority of old and contemporary studies use (Curtis and Zaramody 1998; Defler 1996; Grueter et al. 2008; Kirkpatrick et al. 1998; Liu and Zhao 2004; Palacios and Rodriguez 2001; Riley 2008) grid overlay techniques for estimating home range, studying ranging pattern, resource utilization, temporal variations.

3

Population Status and Distribution of *Macaca fascicularis umbrosus*



Chapter 3:
Population Status and Distribution of *Macaca fascicularis umbrosus*

3.1. Introduction

Natural disasters may pose a serious threat to animal populations (Ewens et al. 1987). Survival of a population after a disastrous event is dependent on plasticity of the species to sudden changes in its population and habitat (Chevin et al. 2010). The plasticity, dependent on evolutionary history and environment of a species (Shaffer 1987), decides the minimum population size necessary for the species to recover. The habitat specialists or the low occurrence species are more risk prone to extinction than the species occurring in large populations or with wide distributions (Shaffer 1987). One of the important environmental determinants of plasticity is the severity of impact and duration of a disaster (Gerber and Hilborn 2001). Thus, natural disasters can be classified into three categories: 1) High severity with short duration e.g., Hurricanes, tsunami, fire, and disease outbreaks, 2) low severity with long duration e.g., Drought, climate change, and 3) high severity with cyclic occurrence e.g., Floods, El Niño event. However, some natural disasters, such as disease outbreaks, which may eliminate a population, have no impact on the structure of its habitat. On the other hand, disasters like the tsunami may affect the habitat and the animal populations both.

There are two kinds of mortalities based on the effects induced by natural disasters; primary and secondary. Primary mortality includes animals dying directly due to natural disasters while secondary mortality occurs due to changes in habitat structure leading to the death of vulnerable individuals (Shilova and Shatunovskii 2005). For example, increased mortality of juveniles and cohorts of various ottariids (seals) due to over harvesting and the El Niño event (Gerber and Hilborn 2001), increased mortality of infants, juveniles and females in *Lemur catta* due to drought (Gould et al. 1999), and breeding failure in *Aptenodytes patagonicus* due to tsunami (Viera et al. 2006). Such differential mortality indeed alters the group composition in a population, affecting its recovery. Recovery is also governed by behaviour and complexity of social systems of a species. For instance, a species with cryptic mating rituals or a complex social system becomes more vulnerable to extinction due to these effects. It is more so with group living species that have cooperative feeding and defence. Thus, such secondary mechanism reduces overall inclusive fitness of the population and reduces its rate of recovery leading to 'Allee effect' and possibilities of multiple Allee effects (Berec et al. 2007; Stephens et al. 1999). Although the prevalence and strength of these effects are poorly known, studies

report these effects on a variety of species, for example *Marmota marmota* occurring in low densities have difficulties in finding mates and their survival is decreased due to less social thermo-regulation (Berec et al. 2007), and *Lycaon pictus* faces reduced breeding capacity, reduced anti-predatory response and reduced cooperative hunting (Berec et al. 2007). Such mechanisms increase the stochasticity of population dynamics making it harder to predict population trends during recovery.

Predicting population trends of animal groups such as primates is particularly difficult because of such high demographic stochasticity which may be due to their social and behavioural complexity. Primates react differently to various disasters. For instance, *Alouatta palliata* recovered, 3 decades after a suspected yellow fever outbreak (Milton 1982), but it showed varied response to regenerating forest (Fedigan et al. 1998). *M. fascicularis* showed behavioural flexibility in response to severely altered environment (Berenstain 1986). Apart from such instances, another limiting factor to population recovery is the rate of recolonizaton of unoccupied habitats by forming new groups. This happens by fission of large neighbouring groups or by dispersed individuals jointly occupying unoccupied patches (Fedigan et al. 1998; Karr and Freemark 1985).

Studies report the immediate impacts of tsunamis on various terrestrial and marine fauna, for example breeding failure in *Aptenodytes patagonicus* at Crozet Archipelago (Viera et al. 2006), reduction in the abundance of sea birds at Latham Island, Tanzania (Crawford et al. 2006) and short term changes in distribution and abundance of *Sephanoides fernandensis* at Robinson Crusoe Island, Chilean coast (Hahn et al. 2015). Similarly, some immediate impacts of the tsunami on fauna in Andaman and Nicobar islands were reported; for example sharp declines in populations of *Megapodius nicobarensis* and *M. f. umbrosus* (Sivakumar 2010b, 2010a), increased population size of fish *Chanos chanos* (Sekhsaria 2009) and loss of nesting grounds for marine turtles due to submergence of sandy beaches (Andrews et al. 2006). Many such studies put emphasis on vulnerability of islands to natural disasters. Such vulnerability of an island depends on size of the island. It has been observed that smaller islands suffer overwhelming natural and socioeconomic impacts compared to continents due to natural disasters (Lewis 1990). Small islands have limited habitats which in turn governs distribution of species making them susceptible to extinction. This was observed in Gwaii Haanas archipelago, where distribution of various bird species was dependent on old growth forests which were correlated with island size and its isolation (Martin et al. 1995).

Macaques are highly adaptable primates to changing habitat (Berenstain 1986), and live in all possible habitat types and environmental conditions (Fooden 1982; Goldstein and Richard 1989). *M. f. umbrosus* is one such island dwelling sub-species of macaque known for its phenotypic plasticity (Gumert 2011). Further, being the only species which was assessed using the same methodologies before and after the tsunami (Sivakumar 2010a; Umapathy et al. 2003), it provides an opportunity to study and understand the long term response by a resilient species in island environment.

I presumed that the impact of the tsunami would be localized to coastal regions, and that, over the time inland population of *M. f. umbrosus* that was unaffected would recolonize coastal regions. Further, the extent of damage to the habitat and population was expected to be more on the smaller islands than on the larger islands. I examined the current status of *M. f. umbrosus* in the Nicobar group of islands using the same field protocol as that of Umapathy et al. (2003) and Sivakumar (2010a) to understand the long-term response of the species that had declined sharply.

3.2. Methods

3.2.1. Study Area: The present study was conducted at Great Nicobar, Little Nicobar and Katchal. The current island size of Great Nicobar, Little Nicobar and Katchal is 895.48, 138.25 and 139.39 km^2 respectively.

3.2.2. Survey Design: I surveyed *M. f. umbrosus* in the three islands between January 2013 and April 2014. Since the undergrowth in the forest was very thick, I used the same trail survey protocol as that of Umapathy et al. (2003). Further, heavy tree falls due to the tsunami made most parts of the islands inaccessible for distance sampling. Therefore, the existing trails and road network were chosen to survey *M. f. umbrosus*. Fixed trails were chosen, and the area was walked between 0700 and 1100 hours at an average speed of 1 km per hour. At every sighting of a macaque group, geographical position was recorded using a handheld GPS (Garmin GPSmap 76CSx). In the case of direct sightings in proximity, group size, age and sex of the visible individuals were also recorded. Group counts were taken when groups were observed crossing clearings such as roads, trails, streams, or narrow open areas. In case all individuals of a group were found to be moving in same direction, macaques intercepting an imaginary line from a vantage point were counted using tally marks for each age and sex class. Basic habitat types and dominant vegetation were noted at each sighting of a group during the population status and distribution survey. During the trail survey, vegetation parameters were

recorded with change in habitat types. Major forest types were distinguished- based on vegetation composition (Sinha 1999).

3.2.3. Analysis: To detect post-tsunami changes in shoreline, I compared current Landsat 8 imageries with 30m spatial resolution (Dated 12- April– 2014 for Great Nicobar, 2-March-2014 for Katchal and Little Nicobar) (downloaded from www.earthexplorer.com, U.S. Geological Survey) with pre-tsunami Landsat 7 imageries (Dated 5- March -2003 for Great Nicobar and Little Nicobar, 23 –Jan– 2003 for Katchal). To extract shorelines from the images, Normalized Difference Water Index (NDWI) was used (McFeeters 1996), which segregated land and water regions from the images.

The current shoreline for the three islands was extracted by converting NDWI raster images to vector formats. For pre-tsunami shoreline, cloud-free data was not available, but the visible portion of shoreline of pre-tsunami NDWI raster matched closely with the vector map down-loaded from DIVA GIS (divagis.org), hence those vector maps were used as reference pre-tsunami shoreline. Pre-tsunami and post-tsunami coastlines obtained thus were used to find out net change in shoreline, degree of inundation and total area submerged. Equidistant parallel transects intersecting both pre- and post-tsunami coastlines were overlaid from an offshore baseline. Distance between consecutive transects was kept at 250 m., intersecting length of each transect in between two shorelines was obtained to estimate degree of inundation. Comparisons for degree of inundation were made between the islands and between west coast and east coast regions of each island.

For processing images and basic GIS operations, I used Quantum GIS (QGIS v2.4.0), while net change in shoreline and degree of inundation was computed using Digital Shoreline Analysis System (DSAS) extension in ArcGIS 10 (Thieler et al. 2009).

The abundance of *M. f. umbrosus* is represented as encounter rate (groups per kilometre) obtained by dividing the number of groups by the length of transects in each place. To compare differences in encounter rate of *M. f. umbrosus* between islands, habitat types and before and after tsunami, I employed generalized linear model (GLM) with Poisson distribution. GLM was run with number of groups as response variable with log transformed trail length as offset parameter. Islands, habitat types and period were set as categorical explanatory variables. Chi square test was used to compare the proportions of males between islands, and abundance of *M. f. umbrosus* before and after tsunami, respectively. Independent sample Student's t-test and one-way ANOVA were used to compare the mean group size and age-sex ratios between the

islands and for before and after tsunami respectively. Overall rate of change in population was computed using intrinsic rate of change (Birch 1948). All statistical analysis was carried out using R statistical language V 3.02 with R Studio IDE for R v0.98.953.

3.3. Results

3.3.1. Population status:

Abundance: I sighted 36, 5 and 38 *M. f. umbrosus* groups during the 119.55, 14.09 and 78.50 km of trail surveys in Great Nicobar, Little Nicobar and Katchal respectively (Table 3.1, Fig. 3.1). The group encounter rate per kilometre in Great Nicobar (0.30) was significantly lower than in Katchal (0.48) (Walds Z=2.03, p=0.04) with no difference between Little Nicobar (0.35) and the other two islands (Table 3.1). The group encounter rate in Plantation (0.58) was significantly higher than in Evergreen (0.28) (Walds Z=2.92, p=0.004) and Littoral forest (0.17) (Walds Z=2.38, p=0.02) with no difference between Mixed forest (0.49) and other forest types (Table 3.2). Similarly, group encounter rate in Coastal habitat (0.49) was significantly higher than in Inland habitat (0.31) (Walds Z=2.05, p=0.04) (Table 3.2).



(Light house on Indira Point, Great Nicobar Island)

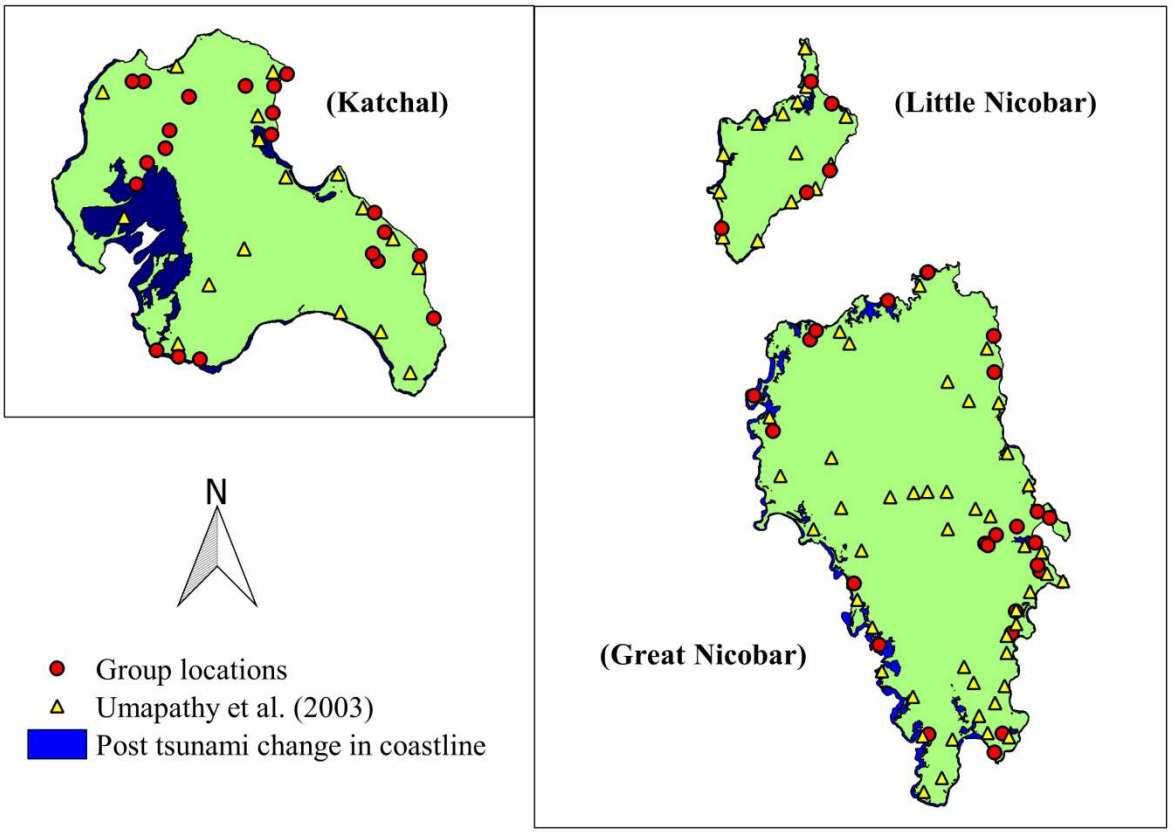


Figure 3.1. Map of the Nicobar Islands depicting inundated area due to tsunami and group location of current study with group locations of pre-tsunami study**.**

Table 3.1. Mean number of *M. f. umbrosus* groups encountered per kilometre in Nicobar Islands

Island	No of trails	Mean trail length ±SD, (min-max)	Total effort (km)	Groups detected (n)	groups/km
Great Nicobar	26	4.59 ± 7.28 (0.3-34.12)	119.55	36	0.30
Little Nicobar	9	1.57 ± 0.96 (0.37-4.20)	14.09	5	0.35
Katchal	21	4.90 ± 2.70 (0.34-16.75)	78.50	38	0.48
Overall	56	2.52 ± 4.32 (0.34-34.12)	212.14	79	0.37

Table 3.2. Mean number of *M. f. umbrosus* groups encountered per kilometre in different forest and habitat type in Nicobar Islands

Type	Overall (of all the three islands)			
	n trails	**Groups**	**km**	**n groups/km**
Forest Type				
Evergreen hill forest	22	32	111.48	0.28
Mixed forest	10	9	18.25	0.49
Plantation	13	34	58.32	0.58
Littoral forest	11	4	23.88	0.17
Habitat Type				
Inland	28	44	141.54	0.31
Coastal	28	35	70.59	0.49

3.3.2. Population characteristics and Social Organisation:

During the study period reliable group counts and demography information on Little Nicobar island could not be recorded, hence data of only Katchal and Great Nicobar Islands was compared. The mean group size between Great Nicobar (39.83±17.47, N=6) and Katchal (43.50±26.15, N= 4) (Table 3.3) did not vary significantly (M-W U test, U= 12.50, p = 0.91).

Table 3.3. Group Size and age-sex composition of *M. f. umbrosus* groups in Nicobar Islands

Island	**Group**	**Adult Male**	**Adult Female**	**Sub-adult + Juvenile**	**Infant**	**Total**
Great Nicobar	B quarry group	6	13	20	6	45
	Temple group	5	7	8	0	20
	Laxman beach group	4	10	16	8	38
	Chinganbasti group	5	13	7	4	29
	09 Km N-S Road	7	19	8	2	36
	20 Km N-S Road	6	25	28	12	71
Katchal	Sea wall group	5	7	17	7	36
	Kapanga group	3	4	8	3	18
	Oil palm I	7	17	36	20	80
	Oil palm II	4	10	22	4	40

Percent adult males, adult females and immature per group between Great Nicobar and Katchal (adult males: $\chi^2 = 5.88$, df = 10, p = 0.82; adult females: $\chi^2 = 5.31$, df = 10, p = 0.86; immature: $\chi^2 = 5.18$, df = 10, p = 0.87) also did not vary significantly (Table 3.4). Although, the number of females per male in the Katchal (1.92±0.63) was less than in Great Nicobar (2.59 ±0.91), it did not differ significantly (t =-1.285, df = 8, p = 0.235). However, the number of immature*s* per adult was significantly higher (t =-3.171, df = 8, p< 0.01) in Katchal (1.94 ±0.32) than in Great Nicobar (1.01±0.52).

Table 3.4. Group structure and age-sex ratio of *M. f. umbrosus* in Nicobar Island

Island	**% Males (±SD)**	**% Females (±SD)**	**% Immature (±SD)**	**Ad ♂: Ad♀**	**Ad: Imm**	**Ad♀: Inf**
Great Nicobar	15.67 (±6.13)	37.17 (±9.97)	47.16 (±13.89)	2.59 (±0.91)	1.01 (±0.52)	3.65 (±3.35)
Katchal	12.33 (±3.63)	21.98 (±2.32)	65.69 (±3.70)	1.92 (±0.63)	1.94 (±0.32)	1.42 (±0.75)

Ad ♂= adult males, Ad♀= adult Females, Imm= immatures, Inf= infants

3.3.3. Impact of 2004 tsunami:

Spatial extent of damage: Rate of shoreline ingress was more on the western coasts of all three islands and the eastern coasts received relatively little damage. The estimated total inundated area using shoreline change due to the 2004 tsunami in Great Nicobar, Little Nicobar and Katchal was 51.91, 10.04 and 21.80 km^2 respectively, thus the current island size is 895.48, 138.25 and 139.39 km^2 respectively (Table 3.5).

Table 3.5. Coastline variation after 2004 December tsunami in Nicobar Islands

Island	Mean Ingress (m)	Max (m)	Inundated area (km^2)	Pre tsunami area	% area submerged
Great Nicobar	228.34	1926.0	51.91	947.39	5.48
Little Nicobar	293.97	1751.0	10.04	148.29	6.77
Katchal	407.21	2800.0	21.80	161.19	13.52

Changes in the population: The group encounter rate during the three surveys carried out in 2000, 2006 and 2014 (Table 3.6) in the three islands was likely to be significantly lower in

2006 (0.10) than in 2000 (0.23) (Walds Z=4.19, p=0.001) and 2014 (0.37) (Walds Z=6.60, p=0.001). Also, the group encounter rate in 2014 was significantly higher than in 2000 (Walds Z=3.11, p=0.002). The population increased at an intrinsic rate (*r*) of 0.12, 0.14 and 0.17 in Great Nicobar, Little Nicobar and Katchal from 2006 to 2014 (Table 3.6).

Table 3.6. Number of *M. f. umbrosus* groups encountered per kilometre during 2000, 2006 and 2014 studies in Nicobar Islands

Island	Pre-Tsunami			Post-Tsunami						Intrinsic rate *r* (2006-2014)
	2000			2006			2014			
	n trails (Km)	n groups	n groups/ km	n trails (Km)	n groups	n groups/km	n trails (Km)	n Groups	n groups/ km	
Great Nicobar	16 (227.9)	53	0.23	41 (211.8)	22	0.104	26 (119.5)	36	0.30	0.12
Little Nicobar	12 (62.7)	17	0.27	23 (99.1)	10	0.101	9 (14.1)	5	0.35	0.14
Katchal	12 (92.5)	18	0.19	17 (76.5)	8	0.105	20 (78.5)	38	0.48	0.17
Overall	40 (383.1)	88	0.23	81 (387.4)	40	0.103	51 (212.1)	79	0.37	0.14

Although statistically not significant ($F_{2, 23}$= 1.057, p = 0.36), the mean group size declined from 36.12 ±7.07 in 2000 to 26.75 (±28.23) by 2006 and increased to 41.30 ± 20.02 by 2014 (Fig. 3.2a). The percent of adult males, adult females and immatures per group differed significantly across the three surveys (Adult males $F_{2, 23}$= 9.45, p = 0.01; adult females $F_{2, 23}$= 10.41, p = 0.01; and immatures $F_{2, 23}$= 17.20, p = 0.01) (Fig. 3.2b, c, d). Percent adult males and females per group increased from 9.87 and 43.63 in 2000 to 23.36 and 48.13 by 2006 and decreased to 14.30 and 31.00 by 2014 respectively. Conversely, percent immature per group decreased from 46.75 in 2000 to 28.50 by 2006 and increased to 54.60 by 2014. The number of adult females to adult males has significantly decreased from 4.74 in 2000 to 2.06 by 2006 and 2.32 by 2014 ($F_{2, 23}$= 7.43, p = 0.01) (Fig. 3.2e). The immature to adult female ratio significantly decreased from 1.09 in 2000 to 0.59 by 2006 and again increased to 1.89 by 2014 ($F_{2,23}$= 12.59, p = 0.01) (Fig. 3.2f).

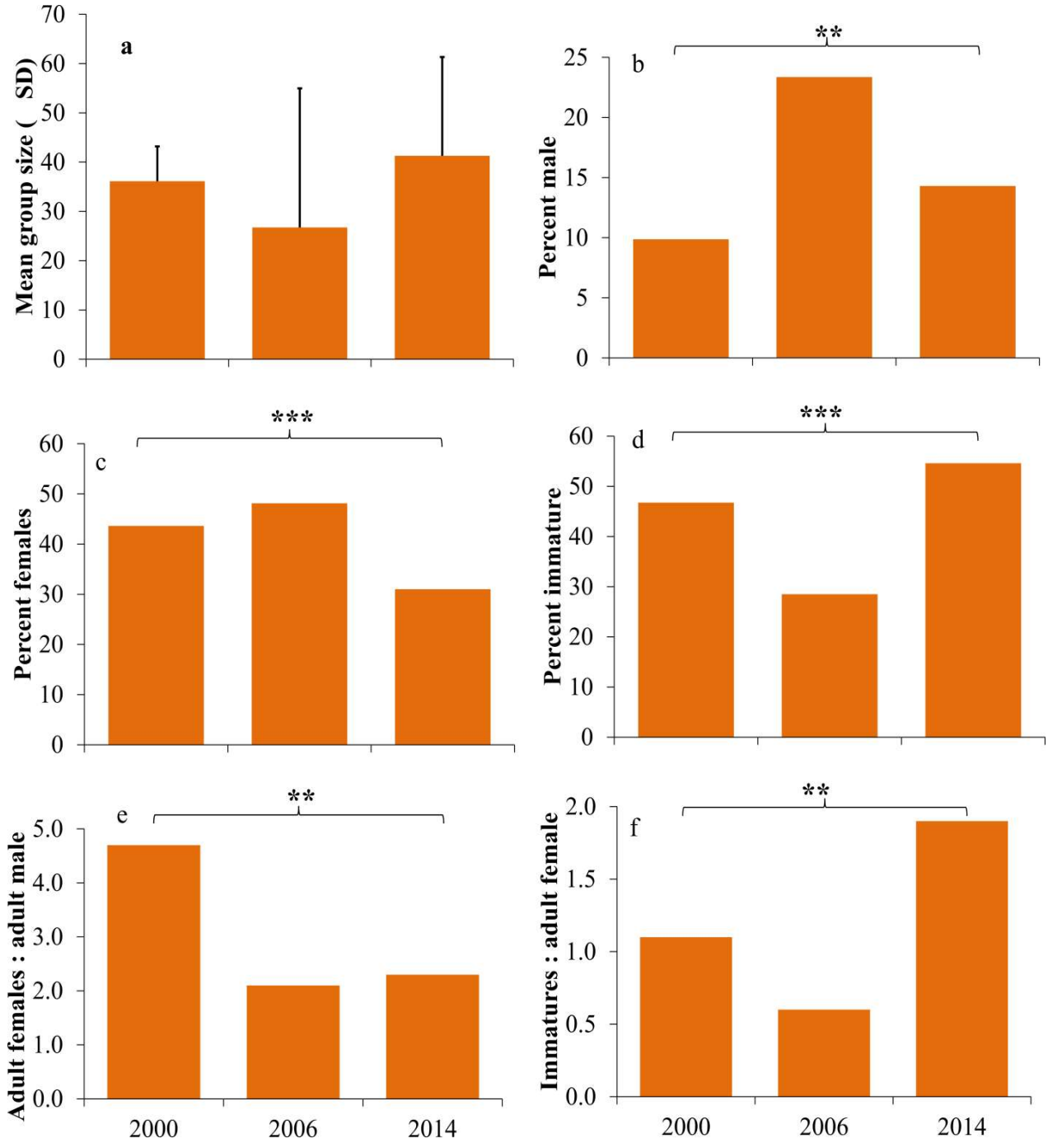


Figure 3.2. Comparison of group structure and age- sex ratios of *M. f. umbrosus* between three study periods. ** $p<0.01$; *** $p<0.001$

3.4. Discussion

I walked 212.14 km and sighted 79 groups of *M. f. umbrosus*. The encounter rate of groups per kilometre was higher in Katchal than in other islands, in plantations and mixed forests than in other forest types and in coastal areas than in inland habitat. Group structure of monkeys did not vary among islands except for Katchal having significantly more immature*s* than Great Nicobar. The Tsunami affected the western coast more than the eastern coast. Population*s* of *M. f. umbrosus*, which had declined immediately after the tsunami, had recovered and became more in 2014 than the pre-tsunami populations. Despite the current population size being higher than pre-tsunami conditions, significant changes in group structure and composition were found.

A tsunami is a category 'I' disaster, which occurs for a short duration but has a severe impact. Apart from direct mortality of individuals, it caused heavy damage to coastal habitats which in turn affected the population. This study reveals that Katchal (13.52%) had lost proportionally *larger* area than Little Nicobar (6.77%) and Great Nicobar (5.48%). Porwal et al. (2011) and Ramachandran et al. (2005) reported similar findings of severe damage to littoral forests, mangroves and low land swamps in all these three islands, and further high intensity of damage in Katchal. This has led the people to leave Katchal or shift their residence by abandoning many coconut and palm plantations to other areas.

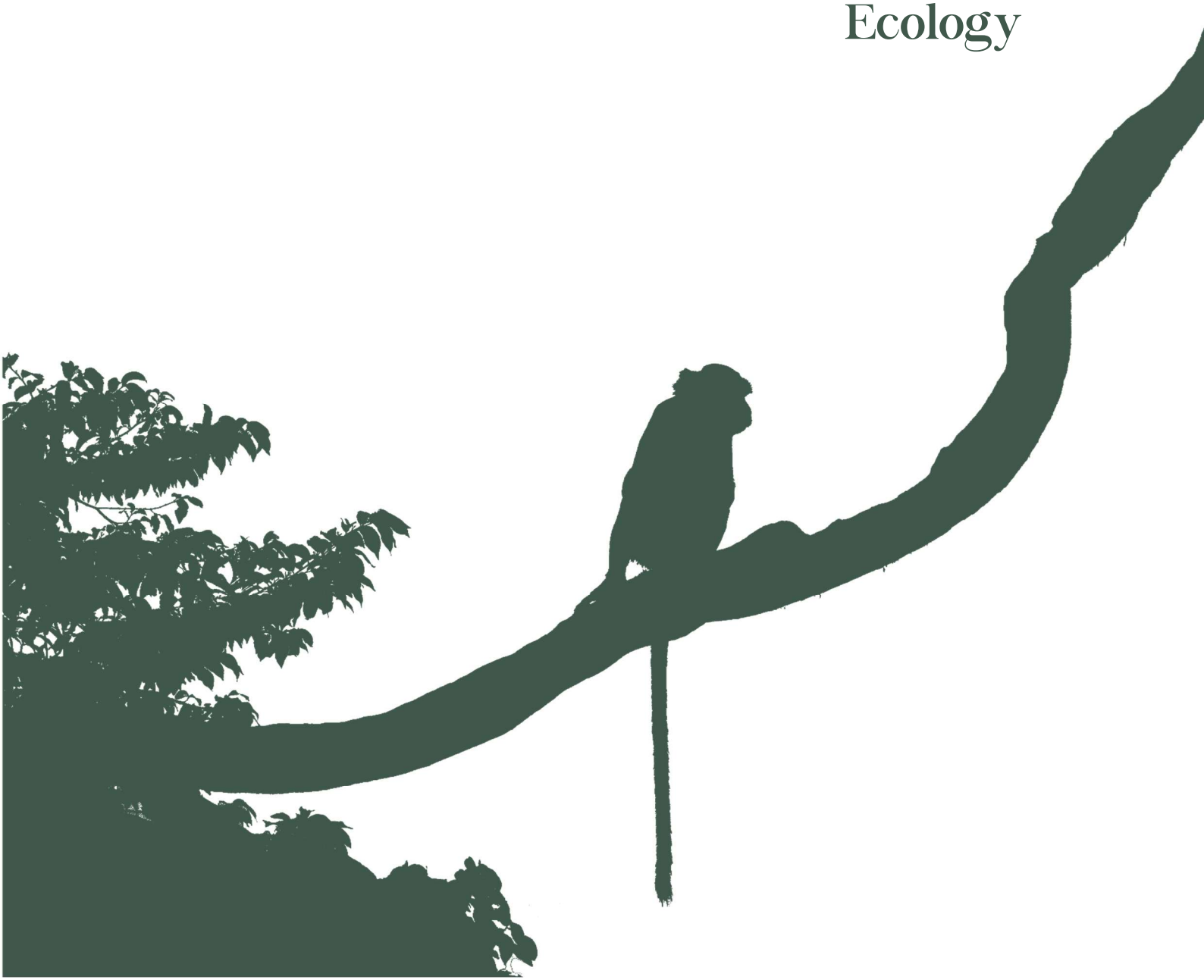
Although *M. fascicularis* is known to refuge in riverine and coastal regions (Salter et al. 1985; vanSchaik et al. 1996; Fittinghoff and Lindburg 1980), they are highly adaptable and adjust their activity pattern to changing conditions even by exploiting novel food sources (Berenstain 1986; Gumert 2011). Due to their phenotypic plasticity, speedy recovery of the population was expected. Umapathy et al. (2003) reported the presence of population*s* in the entire island including inland evergreen forests. Populations in unaffected inland forests could have facilitated re-colonization of *M. f. umbrosus* in all the three islands of Nicobar. Despite the

population of *M. f. umbrosus* suffering a drastic decline following the tsunami (Hahn et al. 2014), they have shown an increase in population size, especially in Katchal Island which had the lowest abundance in previous studies. Umapathy et al. (2003) reported minimal level of crop raiding in certain areas. However, during interactions with the local people in Great Nicobar and Katchal they reported increased crop raiding (coconut and banana) by macaques in villages after the tsunami. This indicates that they have adapted to new food sources. Indeed, *M. f. umbrosus* has shown a high degree of recovery of population size. This is probably due to increased resource availability from abandoned coconut, oil palm plantations, and adapting to feed on different agriculture crops. This may be the reason why Katchal Island shows increased abundance even though it has lost proportionally larger area.

Different species might adopt different strategies to overcome population decrease. One of the strategies may be increasing their population size by increasing the reproductive rate. Although the mean group size did not differ between the three surveys, it showed considerable increase by 2014 and altered the demographic structure. Disasters affected different age-sex classes differently by increasing mortality of weaker individuals in ottarids and ring-tailed lemurs (Shaffer 1987; Gould et al. 1999). In *M. f. umbrosus,* the number of females per adult males decreased from 5 to 2 (ratio 4.74 to 2.32), while the number of immatures per adult females increased from 1 to 2 (ratio 1.09 to 1.89). Increased adult males per group and decreased ratios of adult female*s* to adult males may be due to decreased habitat and total space availability for the dispersal of males. Dittus (1979) reported that after a bad storm, reduced the food supply for toque macaques in Sri Lanka, adult males out competed adult females for what food remained and that both outcompeted immatures, ultimately decreasing the number of immature individuals. In this study, increased numbers of immatures indicate increased reproductive rate, which may be the strategic response to a sudden decline in the population size which is another indicator of population recovery.

4

Activity Budget and Feeding Ecology



Chapter 4:
Activity Budget and Feeding Ecology

4.1. Introduction

The study of the way organisms interact with their environment is essential to understand the ecology of that organism. Monitoring the activity budget of an animal is the easiest way to understand the interdependence of animals and their environment. Unlike resources like food, mate, and space, time is constant and finite throughout the lifecycle of the organism. Hence spatio-temporal changes in the environment, physiology, and social organization of a species are directly reflected in changes in time invested in various activities by that species. Changes in activity pattern due to climatic factors have been observed in Barbary macaques (*Macaca sylvanus*), where macaques spent more time feeding during no snowfall days (Majolo et al. 2013). Activity pattern of rhesus macaques (*Macaca mulatta*) was found to be varying with the degree of commensalism (Jaman and Huffman 2013), where urban groups spent more time resting (46.1%) than the rural group (36.8%) which was lesser commensal. Similarly, the diet pattern of a species dictates its activity budget. A frugivorous and habitat specialist species like lion-tailed macaques were found to move farther during the resource crunch period than the resource-rich period (Santhosh et al. 2015). On the other hand, folivorous species such as Guereza (*Colobus guereza*) and Snub-nosed monkey (*Rhinopithecus roxellana*) are found to spend more time resting (Guo et al. 2007, Fashing 2001). The social organization of the species also influence the time spent on activities, species like long-tailed macaques which involve in scramble competition over limited food resources tend to spend more time moving (van Schaik et al. 1983) than species without scramble competition (Fashing 2001). Also, scramble competition varies within-group structure. Females of *Colobus vellerosus* were observed to partake in scramble competition more than males and the overall frequency of social behaviour was observed to be more in larger groups (Teichroeb et al. 2003). Although group size was seen to influence scramble competition and created 'pushing forward' effect in *M. fascicularis* (van Schaik et al. 1983), its effects on the proportion of time spent moving and feeding were weakly evident in *Cercopithecus aethiops* (Isbell and Young 1993) and *Colobus vellerosus* (Teichroeb et al. 2003).

Accessibility to the food resource is equally important as the quantity of food to determine the availability of food. Some of the food items are encased or embedded in a matrix and are not visible to the naked eye which makes it difficult for an animal to acquire them. To counter such

difficulties and to maximize their foraging efficiency, animals have developed various extractive foraging techniques using distinct manipulative skills (Parker and Gibson 1977). Primates including macaques possess a repertoire of such manipulative skills which help them to optimally forage in heterogeneous environments. Such techniques have been reported in several species of mammals and birds. For example, *Neophron percnopterus* uses a stone as a tool to break the outer shell of the ostrich egg (van Lawick-Goodall and van Lawick 1966), and *Corvus moneduloides* manufacture tools from dry grass to extract lizards from crevices (Troscianko 2008). Various taxonomic groups of mammals from rodents (*Dipodomys ingens*: Ewer 1968) to great apes (*Pan troglodytes*: Watts 2008) employ diverse extractive foraging techniques. Among them, some techniques require a high degree of sensorimotor intelligence and manipulation (Melin et al. 2014). For example, where *Sciurus* sp. use dexterous manipulation to break a nut-shell, *Pan troglodytes* use stone tools to perform the same task (Ewer 1968; Sugiyama and Koman 1979). Similarly, the stone tools are used by *Enhydra lutris* to crack exoskeletons of mussels, crabs, and urchins by pounding them over a stone (Hall and Schaller 1964), and *Macaca fascicularis* break oyster, gastropods and swimming crabs by cracking with axe-shape stones (Malaivijitnond et al. 2007). Expectedly, primates possess a repertoire of wide and diverse foraging techniques. However, the diversity of extractive foraging behavior largely varies between taxonomic groups (King 1986; Yamakoshi 2004). For example, *Papio* sp. and *Macaca* sp. dig out soil for underground bulbs and tubers using their dexterous hands (Dunbar 1977; Wheatley 1988), where *Sapajus* sp. performs the task with the help of tools (Moura and Lee 2004). Though all primate species use their hands, mouth or feet in context-specific extractive foraging techniques, the extractive foraging using tools has been observed only in *Sapajus* sp., great apes and *Macaca* sp. (van Schaik et al. 1999).

Having a high level of sensorimotor intelligence, macaques show a variety of extractive foraging techniques distributed from manual dexterity to tool-aided foraging behaviors (Yamakoshi 2004). However, in the wild, *M. fuscata*, *M. fascicularis*, *M. silenus*, *M. radiata,* and *M. tonkena* have been observed to perform highly dexterous complex extractive foraging tasks (Yamakoshi 2004). *M. fascicularis* is observed to use tools spontaneously in its daily life (Malaivijitnond et al. 2007; Gumert et al. 2009, 2011; Tan et al. 2015). Apart from using stones to break the outer shell of gastropods (Malaivijitnond et al. 2007; Tan 2017), these macaques also perform various food processing techniques such as cleaning the hair of caterpillars, removing the dirt from food items by rubbing them on leaves and washing fruits with water (Chiang 1967; Wheatley 1988). However, among the ten

subspecies of *M. fascicularis*, the two well-studied sub-species (i.e. *M. f. fascicularis* and *M. f. aurea*) were observed to use complex food processing techniques like cracking gastropod shells with stone-tool (Carpenter 1887; Malaivijitnond et al. 2007). The food processing behaviors like leaf washing and washing a food item with water (Wheatley 1988) were observed in *M. f. fascicularis* in Bali, and in Nom Sao Island they have been recorded to process *Opuntia cactai* by using sand, rock, and water (Tan et al. 2016).

M. fascicularis is primarily frugivorous and was found to exploit various resources indicating its generalist nature (Yeager 1996). However, their dietary spectrum is not understood for most of the subspecies including *M. f. umbrosus*. In this chapter, I provide quantitative information on activity budget, feeding habits, and ranging pattern for the group of *M. f. umbrosus* adapted to live in commensal at Great Nicobar.

4.2. Methods

4.2.1. Study Site and Study Group: The study was conducted at Campbell Bay, Great Nicobar Island, which lies between 7° 1′ 30″ – 7° 0′ 0″ N and 93° 4′ 30″ – 93° 57′ 0″ E. I selected a group (TR) with 21 individuals located at the study site for the current study. The group had three adult males, seven adult females, two sub-adult males, seven juveniles, and three infants.

4.2.2. Data collection: The group was followed from dawn (0600 hrs) to dusk (1800 hrs). During this, major activities were recorded using instantaneous scan sampling (Altman 1974) for five minutes at the interval of 30 minutes as per the ethogram provided in Table 4.1. In addition to major activities, I also recorded the details on strata, feeding, and proximity with the nearest and farthest individuals. For feeding activity during continuous feeding bouts as well as during foraging, details of species along with parts consumed and processing and handling are done were documented using *ad libitum* notes. I also recorded the geo-coordinates of visually approximated group center using a handheld GPS receiver (Garmin GPS Map 76csx) for every 30 min.

4.2.3. Analysis: Scan data was sorted season-wise, and contingency tables were prepared as activity vs month and time of the day for the dry and wet season. The time of the day was converted to 6 classes of 2 hours starting from 6:00 am. For daily activity, the proportion of scans for each behavioural state was calculated against the total number of scans aggregated for each time class (Marsh 1981). The overall activity budget between dry and wet seasons was

calculated as relative frequency of scans for a behavioural state compared to the total number of scans in a season.

To compare differences between classes across seasons I performed Kruskal-Wallis (non-parametric test) (Quinn et al. 2002). To check differences within behaviour class but between seasons G-test of proportions was employed. Variation in day activity budget between seasons was compared using non-parametric Wilcoxon's signed-rank test (Quinn and Keough 2002).

All statistical analysis was carried out using R statistical language V 3.02 with R Studio IDE for R v0.98.953.

Table 4.1. Ethogram of the major behavioural states of the macaques recorded during study period along with brief description.

Activity	Description
Movement	Locomotion to spatially different location, vertical movement on same tree and movement within group spread was not considered as movement.
Feeding	Feeding on plant or animal resources. This involves food acquisition, processing and feeding.
Foraging	Moving exploration with intermittent feeding was considered as foraging.
Resting	This comprises of states such as mastication, self-grooming, sleeping, or sitting.
Social	Behaviours comprising of grooming, play, courtship and mating and agonistic interactions with other group members.
Scouting	Individuals giving alarm calls to potential threats or being vigilant after noticing other group in vicinity including behaviours directed towards other groups or organisms were considered as scouting behaviours.

4.3. Results

4.3.1. Activity Budget: A total of 4628 individual scans were collected (Dry N = 546, Wet N = 4082). Activity and season wise breakup of the number of scans is given in Table 4.2. Monkeys spent more time on resting, which is followed by feeding, social and movement, while time spent on foraging and scouting was very less (Fig. 4.1). Although the time spent on each activity varied significantly (Kruskal – Wallis $\chi^2 = 53.96$, df = 5, $P < 0.001$), but the time spent on each activity between dry and wet season did not vary significantly (Table 4.2). There was no significant difference in activities within each day time class between seasons

(Movement: W = 17, P = 0.17, Feed: W= 10, P = 0.50, Forage: W = 11, P = 0.91, Social: W = 14, P = 0.07, Rest: W= 12, P= 0.75, Scout: W= 17, P= 1.70). Throughout the day Resting was the most observed activity and foraging and scouting were the least observed activities (Fig. 4.1a and 4.1b). Activities feeding, social and movement occurred at similar proportion to each other through the day time classes.

Table 4.2. Number of scans recorded for each activity in each season

Activity	Total (N=4628)	Dry (N=546)	Wet (N=4082)	G test of proportions
Move	21.37 (N=989)	16.48 (N=90)	22.02 (N = 899)	G = 4.10, df = 2, P = 0.16
Feed	19.36 (N = 896)	24.54(N = 134)	18.67 (N = 762)	G = 8.23, df = 2, P = 0.057
Forage	3.28 (N = 152)	4.03 (N = 22)	3.18(N = 130)	G= 0.50, df= 2, P = 0.65
Social	18.58 (N = 860)	22.16 (N = 121)	18.10 (N = 739)	G= 3.71, df= 2, P = 0.13
Rest	34.44 (N = 1594)	31.14 (N = 170)	34.88 (N = 1424)	G= 2.20, df= 2, P = 0.20
Scout	2.96 (N=137)	1.65 (N=9)	3.14 (N=128)	G= 1.60, df= 2, P = 0.3

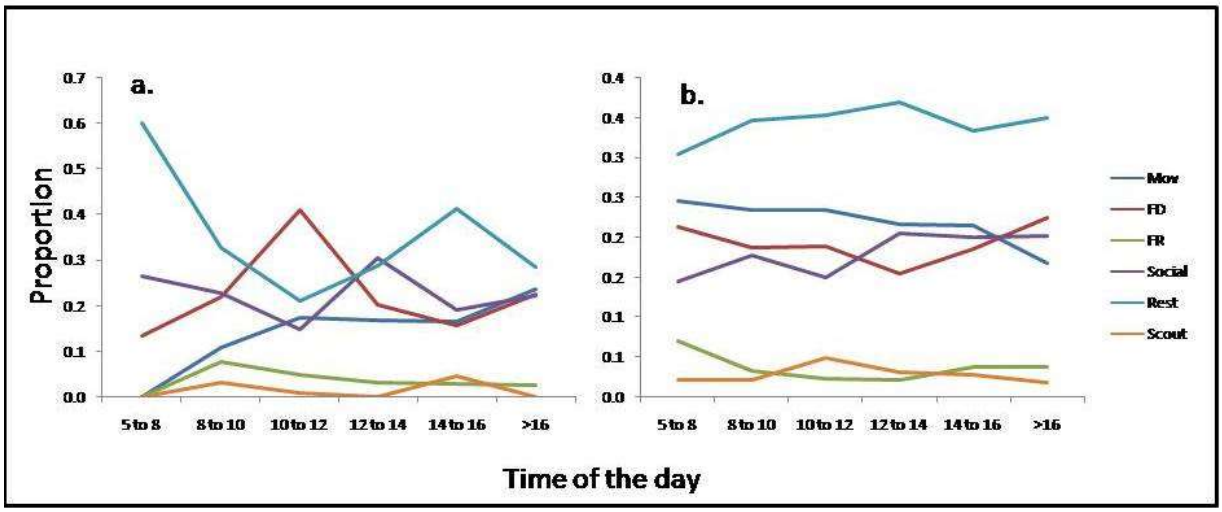


Figure 4.1. Variation in day activity. a. Dry Season, b. Wet Season

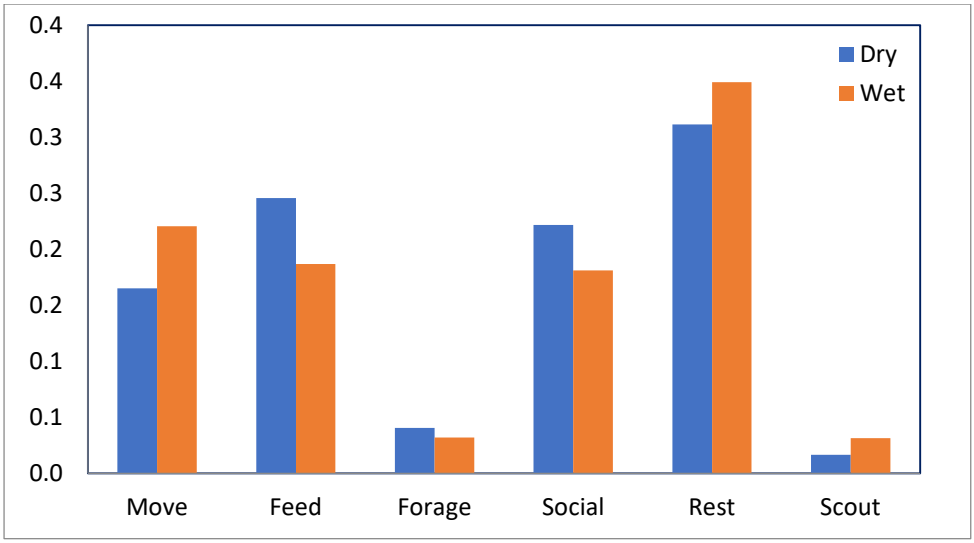
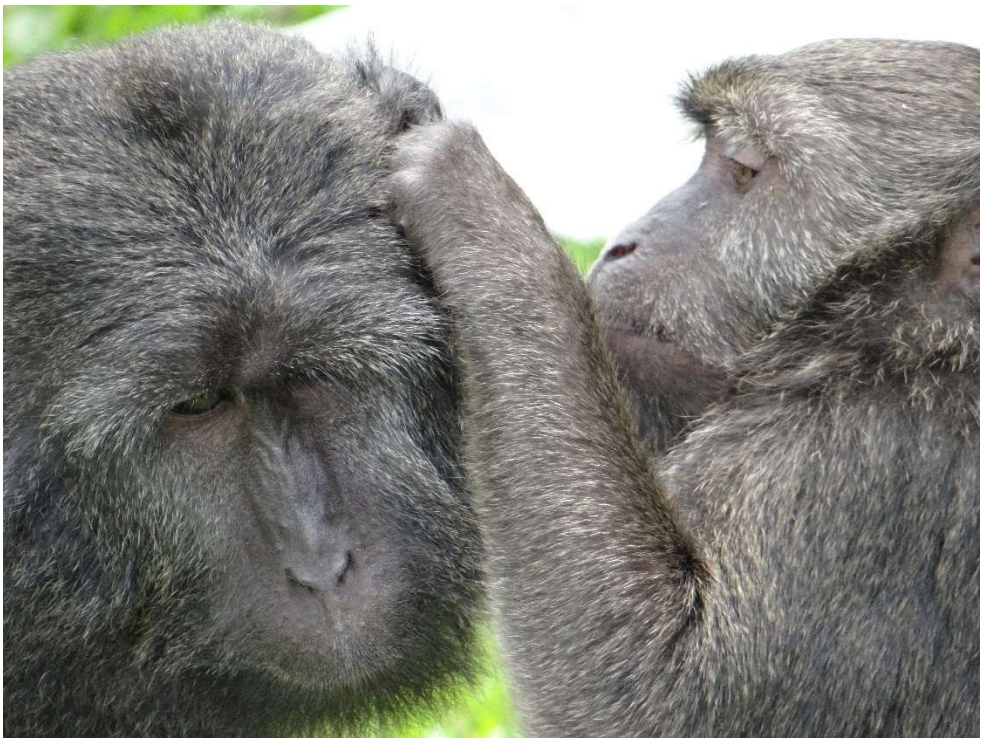


Figure 4.2. Variation in time activity budget during dry and wet seasons.

4.3.2. Feeding Ecology: Study group was observed to feed on 26 major food items of which 12 were introduced by humans and 14 were of native origin (Table 4.3). The relative frequency of feeding on species from the plantation and human habitation was significantly higher (Z = 27.93, $P < 0.01$) than native species (Fig. 4.3). Macaques significantly fed on plant resources than animal or human waste origin resources ($Z = 19.78$, $P < 0.01$) (Fig. 4.4). Among plant resources, macaques fed fruits ($N = 675$) significantly ($Z = 15.38$, $P < 0.01$) over flowers (N = 6), stems ($N = 32$) and leaves ($N = 50$) (Fig. 4.5).



(An allogrooming session between two individuals of TR)

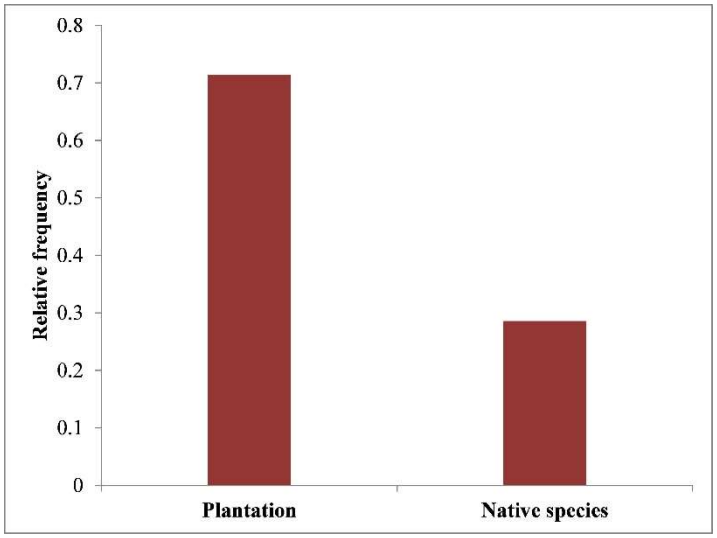


Figure 4.3. Proportion of food items fed by macaques from plantations in human habitations and forest region

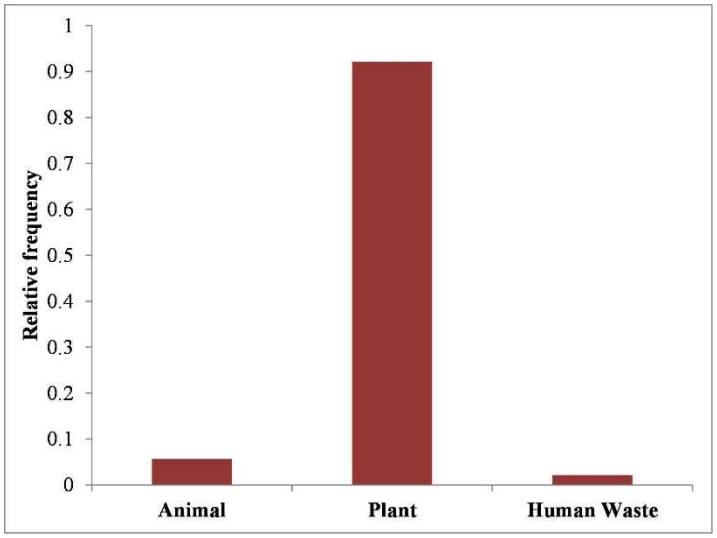


Figure 4.4. Proportion of animal, plant or human origin food items fed by macaques

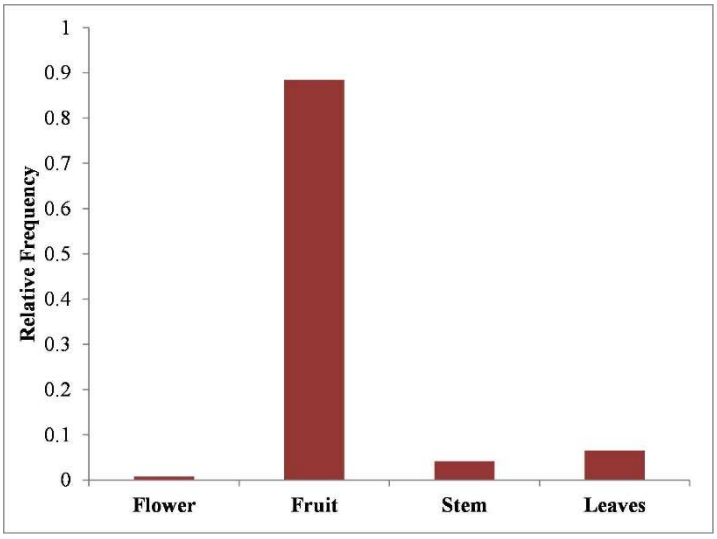


Figure 4.5. Proportion of different plant parts eaten by macaques

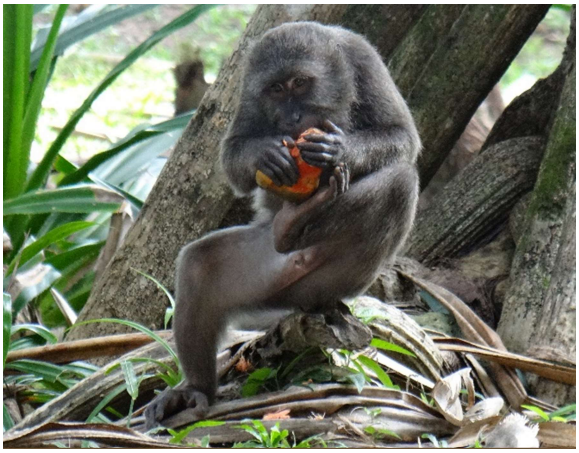
Table 4.3. Relative frequency and source of major food items consumed by Nicobar long tailed macaques.

Common name	Species	Dry season		Wet season		Overall Percent scans
		N (scans)	Percent scans	N (scans)	Percent scans	
Food items of cultivated or human origin						
Australian acacia	*Acacia auriculiformis*	11	6.2	42	6.7	6.60
Custard apple	*Annona reticulata*	4	2.3	12	1.9	1.99
Papaya	*Carica papaya*	4	2.3	12	1.9	1.99
Coconut	*Cocos nucifera*	38	21.5	169	27.0	25.78
Hibiscus	*Hibiscus rosa-sinensis*	0	0.0	3	0.5	0.37
Banana	*Musa paradisiaca*	21	11.9	58	9.3	9.84
Guava	*Psidium guajava*	33	18.6	119	19.0	18.93
Sugarcane	*Saccharum spp*	3	1.7	9	1.4	1.49
Tomato	*Solenum lycopersicum*	2	1.1	6	1.0	1.00
Egg plant	*Solenum melongena*	2	1.1	6	1.0	1.00
Tamarind	*Tamarindus indicus*	3	1.7	9	1.4	1.49
-	Egg (*Gallus domesticus*)	0	0.0	3	0.5	0.37
-	Urban waste	0	0.0	3	0.5	0.37
Native species from forests and secondary growth on fallow land						
Jackfruit,	*Artocarpus spp.*	1	0.6	3	0.5	0.50
Australian pine	*Casuarina equisetifolia*	4	2.3	4	0.6	1.00
Wild musk melon	*Cucumis spp.*	6	3.4	18	2.9	2.99
Banyan	*Ficus bengalensis*	2	1.1	6	1.0	1.00
-	*Ficus spp*	2	1.1	6	1.0	1.00
Infane	*Garcinia spp.*	2	1.1	6	1.0	1.00
Mango	*Mangifera* spp	8	4.5	33	5.3	5.11
Kevda	*Pandanus odoratissimus*	18	10.2	54	8.6	8.97
-	*Semecarpus spp*	1	0.6	6	1.0	0.87
-	unknown spp A	0	0.0	3	0.5	0.37
	Invertebrates	10	5.6	34	5.4	5.48
	Soil	2	1.1	2	0.3	0.50

Further seven extractive foraging and tool use behaviors were observed which include food extraction (husking, coconut pounding), foraging (bush beating: feed on hidden or inconspicuous food items by beating on a bush), food preparation (tool-aided food rubbing, food rubbing by hand and washing) and teeth flossing (Table 4.4). A total of 269 events of extractive foraging behaviors were recorded during the study. Among age-sex classes, sub-adult males and females were observed to perform all seven behaviors, while juveniles were not seen performing food rubbing, bush beating, and teeth flossing. These seven extractive



(Feeding on lizard)



(Feeding on *Pandanus odoratistimus* fruit)



(Feeding on *Artocarpus spp* fruit)



(Feeding on *Gallus domesticus* egg)



(Feeding on *Carica papaya* leaf)



(Feeding on *Musa paradisiae* infloroscence)

foraging behaviors have been grouped into four categories as coconut processing (including husking and coconut pounding), food washing (including tool-aided food rubbing, food rubbing by hand and washing), teeth flossing and bush beating.

Table 4.4. Different types of extractive foraging behaviours observed

Type	Item	Behaviours
Food Extraction	Coconut, *Aegle marmelos* Fruit	Husking, Pounding
Foraging	Grasshoppers and crickets	Bush beating,
Food preparation	*Casurina* seeds, *Anacardium occidentale* seeds, *Aegle marmelos* fruit, dehusked coconut	Leaf wrapping, Hand rubbing, washing

Coconut processing: The macaques were observed to extract edible parts of coconut by employing complex manipulative processes that are described here.

a. Husking: Macaques were observed to use husking to extract endosperm and water by removing the outer fibrous covering (exocarp and mesocarp) of the coconut fruit. Macaques either plucked the coconut or used it directly as it was attached to a tree. They used two different strategies to pluck the coconuts: detaching the coconut by teeth while holding it with forelimbs or twisting it along its horizontal axis using forelimbs. The plucked coconut was carried to a suitable place such as midrib of the leaf of the tree, branches of other trees and concrete walls or dropped to the ground. However, intact coconut processing was done in situ. The animal then removed the outer fibrous layer using teeth. Individuals bit on either terminal of the coconut and tore out a portion of the fibrous covering by pulling the head backward while holding the coconut on the substrate. While husking, both forelimbs and hind limbs were used either alternatively or simultaneously to hold the coconut firmly on the substrate. They repetitively removed the husk until the access was made to the edible part. For a tender coconut, endosperm was exposed once the fibrous covering was removed due to the absence of a hard inner shell (endocarp). Hence, after partial removal of the husk, macaques accessed the endosperm and water. However, in the case of a mature coconut, they had to completely remove the husk because the endosperm is encased in a tough outer shell which also has to be broken to get access to it. A total of 83 husking events were recorded and all individuals of each age-sex class were observed to perform these behaviors, where adult males, subadult males, adult females, and juveniles engaged in 22, 16, 42, and 3 events respectively.

b. Coconut pounding: The pounding was employed by macaques to crack the hard-inner shell of a mature coconut to access the endosperm. After completely removing the exocarp and mesocarp by husking, macaques pounded the dehusked coconut to break the shell. Macaques lifted the coconut and pounded it repeatedly using either one or both forelimbs on a substrate until a fissure was formed on the shell. Then, they used their canines over the fissure to crack open the shell. A total of 37 coconut pounding events were recorded where adult males, subadult males, females, and juvenile performed 15, 9, 12 and 1 events respectively.

Food washing: Food washing includes three techniques where macaques removed the non-edible particles like hair, thorn, mud, soil, and sand from the food items by using various substrates and materials.

Tool-aided food rubbing: If a food item was covered with thorns, hairs, or mud, macaques searched for suitable objects in the vicinity such as leaves, papers, clothes, and polyethene sheets to clean food items that I have considered as rubbing. Macaques also modified these tools before or during the rubbing process. The tool-aided food rubbing behavior was seen with two sequences i.e. wrapping and wiping.

Wrapping: After acquiring the food items, macaques procured materials such as leaves, branches, papers, clothes and polyethene sheets from the vicinity. They wrapped these materials over the food items. In addition to readily available material, macaques also procured and processed those materials from the nearby plants either by breaking the twig with bunches of leaves by forelimbs or they bent the leafy branch using both forelimbs and detached it using their teeth. They also wrapped leafy branch or broad leaves over food items without detaching them from the stalk.

Wiping: After wrapping those materials over the food items, they often wiped the food with the help of forelimbs. Then they bit or ate over the wrapped portion of a food item.

These tool-aided foods rubbing techniques were observed for food items such as husked coconut, cashew nut (*Anacardium occidentale*), Indian bael (*Aegle marmelos*), Pandanus fruit or closed plastic containers with food. Except for juveniles, all other age-sex classes were observed to perform the tool-aided food rubbing behavior (N=56). Adult males, sub-adult males, and adult females were observed to perform the tool-aided food rubbing 12, 27, and 17 times respectively.

Food rubbing by hand: Macaques were observed to clean the small seeds, fruits, and the edible vegetative parts which could fit in their palms before ingestion. The food item was kept between the two palms and they moved the limbs repeatedly in opposing directions, thus rubbing the food item in the process before ingestion. A total of 45 food rubbing by hands events were observed where the adult males, subadult males, adult females, and juveniles performed 7, 16, 19, and 3 times respectively.

Washing: Macaques were observed to wash food items while foraging in puddles, water holes, and freshwater swamps. Food items including tubers and fruits were extracted from the muck and washed in a water body. After extraction, the food items were dipped and rinsed by holding them in a forelimb while swaying it on the water surface to remove the mud. A total of 6 events were performed by subadult males, adult females, and juveniles 3, 2, and 1 time respectively. Adult males were not observed to perform this behavior.

Teeth flossing: Macaques were observed to take a grass blade, Casuarina needle, feather, nylon thread or metal wire and performed teeth flossing. A macaque put one of these objects between its teeth and closed the mouth such that either of the tips of the object was exposed. The exposed tip was then held by a forelimb and pulled out. This behavior was repeated several times while they put the flossing object between different teeth. This behavior was performed while the macaques were resting after a foraging session. Except for juveniles, all other age-sex classes performed teeth flossing. A total of 25 teeth flossing events were recorded where adult males, subadult males, and adult females performed 3, 12, and 10 events respectively.

Bush beating: Bush beating was employed by the macaques to forage on invertebrates from the bushy open scrub vegetation. Macaques were seen to forage on invertebrates like grasshoppers, moths, and other insects from the ground vegetation that comprised grasslands with small scattered bush patches. Macaques beat the bush using their forelimbs. The flushed invertebrates were caught on the ground or from the air. Sometimes when the grasshoppers escaped and relocated to other bushes, macaques followed them and again flushed them out by beating the bush. I recorded 9, 4, and 4 such events by adult males, subadult males, and adult females respectively.

4.4. Discussion

Activity budget: The study group was observed for six behavioural states (Movement, Feeding, Foraging, Resting, Social and Scouting), among them resting was found to be the most common activity over feeding, social, and movement. For diurnal activity budget pattern remained the same between the seasons, that did not vary between seasons.

The order of the behavioural state in the activity pattern varied between the macaque species (Table 4.5). It was attributed to group size, habitat and land cover, food source, and climate for the specific pattern of activity budget. This reveals that the local specific ecological, anthropogenic, and climatic conditions determine the pattern of activity budget in the habitat. Groups in human-dominated landscapes have easy access to enriched food while at the same time such areas have high disturbance from humans and also high competition from neighbouring groups. While provisioned and semi-provisioned groups were found to spend more time on feeding (*M. assamensis*: Koirala et al. 2017; *M. fascicularis*: Sha and Hanya 2013), while forest or non-provisioned groups would spend more time on movement (Hambali et al. 2012; Md-Zain et al. 2010). The focal group TR inhabited mix of primary littoral forests and human-altered landscape perhaps adapted to extract food from many sources from both landscapes. This availability of enriched food may have resulted in less need to spend time on feeding and movement.

Group size was also found to influence group movement and larger groups of *M. fascicularis* were found to move more due to behavioural mechanism termed as "pushing forward effect" (van Schaik et al. 1983). This pushing forward, is attributed to patch depletion rate which increases scramble competition. However, the movement pattern of *M. fascicularis* groups from Kabangasan University, Malaysia did not vary with group size. In the current study, I have found resting to be the most performed activity akin to (van Schaik et al. 1983) and less movement, which indicates patch depletion rate and within-group competition is lower in study group.

Seasonal variation in food availability determined the time-activity budget of *M. Silenus,* where feeding activity was found to be highest when the forests are most productive (monsoon and post-monsoon season) (Kurup and Kumar 1993). In the current study, such variation was not observed as Coconut and Guava were available perennially while *Pandanus odoratissimus* was the only major food species which was seasonal. This may have resulted in the absence of seasonal variation in dry and wet seasons. From this, it can be concluded that, although group

size, habitat, food source, and seasonality do affect the time-activity budget, their effects are stochastic and are highly specific to the group as observed across macaques (Table 4.5).

Table 4.5. Review of activity budget studies for genus *Macaca*

Species	group size	Habitat	food source	Activity 1	Activity 2	Activity 3	Reference
M. assamensis	37-44	*Schima wallichii* forest	Semi-provisioned	feed	rest	move	(Koirala et al. 2017)
M. fascicularis	40	Train station	provisioned	move	feed	rest	(Hambali et al. 2012)
M. fascicularis	20-101	University campus	-	move	rest	feed	(Md-Zain et al. 2010)
M. fascicularis	19-25	Forest and Urban	provisioned	feed	move	rest	(Sha and Hanya 2013)
M. fascicularis	11-33	Forest	-	rest	move	feed	(Schaik et al. 1983)
M. fuscata	47	Temperate forest		social	feed	move	(Maruhashi 1981)
M. munzala	13-22	Forest, secondary scrub and agriculture	-	move	forage	rest	(Kumar et al. 2007)
M. silenus	14-31	Evergreen forest	forest	feed	rest	move	(Kurup and Kumar 1993)
M. nigra	97 61 50	Lowland rainforest and plantations	forest	rest move move	feed feed social	social social feed	(O'brien and Kinnaird 1997)

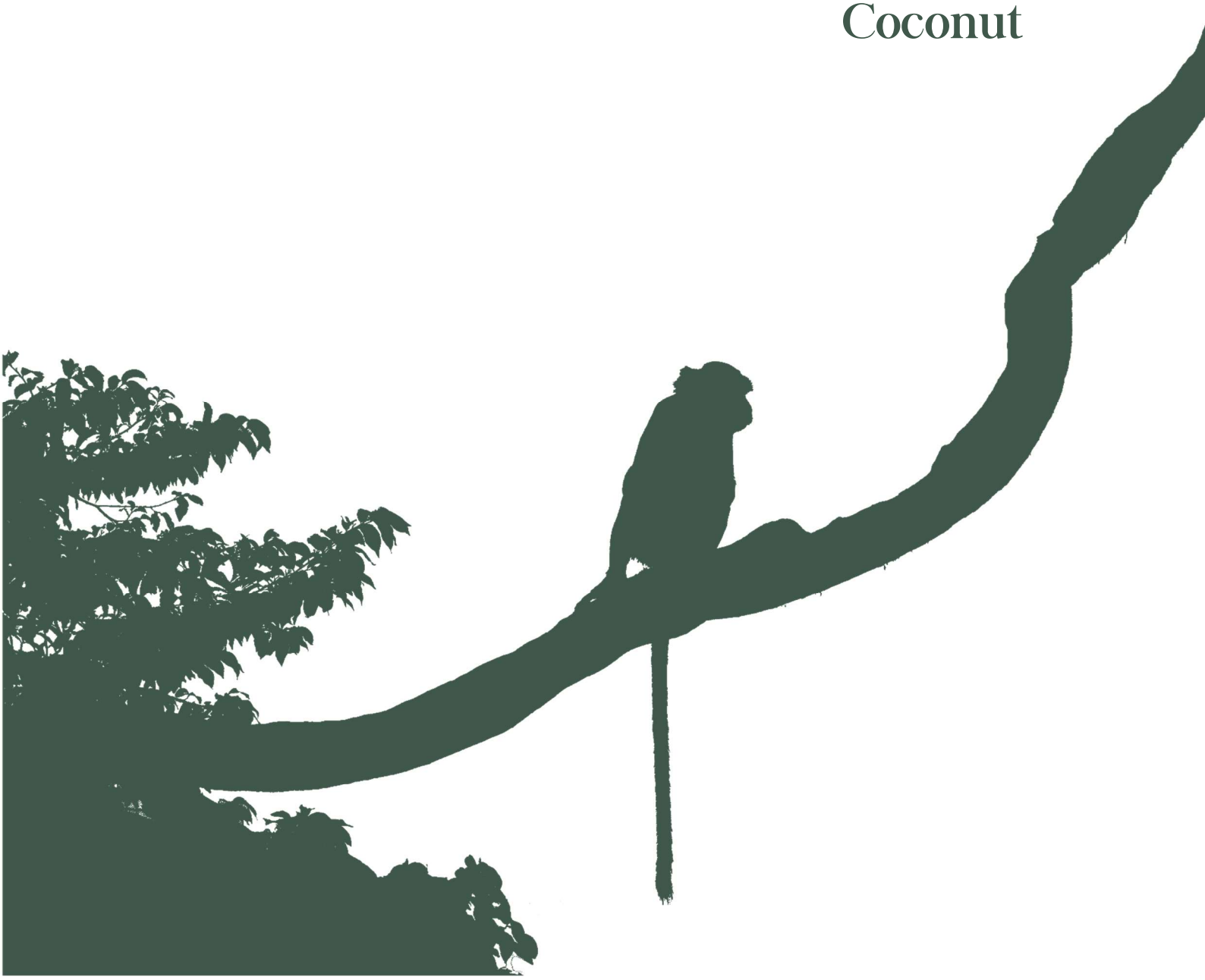
Feeding Ecology: The study group being a partial commensal spends time feeding on food resources from orchards and plantations which may result in the acquisition of low-cost high-energy food and an increase in resting time. Similar observations were reported in *Macaca mulatta* (Jaman and Huffman 2013). Provisioned groups of *Macaca fascicularis* in Vietnam were observed similarly to spend 31.6% to 36.83% of time resting, which again was the most common activity (Son 2003).

Group was observed to feed on 25 food resources of which 4 were most common *viz*., Coconut 27-27%, banana 11.9 – 9.3%, guava 18.6-19%, *Pandanus* spp. 10.2-8.6%. Among them, three resources were from orchards and plantations in human habitation and available throughout the year. Primary forest and orchards spatially cover the majority of the total area (72.2%). Yeager (1996) reported similar findings in *M. fascicularis* in Kalimantan Tengah, Indonesia. There they exploited 33 plant resources of which 5 were most frequent in their diet which were abundant in the habitat. As in both the sites macaques utilized the most abundant and thus low-cost resource first that indicates the generalist nature of the species.

Nicobar long-tailed macaques perform various extractive foraging techniques like husking, coconut pounding, tool-aided food rubbing, washing, and bush beating to extract the inaccessible food items. Therefore, the performing ability of these tool-aided extractive foraging techniques implies that the Nicobar long-tailed macaque has complex manipulative skills with advanced sensorimotor intelligence (van Schaik et al. 1999). The study sets a stage for further exploration about the spread of the foraging techniques among the group members and possible cultural transmission of behaviours across generations.

5

Manipulation and Feeding on Coconut



Chapter 5:
Manipulation and Feeding on Coconut

5.1. Introduction

Prehensile limbs of primates give them ability to manipulate objects in their surroundings. Grasping proficiency in chimpanzees and humans has been attributed to diversity of grips observed (Pouydebat et al. 2011). Similarly, rhesus macaques were observed to use 18 distinct grips for object manipulation (Macfarlane and Graziano 2009). This ability to grasp different objects enables primates to develop motor skills to perform complex tasks (Kummer and Goodall 1985). Various such behaviours in association with tool use and extractive foraging have been documented across primate species. Environmental constraints such as distribution of resource and competition further induce primates to use their physical abilities in innovative ways (Chappell et al. 2015). These innovations are either novel solutions applied to existing problems or existing solutions applied to novel problems (Kummer and Goodall 1985)

Not all species are equally adept at innovation. In captivity, primates are often trained to perform advance cognitive functions such as tool use e.g., tool manufacture and use has been demonstrated in captive *Macaca leonina* (Beck 1976), *Cebus apella* (Visalberghi and Fragaszy 1990), *Pan troglodytes* (D. Hopkins and Rabinowitz 1997) and *Cebus spp.* (Visalberghi 1993). Though individuals of these species show cognitive capability to perform complex tasks in captivity, in the wild such behaviours are not a commonplace (Haslam 2013). Novel behaviours either remain restricted to few individuals or spread to other individuals of the group through sub-cultural propagation (Huffman and Hirata 2003; King 1991). Huffman and Hirata (2003) discuss the vertical and horizontal diffusions during three phases of sub-cultural propagation i.e., Transmission, Tradition and Transformation.

Rate of diffusion of object manipulation vary age and sex wise within a species. In Old World monkeys, immatures show foraging strategies similar to individuals in close proximity which are primarily mothers and other socially tolerant individuals (Rapaport and Brown 2008). Such synchronized co-feeding with mothers was found to be helpful in future survival of offspring of *Papio cynocephalus* (King 1994) and *Cercopithecus aethiops* (Hauser 1994). Also, rate of juvenile play is important in transfer of knowledge between peers as seen in *M. fuscata* in Arashiyama (Burghardt 2015; Fagen 2002). Juvenile play, including objects and contact play between individuals, has been observed to reduce with age in *M. fuscata* (Fagen 2002) and *M. fascicularis* (Tan 2017). Also, if individual is constantly subjected to particular behaviour and

its outcome, there are more chances for that individual to display the behaviour due to local stimulus enhancement (Rapaport and Brown 2008; Visalberghi and Fragaszy 1994). Similarly, sex-wise differences in behaviour patterns have been attributed to differential exposure to perinatal steroid hormones (e.g., *M. mulatta*: Bachevalier 1990), access to resource (e.g., *M. fascicularis*: van Schaik 1989) and rate of mixed play (e.g., M. *fuscata*: Fagen, 2002). Sweet potato washing behaviour (Kawai 1965; Kawamura 1954) and non-functional stone handling (Huffman and Hirata 2003) in *M. fuscata* was not found to be restricted by sex. Availability of resource such as sweet potato, sand, water and stones enables more individuals to pick up the behaviour resulting into local stimulus enhancement. Fagen (2002) reported age and sex tolerance during juvenile play in *M. fuscata* which is favourable for subcultural propagation of these behaviours. However, innovative behaviours have been observed not to diffuse in the group if conditions are not favourable. An innovative coconut handling was observed to be confined to a single individual *M. mulatta* in Cayo Santiago (Comins et al. 2011). However due to the availability of other food items, coconuts are not preferred (Comins et al. 2011) which may lower the local stimulus enhancement affecting the diffusion of the behaviour.

Diffusion of behaviour is not uniform across sexes due to sexual dimorphism, physiology and sociality within primate groups. *Cebus spp.* males show higher tendency to use tools (Fragaszy et al. 2004; Falótico and Ottoni 2014) while in *P. troglodytes*, females acquire tool use more readily than males (Boesch and Boesch 1984; see review by Gumert et al. 2011). In *M. fascicularis aurea*, although both sexes showed proficiency in tool use, their strategies differed significantly based on food source because of differential energy requirements and physical capacities (Gumert et al. 2011).

Further, extrinsic factors have also been found to affect rate of innovation and diffusion among primates. Frugivorous *Ateles geoffroyi* showed tendency to develop complex object manipulation when compared to folivorous *Alouatta palliata* as patchy distribution of resource necessitated the same (Milton 1981). Similarly, frugivorous lemurs (*Varecia spp., Eulemur fulvus)* were found to develop complex motor skills and cognitive abilities when compared to folivorous lemurs (*Lemur katta, Propithecus coquereli*) (Rosati 2017). Dependency on high cost high value food has been linked with higher cognitive function and motor skills (Cords 1992; Gigerenzer 1998; Rosati 2017).

Coconut (*Cocos nucifera*) is one of the complex resources, which requires complex motor skills to obtain the edible part of it (Pal et al. 2018a). This nutrient rich and easily available resource

is perennial on the Nicobar islands (Sinha 1999). Some years ago, only a few groups of *M. f. umbrosus* were found to feed on coconut in these islands (Umapathy et al. 2003). However, the massive tsunami of 2004 caused enormous loss of natural habitat and food resources, such as *pandanus*, of these macaques. As a result, many groups were pushed towards villages and crop fields in these islands, and consequently, coconut became a primary part of their diet (Velankar et al. 2016; Pal et al. 2018a). *M. f. umbrosus* have been observed to use complex extractive foraging techniques and tool use for various food items (Wheatley 1988) including coconuts (Pal et al. 2018a). Therefore, I hypothesize that this should provide enhanced local stimulus to these macaques enabling coconut manipulation prevalent between both sexes while adults showing more proficiency. However, hard shell and thick husk of coconut may be a hindrance to smaller and weaker individuals which may make differences between age and sex profound. To test this, coconut feeding behaviour was graded in to 33 specific acts based on differential patterns in choice, plucking, dehusking, drinking and feeding of coconuts. I observed the sequences of these acts used by different age and sex individuals to find out variation in coconut processing behaviour by *M. f. umbrosus*.

5.2. Methods

5.2.2. Study animal: The home range of TR group is in the juxtaposition of coastal littoral forest and human settlements, consist of a vegetation matrix of hilly tropical rain forest, low-land littoral forest dominated by *Pandanus odoratissimus*, coconut (*Cocos nucifera*) and *Areca* nut plantations. This also provided good vantage to observe individuals of TR groups from proximity. Hence, the study was conducted on this multi-male multi-female group (TR) between October-2014 to May-2015. During the study period, TR group was composed of 16 individuals with of 3 adult males (FY, HK and MA); 6 adult females (AU, BY, RE, NI, TE and ST); 3 sub-adult males (KU, BA and AI) and 4 male infants (AN, BL, RI and TA).

5.2.3. Survey: The TR group was followed between August 2013 and December 2015 to study their ecology and behaviours including feeding ecology. In the first three months of study, the group was habituated and individuals were identified using physical features like facial markings, wound marks and other variation in their morphological characteristics.

During the study period, macaques were seen to feed on different stages of coconut fruits by employing various processing and feeding techniques (here onwards ‘coconut processing’). The coconut trees naturally grow in Andaman and Nicobar archipelago and cultivated by

islanders as an economic crop. In Campbell Bay, the coconut plantation is a common in and around Campbell Bay. The weight of a mature coconut fruit is about 1.5 kg which takes 12 to 15 months to get mature. At 3rd month, water starts developing inside fruit while the outer covering (exocarp) remains green with thin soft husk (mesocarp) beneath it encased water. From 6th month, endosperm starts developing which takes another 6 months to complete development. Along with endosperm, inner shell (endocarp) also develops which embedded endosperm with a seed wall. During this period the mesocarp becomes thick, tight and fibrous with yellowish-green heard exocarp. After maturation, fruit starts drying and falls on the ground with stiff, gray exocarp; thick, tight mesocarp and heard endocarp. That fallen fruit sometime germinated after seven months of falling. Fruits in grounds are sometimes rotten due to natural seasoning while the endocarp becomes weak, and endosperm dissolved with cotyledon as oily sap. Due to non-seasonal continuous fruiting and long development period, there are always different mature stages of coconut available in tree and fallen ones on the ground. Macaques feed on coconut regularly (Pal et al. 2018a). A pilot study using *ad libitum* sampling was conducted to prepare an ethogram of the coconut processing techniques.

Thereafter, data was collected between November 2014 and May 2015. Feeding ecology data was collected with instantaneous scan sampling at 30 min intervals (Altmann 1974). I recorded activities and food items consumed by everyone along with group's behavioural states by the scan sampling. Continuous focal animal sampling with structured datasheet was used to collect coconut processing data (Altmann 1974). Samplings were started just after an individual made physical contact with a coconut and continued up to the next 60 seconds of non-contact phase. This entire event was considered as a behavioural bout. Sometime during one's sampling bout another individual snatched the coconut from the focal individual. In that case, if within 30 seconds focal individual was unable to repossess it and the intruder continued feeding on it then that was considered as a termination of that bout, and next bout started with intruder as a focal animal. All coconut approaching activity *viz.* processing, drinking and feeding data were collected in time bout (seconds) where types of activities were recorded separately as one count until it replaced by another. If in a single bout or even in a continuous event of a bout any type of behaviour appeared more than once with discontinuation, was recounted. Pluck and leftover content of coconut were recorded as a single event in each sampling bout.

5.2.4. Analysis: In the pilot study, Infants were not seen to process coconut independently; therefore, they were excluded from the study. One adult male HK whose left hand was amputated from elbow, was not included in the study. The study was conducted by collecting

data on 11 individuals, were subdivided independently into two groups with two categories in each (Table 5.1). First one was sex-wise *i.e.,* male (5) and female (6), and the second one was age-wise *i.e.,* adult (7) and young (4). Along with three sub-adult male's female ST was put in the young class due to her body size and absence of sexual swelling.

Table 5.1. Age and sex wise classification of TR group individuals:

Sex-wise classification		**Age-wise classification**	
Male	**Female**	**Adult**	**Young**
5 (FY, KU, BA, BM and AI)	6 (AU, BY, RE, NI, TE and ST)	7 (FY, AU, BY, RE, NI, MA and TE)	4 (ST, KU, BA and AI)

After a pilot study, according to the maturity levels and processing techniques, the coconut fruits were categorized in to four classes i.e., tender (T), mature (M), dry (D) and dry-dehusked (DD) (Table 5.2). During the pilot study, I recorded 25 coconut processing behaviours which were composed of drink (6), feed (4), pluck (4) and process (11) (Table 5.3). After each bout, according to success of processing and the left-over states coconuts were categorized into seven categories (Table 5.3).

Statistical analysis: Preference of coconut feeding of each individual was calculated as the proportion of coconut feeding scan from the total feeding scans of an individual**.** I employed independent sample student's t test to compare the preferences of coconut feeding among age and sex classes. Similarly, mixed effect of coconut type, choice of coconut types, pluck pattern and mean time spent for processing, drinking and feeding with age and sex classes was determined using two-way ANOVA with repeated measures. Similar approach was used to examine whether there is differential success for each coconut type with age and sex classes. Spearman's rank correlation was used to check the relation between hand and leg laterality of study individuals.

Table 5.2. Coconut types according to the maturation:

Type (Code)	Fruit age (Months)	Exocarp (Outer covering)	Mesocarp (Fibrous husk or coir)	Endocarp (Inner shell)	Coconut-water	Endosperm (Flesh or meat)
Tender (T)	3 – 6	Soft; green	Thin, loose	Not developed	Present	Not developed / Thin and soft
Mature (M)	6 – 10	Heard; yellowish green	Thick; tight	Soft	Present	Thick and soft
Dry (D)	> 10	Stiff; gray	Thick; rigid	Hard	Present (little)	Thick and fleshy
Dry dehusked (DD)	> 10	Removed	Removed	Hard	Present (little)/ Absent	Fleshy / dissolved and absorbed in cotyledon or oily sap

I included age and sex as grouping variables to the transformed dataset. Non-metric Multi-Dimensional Scaling (nMDS) was performed on this dataset by using Bray-Curtis dissimilarity measure (Quinn et al. 2002). Further, ANOSIM was used to check the mean rank dissimilarities between both age and sex classes differed from within group dissimilarities (Quinn and Keough 2002). All statistical analyses were performed using R statistical language V3.4.1 with R Studio IDE for R V1.0.143. I used 'vegan': Community Ecology Package, Vegan 2.4-3 for nMDS and ANOSIM (Oksanen et al. 2015).

To assess the differences in behavioral repertoire among immatures and subadults, I collected sequence of behaviors for each type of coconut. For this each behavioral act was differentiated and coded based on type of behavior (Pluck, Process, Carry, Drink, Eat), use of body parts (Hands, Legs, Mouth) and function (strike, bite, scrape, rip, pull, hold). A total of 32 unique behaviors were identified. I assumed that transition between these behaviours will follow single order Markov chain. Markov chain transitional frequencies have been used to assess efficiency of behaviours such as social grooming in Japanese macaques (Espitia-Contreras et al. 2020), and foraging in lizard species (McElroy et al. 2012). To employ the same technique I developed transition probabilities using package 'markovchain' (Spedicato 2017) using Laplacian smoothing parameter. Transition matrix for immatures and adults were created separately for each coconut type. These matrices were plotted as flowchart using plot function provided by package.

Table 5.3. Description of coconut processing behaviours and left-over coconut stages:

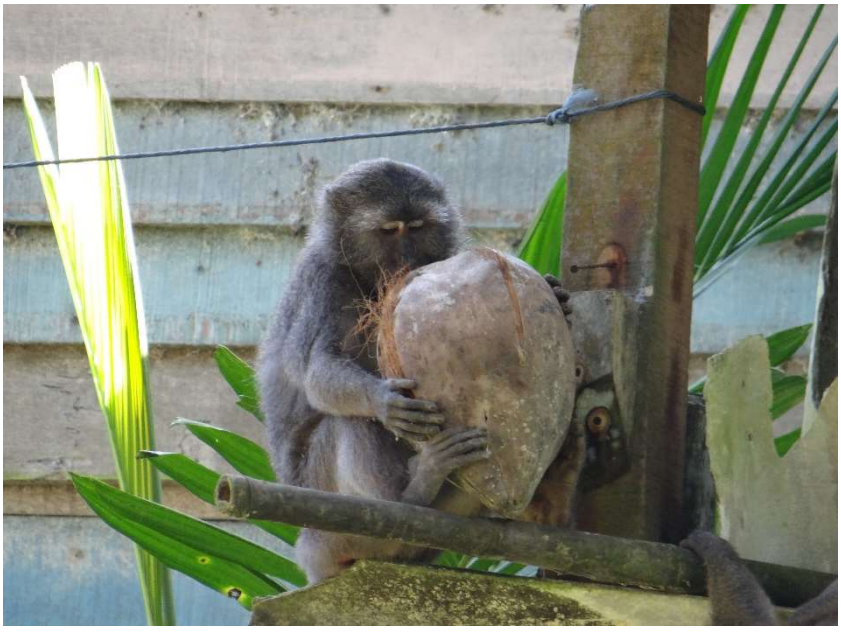
Activity	Code	Description
Pluck	**IT**	Stalk intact on tree after unsuccessful plucking attempt
	PC	Cut by teeth
	PCR	Cut by using both PC and PR process
	PR	Cut by rolling
Process	**BHH**	Holding with both hands and husking by mouth
	BHLH	Holding with both hands and both legs and husking by mouth
	CBH	Carry with both hands
	CH	Carry with one hand
	CM	Carry with mouth
	DHC	Drag by one hand
	EBE	Bite eye to make an opening while holding with both hands and one leg
	HLH	Holding with both hands and one leg and husking by mouth
	SEFB	Strike on hard surface with both hands
	WB	Wipe with leaf or twig with both hands
	WH	Husking with hand while holding with another hand and one leg
Drink	**BHD**	Lift with both hands
	HD	Tilt with one hand over substrate
	HLD	Lift with both hand with support of one leg
	HST	Lift with both hands while standing upright
	MD	Put mouth in the opening while holding with both hand over substrate
	SD	Put one hand in the opening and splash water into mouth while holding with another hand
Feed	**EE**	Eat from eye with one hand
	EH	Scrap with one hand while holding with other
	SH	Scrape by teeth while holding with both hands
	THE	Scrape by teeth while holding with both hands and one leg
End	**ACF**	Unable to repossess accidental dropped
	AD	Accidental dropped but not retrieve
	C	Completely eat and/or drink flesh and/or water
	LG	Left coconut and join moving group
	NS	No success in eating
	RL	Snatched by other individual and not retrieved
	UL	Incompletely eaten



(Sequence of adult male FY using both hands and mouth (BHH) to dehusk tender coconut)



(Tender coconut manipulated intact on tree without plucking (IT))



(Sub-adult female feeding on dry coconut)

5.3 Results

The macaques of the TR group were found to feed on coconut in 279 scans (21.15%) out of the total 1319 feeding scans. The mean proportion of coconut feeding by individual macaques in the group was $0.21\pm0.03_{SD}$, where coconut feeding by male and female were $0.23\pm0.03_{SD}$ and $0.18\pm0.02_{SD}$, and adult and immature were $0.19\pm0.04_{SD}$ and $0.22\pm0.02_{SD}$ respectively (Fig 5.1). Males fed significantly more coconuts than females (t = -3.48, df = 11, P = 0.005), however, proportion of coconut feeding did not differ between adults and immature (t = -1.81, df = 11, P = 0.09).

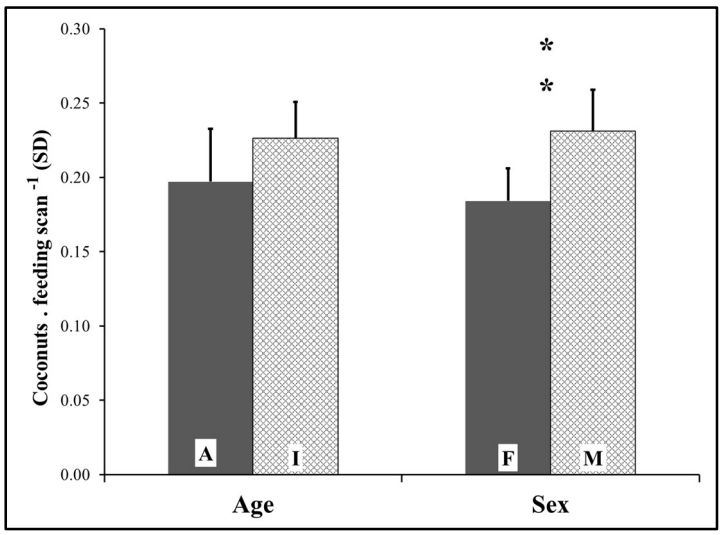


Figure 5.1. Mean proportion of coconut feeding proportion: coconut feeding per respective feeding scans different age-sex macaque individuals (A- adult, I- immature, F- female, and M-male).

Macaques fed on coconut water, coconut flesh/copra (endosperm) and oily cotyledon from different stages of coconuts using 25 distinct manipulative techniques. These techniques were segregated in to four categories as pluck, process, drink and feed (Table 5.3).

Description of coconut feeding behaviour

Macaques procured tender (T), mature (M) coconuts from the tree and the fallen dry coconut (D) from the ground. After choosing the coconut in the tree, macaques plucked the coconut by teeth and hand, or fed without plucking from the tree. The plucked coconuts were either processed on the tree or were carried to the ground by their hand/s and mouth. Macaques de-husked the exocarp and mesocarp of coconut by using teeth and hands and legs. Macaques bit

one terminal of the coconut and tore out fibrous mesocarp by using their hands or mouth while using other limbs to secure coconut during husking. This process was repeated until the hard endocarp was exposed. In tender coconuts, after partial husking, the exposed endocarp was opened by canines. They drank the coconut water through the opened portioned by holding the fruit by both hands and legs; or used one hand to splash water into the mouth while supporting it with the other hand. After drinking the coconut water, soft endosperm was scooped out and eaten with one hand, while other hand and legs were used to support or position the coconut. Sometimes, macaques again husked the tender coconut to widen the opening.

Mature and dry coconuts were de-husked completely. Macaques employed two approaches to extract the endosperm and water. Macaques used their fingers and canines to make a hole through eye (functional pore) of the coconut and drank coconut water through the hole by holding the pore above mouth. They scraped the endosperm by inserting fingers and/or canine into the pore. Secondly, macaques pounded the completely de-husked coconut using both hands on a hard surface such as paved ground or tree trunk by standing on the legs. Pounding was done until a fissure was formed in the shell. They drank water by holding the fissured portion over the mouth by hands and one of the legs. They again pounded the coconut or used their canines to break the endocarp completely. Finally, they ate the endosperm by scraping it with hand or teeth while other limbs were used for support. Often macaques were observed to leave the de-husked coconut after partial processing which were later re-processed similarly as dry coconut. Those complete de-husked coconuts were described as dry de-husked (DD) coconut. Macaques were observed to use leaf, branch, paper, cloth or plastic bags from the vicinity and wrap them over the de-husked coconut. They were also seen to break twigs from plants and wrap it over coconut. After wrapping coconut with such materials, they wiped coconut by rubbing it with hands or rolling it on the ground. In some cases, macaques were observed to bite the functional pore while it was wrapped.

The different coconut types (described in Table 5.2) were not chosen equally by the macaques ($F=8.16$, $df=3$, $p < 0.001$) as TR group more fed on tender coconuts ($0.51\pm0.41_{SD}$) than mature ($0.21\pm0.26_{SD}$), dry coconuts ($0.04\pm0.11_{SD}$) and dry dehusked coconuts ($0.22\pm0.19_{SD}$)(Table 5.4). Descriptive statistics for coconut choice and feeding success for each coconut type and age-sex classes were tabulated (Table 5.4). Overall, mean proportion of choosing coconut for age and sex classes did not vary however was higher for tender coconuts (0.47-0.66), while that for dry coconuts was least (0.04-0.11). Similarly, feeding on tender coconuts was always successful, proportion of success for other coconut types showed high variance between age

and sex classes (0.0-0.57) (Table 5.4). Two-way ANOVA test did not reveal significant difference in coconut choice and feeding success between age and sex classes (Table 5.5) However, pluck pattern (Table 5.5) varied between immature and adults. Immatures fed on coconuts without plucking them from the parent tree while adults plucked coconuts by cutting with teeth (Fig 5.2).

Table 5.4. Descriptive statistics of coconut choice, and feeding success between different coconut types and age-sex classes (*<0.001p).

	T	**M**	**D**	**DD**
Coconut choice				
Overall	0.51 (±0.41)	0.21 (±0.26)	0.04 (±0.11)	0.22 (±0.19)
Male	0.60 (±0.26)	0.18 (±0.08)	0.11 (±0.03)	0.28 (±0.13)
Female	0.50 (±0.18)	0.28 (±0.15)	0.10 (±0.01)	0.20 (±0.06)
Adult	0.47 (±0.03)	0.3 (±0.13)	0.07 (±0.01)	0.26 (±0.08)
Immature	0.66 (±0.27)	0.15 (±0.07)	0.10 (±0.03)	0.20 (±0.14)
Feeding success				
Overall	1.00 (±0)	0.80 (±0.32)	0.62 (±0.33)	0.17 (±0.24)
Male	1.00 (±0)	0.28 (±0.57)	0.11 (±0.19)	0.42 (±0.28)
Female	1.00 (±0)	0.96 (±0.32)	0.25 (±0.33)	0.79 (±0.28)
Adult	1.00 (±0)	1.00 (±0)	0.81 (±0.35)	0.25 (±0.21)
Immature	1.00 (±0)	0.50 (±0.34)	0.11 (±0.19)	0.29 (±0.21)

(Coconut types T- Tender, M- Mature, D- Dry, DD – Dry dehusked)

Table 5.5. Variation in coconut choice, pluck pattern and feeding success between different coconut types and age-sex classes (*<0.001p).

Factors	**Coconut Choice**			**Pluck pattern**			**Feeding success**		
	df	F	p	df	F	p	df	F	p
Coconut type	3	16.17	<0.001*	3	8.16	<0.001*	3	7.3	<0.001*
Age	1	0.05	0.83	1	0.02	0.88	1	0.01	0.92
Sex	1	0.5	0.49	1	0.01	0.91	1	0.03	0.87
Coconut type: Age	3	2.6	0.07	3	15.35	<0.001*	3	0.88	0.46
Coconut type: Sex	2	0.72	0.5	3	2.48	0.08	3	0.98	0.41

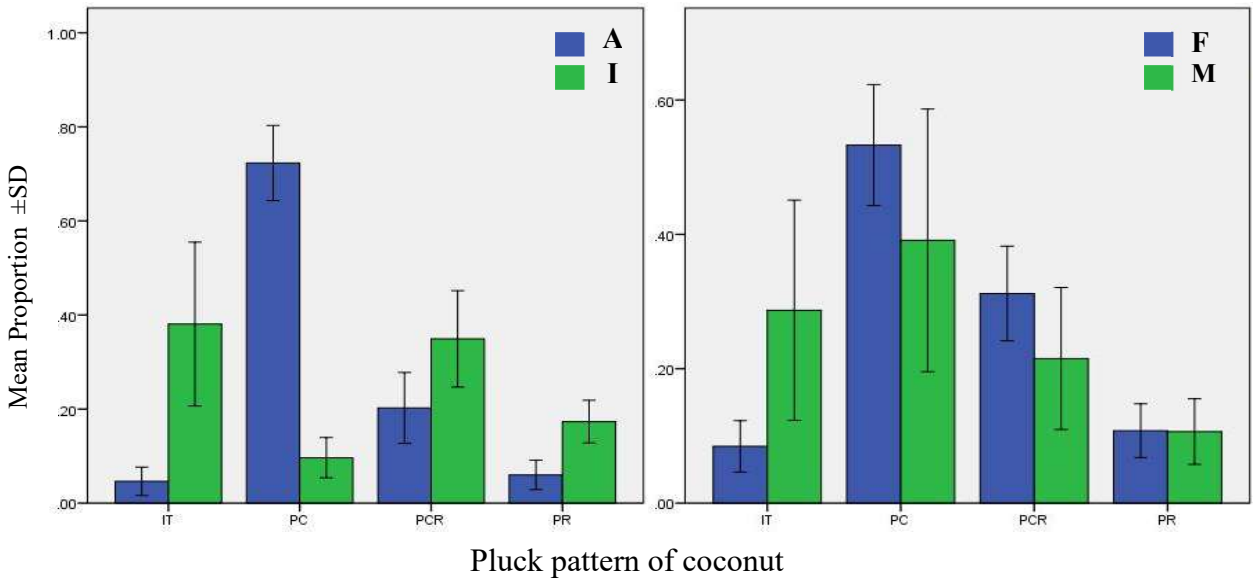


Figure 5.2. Mean proportion of coconut plucking pattern between different age-sex classes (A- adult, I- immature, F- female, and M- male, IT- Intact, PC – Cut by teeth, PR- Cut by rolling, PCR- cut using PC and PR).

Two dimensional nMDS performed for dissimilarities in behavioral diversity for coconut manipulation (Table 5.3) showed age-wise segregation in individuals (Fig. 5.3), while male and female individuals didn't group separately (dissimilarities = Bray – Curtis, stress = 0.104, non-metric R^2 = 0.98). Further, ANOSIM performed between ages revealed that adults and immature were significantly dissimilar in their behavioral repertoire in processing coconuts (R = 0.52, P = 0.01). Although ANOSIM between sexes indicated more within group variation among males and females than between group (R = -0.072, P = 0.72).

Markov chains for dry, mature and tender coconuts by adult and immature showed differences in behavioural transitions (Fig. 5.4). For dry coconuts (D), adults transitioned between 16 distinct behaviours while immatures used 14 behaviours. Adults can be seen to transition between feeding and drinking behaviours and processing behaviours (EH and BHD to BHLH and BHH, SH and HLD to EBE) while immatures displayed fewer transitions to feeding and drinking behaviours. Immatures showed fewer transitions from feeding behaviours back to processing behaviours (N=4, SD to BHH and BHLH, EBE to SFEB and WB). Adults showed tendency to bite coconut eye (EBE) after feeding and drinking behaviours (HLD, EH, SH) and other processing behaviours such as wrapping and husking (WB, HLH, BHLH). Immatures displayed only two drinking (HST, MD) and one feeding behaviour (EE) while adults used two drinking (HLD, MD) and four feeding (EE, EH, SH, THE) behaviours.

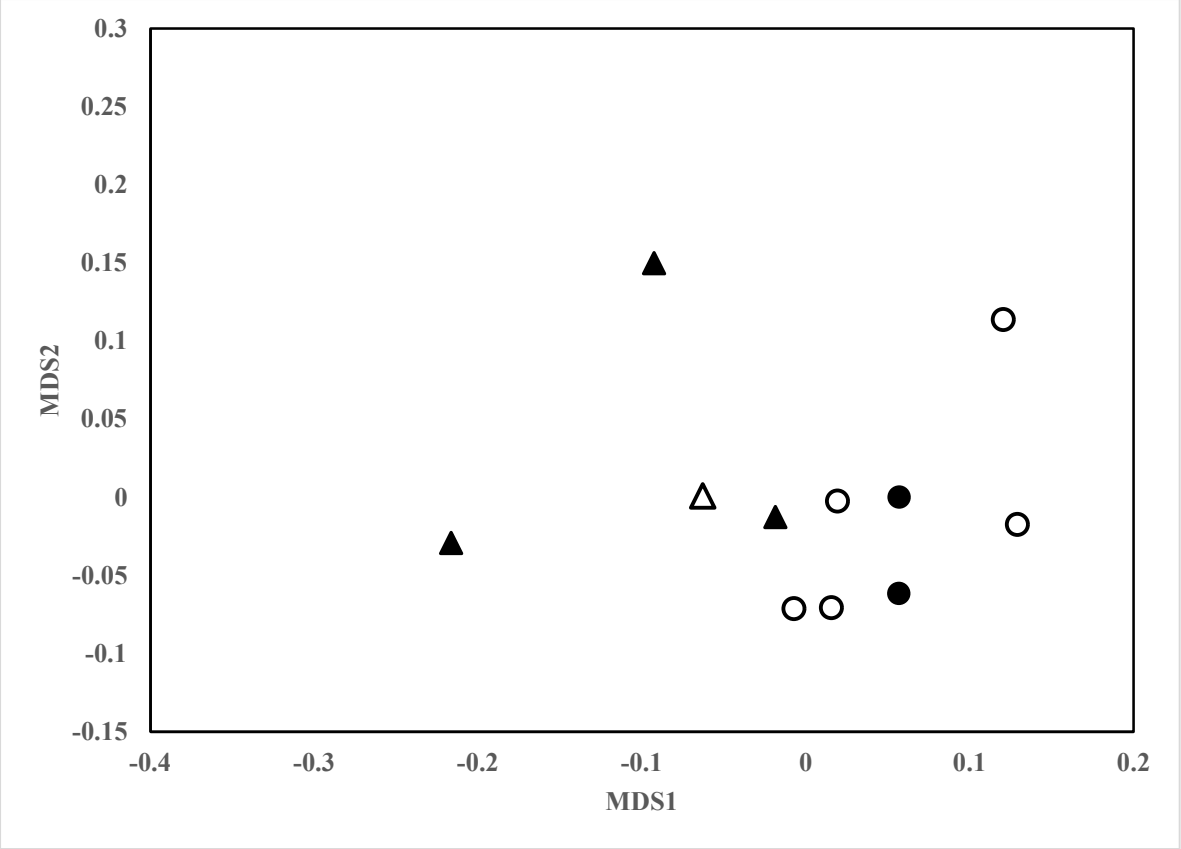


Figure 5.3. Ordination plot of nMDS showing age wise segregation in coconut processing behaviours with dots representing adults, triangles representing immature, solid marker showing male and hollow markers as female individuals.

Similarly, for tender coconuts immatures showed lesser tendency to transition from feeding behaviours to processing behaviours. Many processing behaviours (WH, BHH, HLH, BHLH) transitioned to feeding with hand (EH) and drinking behaviours (MD, SD). A similar pattern is evident in adults except they show more transitions from feeding and drinking behaviours to processing behaviours (EH to HLH, BHLH and BHH, HLD to HLH and BHH).

For mature coconuts, immatures and adults showed fewer transitions. Some behaviours were exclusive to the age such as immatures used dragging (DHC) with one hand to carry coconut and HLD and MD were seen only in adults.

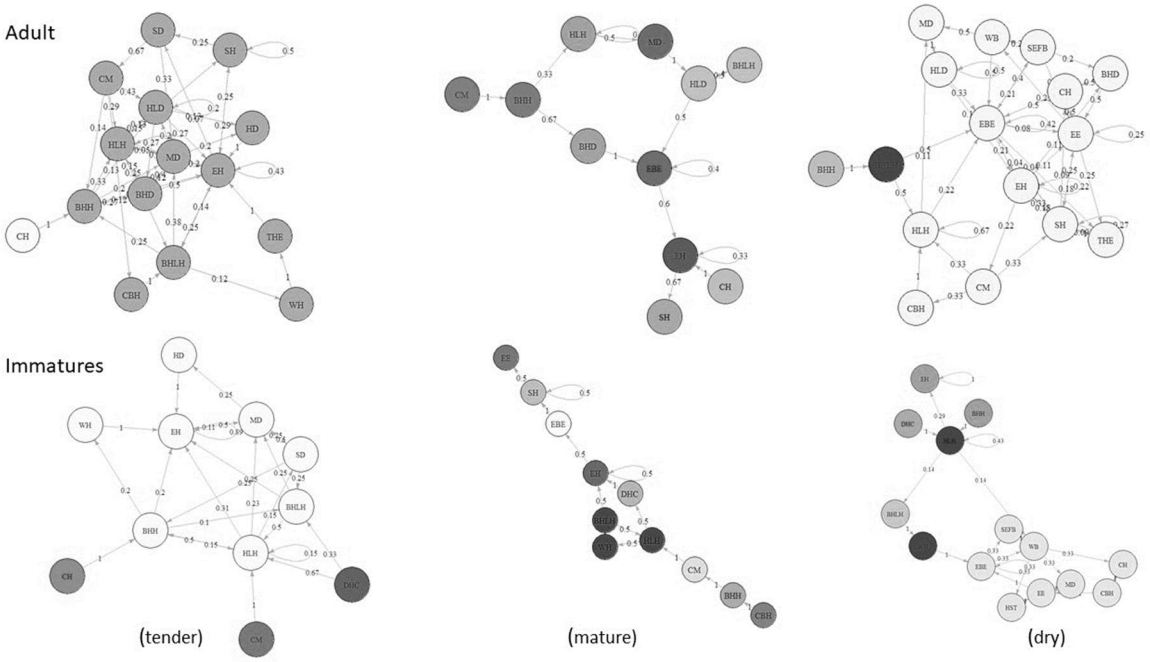


Figure 5.4. Markov chain transition diagram showing transitional probabilities between behavioural states used by macaques to process, feed and drink coconuts

5.4. Discussion

The results from the study discerned three major patterns i.e., 1). females significantly fed on less coconuts compared to males despite showing equal proficiency in manipulation of all coconut types, 2). although immatures and adults used same behavioural units for coconut manipulation, but they differed in transition between them, and 3). there was no visible ontogeny or model behaviour for coconut manipulation towards which individuals were seen converging to. These observations, considering social organization within and between groups (Velankar et al. 2016; Pal et al. 2018a), corroborates with current understanding of behavioural diffusion among primates.

Differences in coconut manipulation between sexes: Differences between sexes in object manipulation and tool use have played crucial role in emergence of division of labour in human evolution (van Schaik et al. 1999). Sexual dimorphism and differences in physical capabilities arises in species at developmental stages, e.g., male and female *M. mulatta* are differentially exposed to hormones in perinatal conditions (Bachevalier and Hagger 1991). Differences in sociality along with sexual dimorphism were found to be responsible for sex differences in nut cracking efficiency among chimpanzees (Boesch and Boesch 1984). Such differences in tool

use strategies due to different energy requirements have been observed in long-tailed macaque (Gumert et al. 2011). The less feeding on coconut by a *M. f. umbrosus* female may be a strategic choice rather than lack of proficiency. Coconut manipulation involves more energy costs for females than males due to which females might less feed on the coconuts.

Age wise differences in coconut manipulation: The age specific behaviour can be attributed to differences in the physical capabilities like immatures unable to lift and carry entire coconuts, thus often dragged them on the ground. Immatures manipulated more coconuts without plucking or used combination of bite and roll to pluck the coconut from the tree, while adults plucked the coconut with less effort due to their physical prowess. There were also major differences in transition between processing, feeding and drinking among adults and immatures. Adults often utilized the coconuts by reprocessing it more than immatures.

Presence of same unit behaviours for coconut manipulation in both the age classes also alludes to high diffusion rate of these behaviours within group. Transmission rate of behaviour depends upon social organization, gregariousness (Fagen 2002; van Schaik et al. 1999) and presence of enhanced stimulus (Visalberghi and Fragaszy 1994; Zuberbühler et al. 1996). This study group is socially tolerant (Mishra et al. 2020b, Mishra et al. 2020c), increased coconut crop depredation by other groups after 2004 Indian ocean Tsunami (Mishra et al. 2020a), and highly contested home range with neighbouring groups (Pal et al. 2018b), allude to gregarious nature of the study group as well as presence of enhanced stimulus which facilitates young individuals to pick up coconut manipulation at early age.

These results show that behavioural repertoire between age and sex is not much different but differ in frequency of use of these behaviours. Among 25 behaviours 2 behaviours SFEB (Strike on hard surface) and WB (wipe with leaf or twig) involve active tool use. However, similar behaviours have been observed in other populations of long tailed macaques e.g., striking coconut on hard surface is very similar to use of stone hammers to open oysters and sea almonds (Falótico et al. 2017; Gumert et al. 2011; Gumert and Malaivijitnond 2012), and leaf washing (Wheatley 1988) in Bornean *M. fascicularis*. These geographically isolated populations showing similar behaviours indicate that source population of Nicobar Islands had these behaviours.

Non convergence of coconut manipulation behaviour pathway by all individuals may be the evidence of every individual learning by trial and error in presence of enhanced stimulus rather than imitation of model behaviour. It can be concluded that, although individuals gain

proficiency quickly across age and sex, efficient use of these behaviours depends upon age and sex of the individual.



(Coconut grove abandoned after tsunami)

6

Ranging Pattern and Habitat Use



Chapter 6:
Ranging Pattern and Habitat Use

6.1 Introduction

Habitat utilization of an animal depends upon many constraints such as spatial distribution of the resources, its quantity and quality, intra-inter specific competitions, and physical limitations of the animal to extract the resources. Animals have to cope with all these constraints to keep the costs incurred by them as low as possible. Through evolutionary processes, animals have developed various adaptive strategies which help them to maximize their gains. The constraints mentioned above allude to animal movement to be a deterministic process rather than random. The traditional definition of home range is described as an area traversed by an individual in its natural activities (Burt 1943). However, this definition was found inadequate to explain the spatio-temporal dynamics of an animal or delineate boundaries effectively (Kie et al. 2010). With the advent of tracking and computation and GIS, it was possible to study nuanced relationship animal has with its surroundings. To incorporate these techniques, Powell (2000) defined home range as the cognitive map, or the area animal knows and remembers for its value. This definition allows us to study home range as a mechanistic function of the spatial distribution of resources, competition, seasonal variation, and disturbance, which can be statistically tested.

To understand cognitive maps of group-living primates, researchers have used various techniques such as minimum convex polygon (MCP) (Bonadonna et al. 2020; Chen et al. 2015), Kernel Density (Patzelt et al. 2014), Grid use (Boyle et al. 2009; Grueter et al. 2008) and Daily Path Length (DPL) (Kumar et al. 2015). These techniques help us to examine spatio-temporal variations in ranging patterns.

Changes in diurnal activity due to environmental, physiological or social limits manifest as variations in ranging patterns within and between primate species. Lion-tailed macaques were reported to use regions with high fruit availability and shifted their home range accordingly during wet and dry seasons (Santhosh et al. 2015). Similar results were reported in red colobus (*Colobus badius*), where time spent in the area correlated with the availability of food resources (Clutton-Brock 1975). Seasonal shrinkage in home range size was observed in Japanese macaque (*Macaca fuscata*) due to the availability of supplemental food during tourist season(Koganezawa and Imaki 1999). Just like within-group scramble competition affects ranging patterns (van Schaik et al. 1983), between-group competitions have also been observed

to play an important role. Nilgiri langurs were observed to shift their home range to avoid between-group encounters (Kavana et al. 2014). Availability of food also influences tolerance between neighbouring groups. Japanese macaque (*Macaca fuscata*) was reported to have more overlapping home ranges in resource-rich areas than resource-poor areas (Maruhashi et al. 1998).

In this study, I attempt to understand the spatial cognitive ability of *M. f. umbrosus* through the intensity of grid use and analysing variation in Daily Path Lengths.

6.2 Methods

6.2.1 Study site and study group: The study was conducted at Campbell Bay, Great Nicobar Island (Fig. 6.1). The study site includes a mosaic of natural as well as human-altered land cover types. The coastal region of the study area is dominated by littoral forest with extensive patches with *Pandanus spp* and intermittently mixed forest. The inland region contains human habitation and plantations of coconut (*Cocos nucifera*) and beetle nut (*Areca catechue*) (Sinha 1999; Velankar et al. 2016). Human habitation consists primarily of small single-story households with small orchards intermittent with open and dense secondary scrub vegetation. This region is dominated by introduced vegetation comprising of banana (*Musa paradisiaca*), Guava (*Psidium guajava*), Mango (*Mangifera indica*). The altitude of the study area ranges from 0 m MSL to 218 m MSL. The study area receives an annual rainfall of about 3200 mm. A significant portion of rainfall is received between May to November, where December to April remains relatively dry. I selected the group (TR) located at Campbell Bay as the focal group for the current study owing to its accessibility to follow compared to other groups (PI, MG, LB and MA). During the study period, groups PI and MA were also observed to use the same habitat as that of the focal group (Fig 6.1).

6.2.2 Data collection: The study group (TR) was followed from dawn (0600 hrs) to dusk (1800 hrs). I recorded the geo-coordinates of visually approximated group centre using a handheld GPS receiver (Garmin GPS Map 76csx) at 30 min intervals (Altmann 1974). During study period groups. Overlap of the home range of TR with PI and MG was obtained using data on between-group encounters (Pal et al. 2018c).

Data on vegetation in each grid cell using quadrat sampling was collected to determine the governing factors for grid use. Details of tree, shrub and herb species were collected in nested circular quadrats (10m: trees, 5m: Shrubs, 1m: Herbs) (Newton 2007).

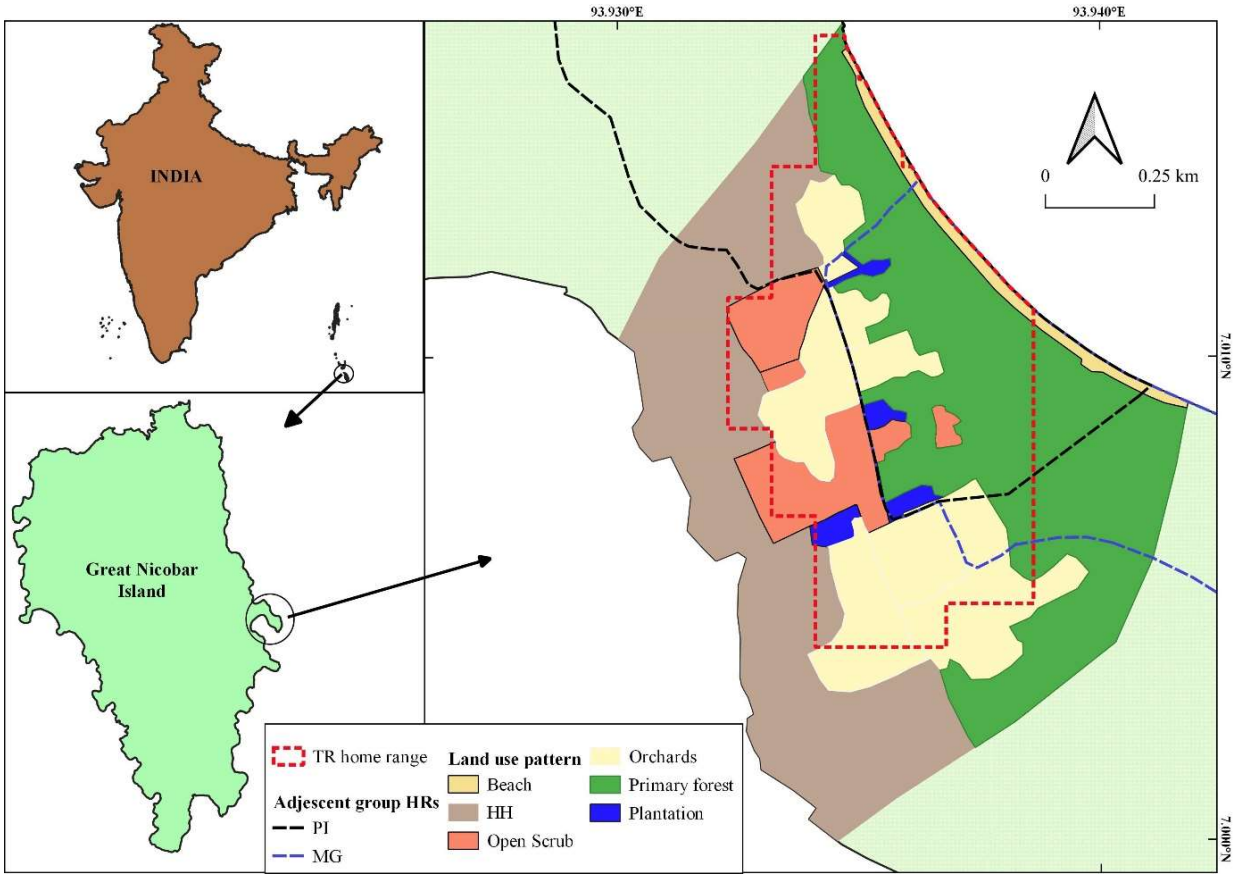


Figure 6.1. Map of study sites in Campbell Bay region with the home range of study group (TR)**.**

6.2.3 Analysis: Group locations were converted as shapefiles. Points for each day of the following were connected to obtain daily paths. Complete follows from dawn to dusk were used to estimate daily path length. Distance between 2 consecutive observations was taken as step length. Step lengths less than 20 meters were truncated from the data set to compensate for the group spread.



(Human Habitation with small orchards)



(Beach)



(Human habitation with Coconut plantation)



(Primary forest: *Pandanus spp*)



(Primary Forest: Mixed Littoral Vegetation)

The study area was overlaid with a vector grid of 100 m X 100 m cell dimensions (Santhosh et al. 2015). The frequency of grid cell use was computed by counting the number of point locations within a grid cell. The frequency of use of grid cells was calculated separately for wet and dry seasons. The frequency was converted to proportions by dividing the number of points within a grid cell by the total number of points recorded during each season. The study area was classified into six broad land cover types as habitats viz. Beach, Household, Orchards, Primary Forest, Open scrub and Plantation. The spatial availability of each habitat type was estimated as the proportion of habitat type within the area of each grid cell.

Variation in intensity of grid use between seasons was compared using non-parametric Wilcoxon's signed-rank test. Similarly, to test if the group used the same grids during different seasons, McNemar's chi-square test was employed (Quinn et al. 2002). To assess variations in spatial availability of habitat types within each grid cell, one-way ANOVA was employed, and comparisons between classes were made by Tukey's posthoc test of honest significant difference (HSD). To check the association between the intensity of grid use and the proportion of each habitat type available, Pearson correlation was used.

Tree density and food species density was calculated for each grid. Similarly, proximity from human settlements, home range overlap with other groups and the number of between-group encounters observed in each grid were also taken as explanatory variables. To test the influence of these covariates on the grid-use pattern, GLM was performed.

All statistical analysis was carried out using R statistical language V 3.02 with R Studio IDE for R v0.98.953. To prepare land-use and landcover maps as well as extract information of ranging, GIS package QGIS v 2.13 was used.

6.3 Results

The spatial availability of all the habitat types within each grid cell differed significantly ($F_{5, 390} = 19.11$, $P < 0.001$). The mean spatial availability of Primary Forest (0.39 ± 0.40 SD) and Orchards (0.32 ± 0.38 SD) was significantly higher than that of other habitat types (Fig 1). The overall proportion of each habitat type within the home range was 2.9% for Beach, 7.7% for households, 14.0 % for open scrub, 33.7 % for orchards, 38.5% for primary forest and 3.1% for plantation (Fig 6.2).

However, Pearson correlation between habitats and proportion of grid use shows no significant association between all habitats and intensity of use, except plantation, which shows weak but significant association (Table 6.1).

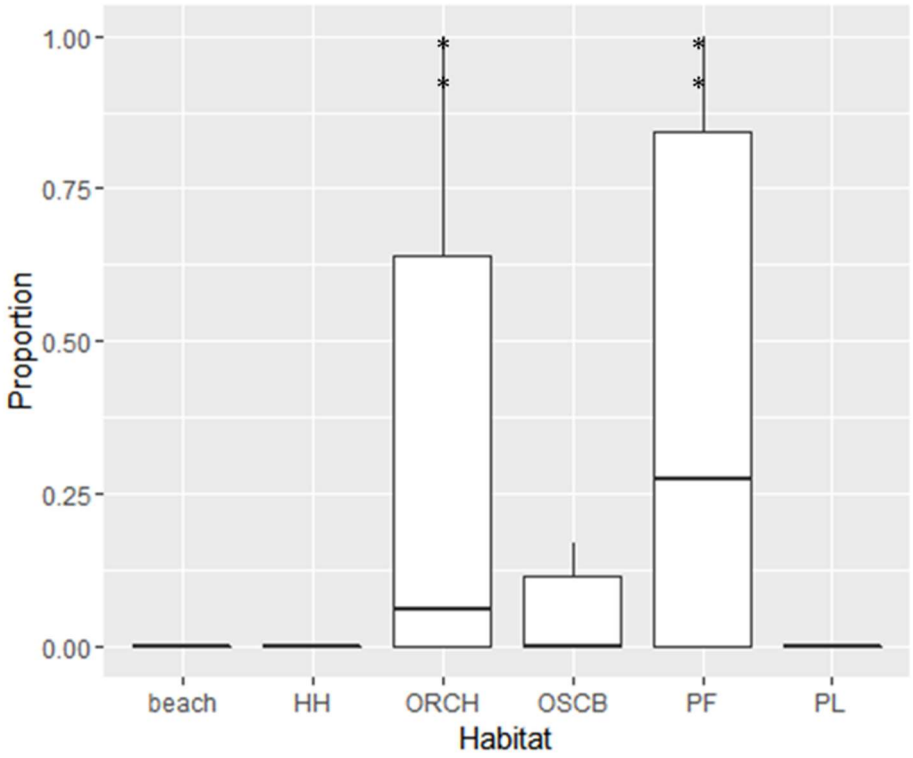


Figure 6.2. Proportion of habitat type in the grid cells within the home range of study group Nicobar long-tailed macaque. HH = Households, ORCH = Orchards, OSCB = Open Scrub, PF = Primary Forest, PL = Plantation. ** Tukey HSD test Padj<0.001

Table 6.1. Pearson's product-moment correlation between the intensity of grid use by *M. f. umbrosus* group TR and habitat types available in Campbell Bay, GNI.

	Beach	Households	Open Scrub	Orchards	Primary Forest	Plantation
Correlation coefficient	0.161	-0.164	-0.140	-0.10	-0.12	0.344
P	0.192	0.186	0.263	0.931	0.923	0.005

A total of 830 group locations (Dry N = 357, Wet N = 473) were collected during the study period, spread over in 66 grid cells. Of 66 grids, only six grids were used for > 7 % of observations (Fig 6.3). The intensity of grid cells uses did not vary significantly between wet

and dry seasons (Wilcoxon signed-rank test: V= 969, P = 0.69). However, the number of grid cells used by the group between seasons differed significantly (McNemar's: χ^2 = 16.36, p< 0.000).

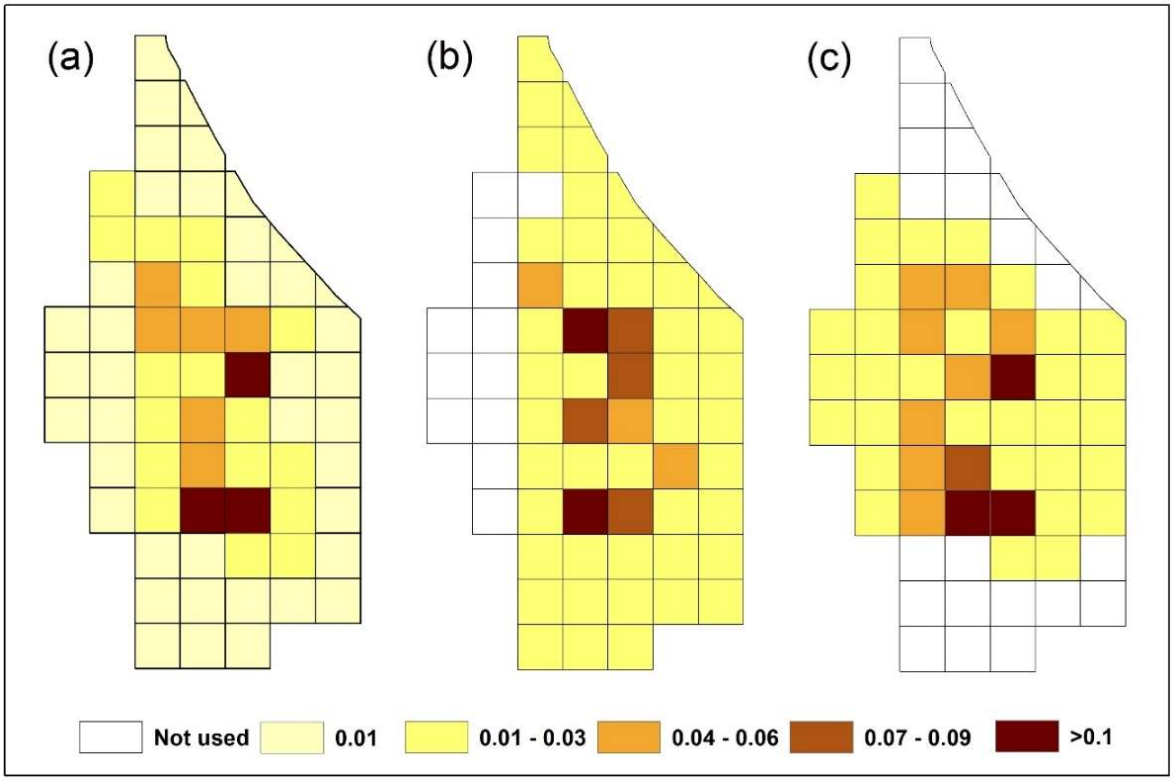


Figure 6.3. Proportion of grid cells used by the study group TR in, a. overall study period, b. the dry season, c. wet season.

Table 6.2. Seasonal variation in daily path length (DPL) by TR.

Season	N	Range	Mean (± SD)	**T test**
Dry	27	712.82-1280.41	916.13 (±121.79)	t = -2.3546, df = 46.221, p < 0.05
Wet	30	704.18 – 1336.76	1025.40 (±219.35)	
Overall	57	704.18 – 1336.76	973.64 (±186.63)	

GLM was run with grid-use as a response variable and predictors. Model was significantly explanatory when compared with null model (Residual deviance = 913.19, Null deviance = 1642.58, DF = 65, residual DF =61, p<0.0001). The model showed the affinity of the group to grids with overlapping home ranges of adjacent groups. Group also did not avoid the area with frequent between-group encounters (Table 6.3).

Table 6.3. Influence of covariates on the intensity of grid use by *M. f. umbrosus* in Campbell Bay, GNI.

Grid Use ~ HR Overlap + BGE + Tree Cover + Food Tree Density				
Predictor	**B**	**SE**	**Walds Z**	**P**
Intercept	1.462	0.104	13.965	<0.0001
Home range overlap	0.724	0.120	6.050	<0.0001
Between group encounters	0.240	0.010	23.724	<0.0001
Tree cover (%)	0.034	0.166	0.027	0.836
Food tree density	-0.903	1.078	-0.837	0.403

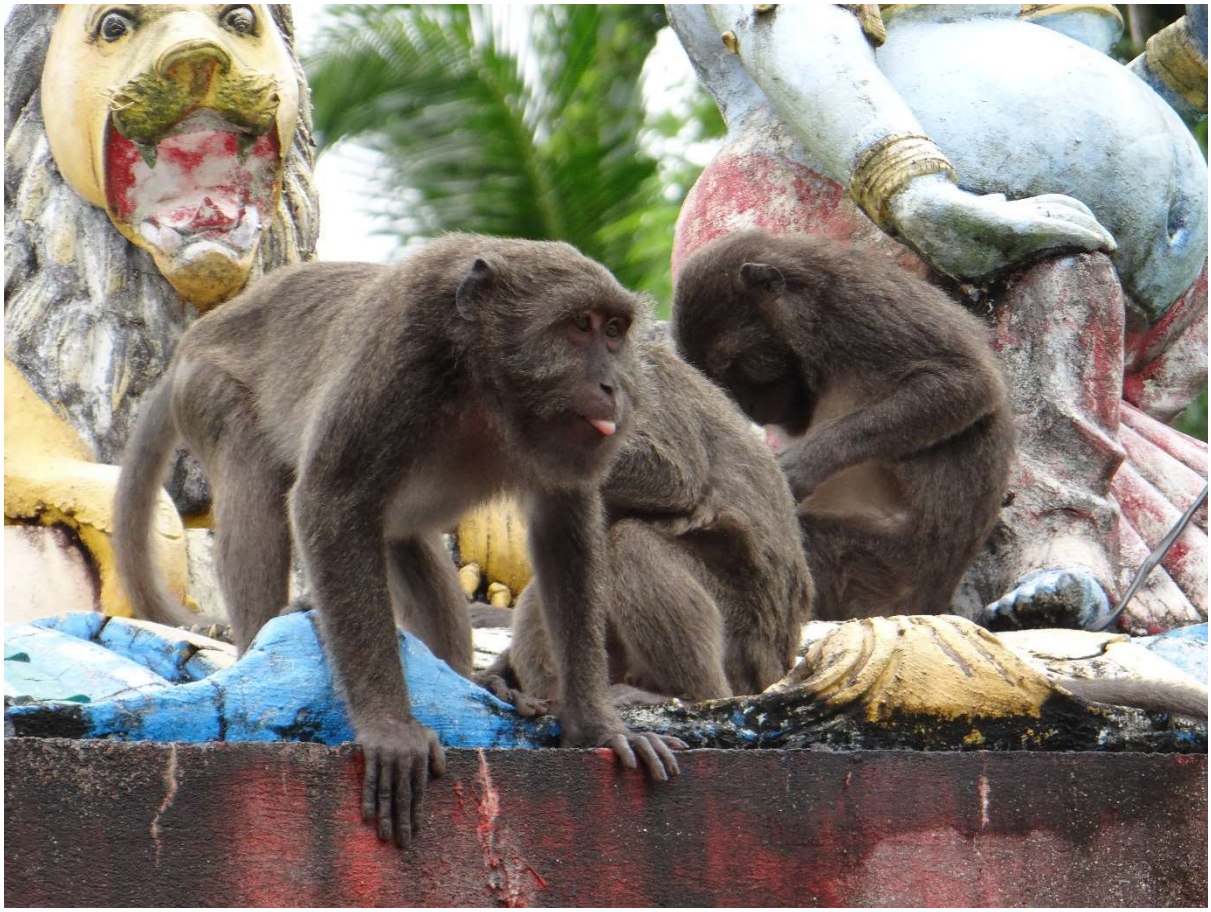
6.4 Discussion

The study group being a partial commensal, spends time feeding on food resources from orchards and plantations, which may result in the acquisition of low-cost, high-energy food and an increase in resting time. Similar observations were reported in rhesus macaque *M. mulatta* (Jaman and Huffman 2013). Provisioned groups of *M. fascicularis* in Vietnam were observed similarly to spend 31.60% to 36.83% of time resting, which again was the most common activity (Son 2003).

Group was observed to feed on 25 food resources, of which four were most common viz. Coconut 27.0-27.0%, banana 11.9 – 9.3%, guava 18.6-19.0%, Pandanus spp. 10.2-8.6%. Among them, three resources were from orchards and plantations in human habitation and available throughout the year. Primary forest and orchards spatially cover most of the total area (72.2%). Yeager (1996) reported similar findings from Kalimantan Tengah, Indonesia. There the long-tailed macaque exploited 33 plant resources, of which five were most frequent in their diet. This indicates the generalist nature of the species, as in both the studies, macaques utilized the most abundant and thus low-cost resource first. Due to this high dependency on perennially available food sources, the group did not exhibit seasonality and most heavily used grids, or core home range remained unchanged between seasons. However, they were observed to utilize more grids, especially littoral patches, to feed on pandanus, available during the dry season. Despite using significantly fewer grids during the wet season, daily path length remained similar to dry.

GLM analysis shows that between-group competition and not food availability was the most influencing factor on grid-use by *M. f. umbrosus*. Study group TR was among the smallest compared to the neighbouring group PI and MG, having massive handicap during aggressive encounters (Pal et al. 2018c). Hence affinity of study group towards home range overlap and

between-group encounters seems apparently counter-intuitive. However, it can be explained due to the following reasons. Schaik et al. (1983) showed that daily path length increases with group size due. This is due to individuals in a group attempts to reach intact foraging patches, and larger groups move often and spend less time in a patch. Conversely, a smaller group will deplete the patch at a much slower rate and will not be influenced by 'the pushing forward effect'. This may have allowed smaller group TR to utilize the smaller patches within home range overlap more efficiently. Also, resource requirement by smaller group is lesser enabling them to exploit smaller patches which larger groups cannot.



Conclusion

- Islands host a stable population of the species. Population recovered after sharp decline, but age-sex ratios are skewed.
- Resting, Feeding and Movement were the most common activities and time activity budget did not vary between dry and wet season.
- Macaques were observed to be primarily frugivorous and coconut, guava and pandanus were found to be major source of food.
- Though 90% diet was plant based, macaques also opportunistically fed on insects, reptiles, eggs and processed food from municipal solid waste.
- Coconut being most abundant and high energy food source, macaques have developed complex manipulation behavior to forage on coconuts efficiently.
- Macaques were observed to use combination of 25 distinct behaviours for plucking, processing, drinking and feeding on 3 types of coconuts (tender, mature and dry).
- Males and Females were found to be equally proficient in coconut manipulation but there was significant difference between immature and adults.
- During study period, the study group of macaques occupied 66 ha. Of these six hectares were used majority of the time. Plantation was found to be preferred habitat type for the macaques.

7

Summary



Chapter 7:
Summary

The observational study is the only tool that helps us study a species in its natural environment without affecting ecological processes. Observations of a species start from the most basic recording presence/absence and social organisation of a species to observing behavioural acts for an individual. Each chapter of this study is at different observation levels involving an overview of population status across the distribution of *M. f. umbrosus*, assessment of activity budget, ranging pattern and feeding ecology of one group and case study on how individuals within group manipulate coconuts. Here, I highlight the broad outcomes of these observations at each level.

A population-level assessment was carried out using the same trail survey method followed by previous studies for unbiased comparison. Following the 2004 Indian ocean tsunami, a sharp population decline was reported. The current study shows increased population and positive intrinsic rate of change on all three islands indicating recovery. However, the population structure is significantly different from previous studies. An increased number of males per female and an increased number of immatures per female indicate changes in reproductive traits.

Further, the tsunami also destroyed coastal habitat and permanent changes in land use and land cover on these islands. However, *M. f. umbrosus* was observed to recolonize the coastal habitat and adapt to changed land-use patterns. This population recovery can be attributed to the effect of the tsunami being localized to coasts, leaving the inland population intact and behavioural plasticity and generalist nature of *M. f. umbrosus*. However, differential mortality favouring fitter individuals may have resulted in shuffling of individuals, which cascaded to intact inland population. Hence, although this study indicates population recovery, its stability cannot be ascertained. Population recovery was the result of the behavioural plasticity of the species. To study this behavioural plasticity, I studied resource utilization by *M. f. umbrosus*. Time, space, nutrition and mate are the primary resources for all living organisms. Individuals of species develop strategies to maximize the utilization of these resources as per their capabilities. In social species such as *M. f. umbrosus*, such capabilities vary between and within the group resulting in a myriad of strategies by individuals and groups. The range of these variations indicates the behavioural plasticity of a species. In this study, I discuss the behavioural

plasticity of *M. f. umbrosus* through observations on time-activity budget, feeding ecology and ranging pattern of a group inhabiting altered landscape on Great Nicobar Island.

Time activity budget was studied using instantaneous scan sampling carried out at regular intervals. Resting, Feeding and Movement were found to be the most common activities. Although most of the studies show movement or feeding as a primary activity, the amount of time spent on activity was found to be determined by group size, food availability, between-group competition and anthropogenic provisioning and disturbances. Food availability and group size determine how quickly a group will deplete a patch. Due to this, larger groups tend to move more to reach less depleted patches. For the focal group of the study, the patch depletion rate is low due to its small group size. Further, the activity budget did not vary between dry and wet seasons due to less seasonal variation in food availability.

The group was observed to utilize 26 different species as food during feeding and foraging bouts. Group was primarily frugivorous, depending upon fruits of coconut, guava and pandanus as a major food source. Although 90% of the diet was found to be plant-based, macaques also opportunistically fed on insects, reptiles, domestic fowl eggs and processed food from municipal solid waste. Apart from direct feeding, macaques were also observed to utilize seven distinct extractive foraging behaviours. Husking, pounding, leaf wrapping, hand washing and rubbing were used to manipulate hard to breach food items such as coconut, *Aegle marmelos* and Cashewnut. Bush beating was used to catch invertebrates. Macaques were also observed to use fibrous stems as floss to clean the teeth.

Coconut was one of the most abundant and high energy food sources for the focal group. For efficient utilization of this resource, macaques were observed to possess complex manipulation behaviour. Males and Females were equally proficient in coconut manipulation, but males were observed to feed on coconuts more often than females. Males and females showed similar coconut choice and coconut plucking techniques, but feeding success varied significantly. However, significant disparity was observed between adult and young individuals in coconut choice, plucking technique and success rate. Macaques were observed to use a combination of 25 distinct behaviours for plucking, processing, drinking and feeding on four types of coconuts (tender, mature, dry and dry dehusked). Adults showed a tendency to go back to processing behaviours from feeding and drinking behaviours than young ones. High availability of coconuts at every stage of manipulation result in the enhanced local stimulus. Further, the tolerant nature of the group aids in vertical and horizontal diffusion of behaviours within the

group. This may have helped to the manifestation of all individuals demonstrating the capability to manipulate coconuts.

Space use by macaques was assessed through observations of the intensity of grid use and daily path length. Macaques were observed to utilize 66 ha of the area as their home range during the study period. The intensity of grid use, as well as DPL did not vary between seasons. As discussed earlier, less seasonal variation in food availability can cause the lack of seasonal variation in the intensity of grid use and DPL. Further, home range overlap and between-group encounters were positively associated with the intensity of grid use. Although primary forest and home gardens were dominant habitat types in the grids, macaques primarily utilized grids with coconut plantations. Although the between-group encounter is a deterrent and should affect negatively to intensity of grid use, most of these encounters were localized to grids with plantations. Due to the availability of high-energy food, these plantations are highly contested areas resulting in home range overlap and between-group encounters. However, as neighbouring groups are larger than the focal group, they are subjected to the 'pushing forward effect' and tend to move quickly to less depleted patches. This gives more time for the smaller group to utilize these patches.

From these observations, it can be inferred that the *M. f. umbrosus* are capable of developing individual and group level strategies to maximize utilization of resources in a diverse landscape with recent anthropogenic alterations. The study group shows strategic utilization of highly contested plantations, extractive foraging behaviours used to manipulate cryptic food sources, broad food spectrum of 25 species from native as well as novel origins and mixed diet of animal and plant resources. Study on coconut manipulation behaviour also gives us insight into how novel behaviours can diffuse within the group. Although patterns of ranging, feeding ecology and activity budget are highly specific to the study group, they provide us with a window to comprehend the variability of these patterns in different groups occupying different habitats. *M. fascicularis* was found to be resilient in the past studies to calamities such as drought and fire. This study further emphasizes the role of behavioural diversity in species' resilience to natural disasters like a tsunami. These capabilities have enabled *M. fascicularis* to be one of the most widespread primates next to humans. It is the only species that has been listed in both IUCN Red List as vulnerable and the IUCN list of 100 worst invasive species. Current biodiversity collapse, also considered the sixth mass extinction, may adversely impact *M. f. umbrosus*. Still, overall, *M. fascicularis* will endure and eventually prevail the most significant calamity humans have subjected onto them.

8

References



References

Abegg, C., & Thierry, B. (2002). Macaque evolution and dispersal in insular south-east Asia. *Biological Journal of the Linnean Society*, *75*(4), 555–576.

Aggimarangsee, N. (1992). *Survey for semi-tame colonies of macaques in Thailand* (Doctoral dissertation, Mahidol University).

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, *49*(3), 227–267.

Andrews, H. V., Chandi, M., Vaughan, A., Aungthong, J., Aghue, S., Johnny, S., et al. (2006). Marine turtle status and distribution in the Andaman and Nicobar islands after the 2004 M 9 quake and tsunami. *Indian Ocean Turtle Newsletter*, *4*, 3–11.

Bachevalier, J. (1990). Ontogenetic Development of Habit and Memory Formation in Primates. *Annals of the New York Academy of Sciences*, *608*(1 The Developme), 457–484. https://doi.org/10.1111/j.1749-6632.1990.tb48906.x

Bachevalier, J., & Hagger, C. (1991). Sex differences in the development of learning abilities in primates. *Psychoneuroendocrinology*, *16*(1–3), 177–188.

Balakrishnan, N. P., Hore, D. K., & Dwivedi, R. P. (1989). Great Nicobar Biosphere Reserve Project Document 11. *Ministry of Environment & Forest, Govt. India, New Delhi, 70pp*

Beck, B. B. (1976). Tool use by captive pigtailed macaques. *Primates*, *17*(3), 301–310.

Berec, L., Angulo, E., & Courchamp, F. (2007). Multiple Allee effects and population management. *Trends in Ecology & Evolution*, *22*(4), 185–191.

Berenstain, L. (1986). Responses of long-tailed macaques to drought and fire in eastern Borneo: a preliminary report. *Biotropica*, 257–262.

Birch, L. (1948). The intrinsic rate of natural increase of an insect population. *The Journal of Animal Ecology*, 15–26.

Boesch, C. and Boesch, H. (1984). Mental map in wild chimpanzees: an analysis of hammer transports for nut cracking. *Primates*, *25*(2), 160-170.

Boer, C. (1989). Effects of the forest fire 1982-83 in East Kalimantan on wildlife. *FR Report*, (7), 1–7.

Bonadonna, G., Zaccagno, M., Torti, V., Valente, D., De Gregorio, C., Randrianarison, R. M., et al. (2020). Intra-and intergroup spatial dynamics of a pair-living singing primate, Indri indri: a multiannual study of three indri groups in Maromizaha Forest, Madagascar. *International Journal of Primatology*, *41*(2), 224–245.

Boyle, S. A., Lourenço, W. C., da Silva, L. R., & Smith, A. T. (2009). Home Range Estimates Vary with Sample Size and Methods. *Folia Primatologica*, *80*(1), 33–42. https://doi.org/10.1159/000201092

Brotcorne, F., Maslarov, C., Wandia, I. N., Fuentes, A., Beudels-Jamar, R. C., & Huynen, M.-C. (2014). The role of anthropic, ecological, and social factors in sleeping site choice by long-tailed Macaques (*Macaca fascicularis*): Sleeping Sites of Balinese Macaques. *American Journal of Primatology*, *76*(12), 1140–1150. https://doi.org/10.1002/ajp.22299

Burghardt, G. m. (2015). Creativity, Play, and the Pace of Evolution. In *Animal Creativity and Innovation* (pp. 129–159). San Diego: Academic Press. https://doi.org/10.1016/B978-0-12-800648-1.00010-3

Burt, W. H. (1943). Territoriality and home range concepts as applied to mammals. *Journal of mammalogy*, *24*(3), 346–352.

Carew-Reid, J. (1990). Conservation and protected areas on South-Pacific Islands: the importance of tradition. *Environmental Conservation*, *17*(1), 29-38.

Carpenter, A. (1887). Monkeys opening oysters. *Nature*, *36*(916), 53-53.

Chappell, J., Cutting, N., Tecwyn, E. C., Apperly, I. A., Beck, S. R., & Thorpe, S. K. S. (2015). Minding the Gap: A Comparative Approach to Studying the Development of Innovation. In A. B. Kaufman & J. C. Kaufman (Eds.), *Animal Creativity and Innovation* (pp. 287–316). San Diego: Academic Press. https://doi.org/10.1016/B978-0-12-800648-1.00010-3

Chiang, M. (1967). Use of tools by wild macaque monkeys in Singapore. *Nature*, *214*(5094), 1258-1259.

Chen, Y., Xiang, Z., Wang, X., Xiao, W., Xiao, Z., Ren, B., et al. (2015). Preliminary study of the newly discovered primate species Rhinopithecus strykeri at Pianma, Yunnan, China using infrared camera traps. *International Journal of Primatology*, *36*(4), 679–690.

Chevin, L.-M., Lande, R., & Mace, G. M. (2010). Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLoS biology*, *8*(4).

Chitale, V. S., Behera, M. D., & Roy, P. S. (2014). Future of endemic flora of biodiversity hotspots in India. *PloS one*, *9*(12), e115264.

Clutton-Brock, T. H. (1975). Ranging behaviour of red colobus (Colobus badius tephrosceles) in the Gombe National Park. *Animal behaviour*, *23*, 706-722.

Comins, J. A., Russ, B. E., Humbert, K. A., & Hauser, M. D. (2011). Innovative coconut-opening in a semi free-ranging rhesus monkey (Macaca mulatta): a case report on

behavioral propensities. *Journal of Ethology*, *29*(1), 187–189. https://doi.org/10.1007/s10164-010-0234-0

Cords, M. (1992). Social versus ecological intelligence. *Behavioral and Brain Sciences*, *15*(1), 151–151.

Corlett, R. T., & Lucas, P. W. (1990). Alternative seed-handling strategies in primates: seed-spitting by long-tailed macaques (Macaca fascicularis). *Oecologia*, *82*(2), 166–171.

Crawford, R. J. M., Asseid, B. S., Dyer, B. M., Hija, A., Mwinyi, A. A., Shinula, P., & Upfold, L. (2006). The status of seabirds at Latham Island, Tanzania. *African Journal of Marine Science*, *28*(1), 99–108.

Curtis, D. J., & Zaramody, A. (1998). Group size, home range use, and seasonal variation in the ecology of Eulemur mongoz. *International Journal of Primatology*, *19*(5), 811–835.

D. Hopkins, W., & Rabinowitz, D. M. (1997). Manual specialisation and tool use in captive chimpanzees (Pan troglodytes): the effect of unimanual and bimanual strategies on hand preference. *Laterality: Asymmetries of Body, Brain and Cognition*, *2*(3–4), 267–277.

Defler, T. R. (1996). Aspects of the Ranging Pattern in a Group of Wild Woolly Monkeys (Lagothrix lagothricha). *American Journal of Primatology*, *38*, 289–302.

Dittus, W. P. (1979). The evolution of behaviors regulating density and age-specific sex ratios in a primate population. *Behaviour*, *69*(3-4), 265-301.

Dunbar, R. I. (1977). Feeding ecology of gelada baboons: a preliminary report. *Primate ecology*. In: Clutton-Brock TH (ed) Primate ecology. Academic, London, pp 251–273

Espitia-Contreras, J. P., Fedigan, L. M., & Turner, S. E. (2020). Social grooming efficiency and techniques are influenced by manual impairment in free-ranging Japanese macaques (Macaca fuscata). *PLOS ONE*, *15*(2), e0228978. https://doi.org/10.1371/journal.pone.0228978

Eudey, A. A. (2008). The crab-eating macaque (Macaca fascicularis): widespread and rapidly declining. *Primate conservation*, *23*(1), 129–132.

Ewens, W. J., Gani, J., Brockwell, P. J., & Resnick, S. I. (1987). Minimum viable population size in the presence of catastrophes. *Viable populations for conservation*, 59.

Ewer, R. F. (1968). *Ethology of Mammals*. Springer, Boston, MA.

Fagen, R. (2002). Primate Juveniles and Primate Play. In M. E. Pereira & L. A. Fairbanks (Eds.), *Juvenile Primates: Life History, Development and Behavior, with a New Foreword* (pp. 182–196). University of Chicago Press.

Falótico, T., & Ottoni, E. B. (2014). Sexual bias in probe tool manufacture and use by wild bearded capuchin monkeys. *Behavioural Processes*, *108*, 117-122.

Falótico, T., Spagnoletti, N., Haslam, M., Luncz, L. V., Malaivijitnond, S., & Gumert, M. (2017). Analysis of sea almond (Terminalia catappa) cracking sites used by wild Burmese long-tailed macaques (Macaca fascicularis aurea). *American Journal of Primatology*, *79*(5), e22629. https://doi.org/10.1002/ajp.22629

Fashing, P. J. (2001). Activity and ranging patterns of guerezas in the Kakamega Forest: intergroup variation and implications for intragroup feeding competition. *International Journal of Primatology*, *22*(4), 549-577.

Fedigan, L. M., Rose, L. M., & Avila, R. M. (1998). Growth of mantled howler groups in a regenerating Costa Rican dry forest. *International Journal of Primatology*, *19*(3), 405–432.

Fittinghoff, N. A., & Lindburg, D. G. (1980). Riverine Refuging in East Bornean Macaca fascicularis. In D. G. Lindburg (Ed.), *The Macaques : Studies in ecology, behaviour and evolution* (pp. 182–214). Van Nostrand Reinhold Company.

Fooden, J. (1982). Ecogeographic segregation of macaque species. *Primates*, *23*(4), 574–579.

Fooden, J. (1995). Systematics review of Southeast Asian longtail macaques, Macaca fascicularis (Raffles, 1821). *Fieldiana: Zool., ns*, *81*, 2-3.

Fragaszy, D., Izar, P., Visalberghi, E., Ottoni, E. B., & de Oliveira, M. G. (2004). Wild capuchin monkeys (Cebus libidinosus) use anvils and stone pounding tools. *American Journal of Primatology: Official Journal of the American Society of Primatologists*, *64*(4), 359-366.

Gerber, L. R., & Hilborn, R. (2001). Catastrophic events and recovery from low densities in populations of otariids: implications for risk of extinction. *Mammal Review*, *31*(2), 131–150.

Gigerenzer, G. (1998). Ecological intelligence: An adaptation for frequencies. In *The evolution of mind* (pp. 9–29). Oxford University Press.

Goldstein, S. J., & Richard, A. F. (1989). Ecology of rhesus macaques (Macaca mulatta) in northwest Pakistan. *International Journal of Primatology*, *10*(6), 531–567.

Gould, L., Sussman, R. W., & Sauther, M. L. (1999). Natural disasters and primate populations: the effects of a 2-year drought on a naturally occurring population of ring-tailed lemurs (Lemur catta) in southwestern Madagascar. *International Journal of Primatology*, *20*(1), 69–84.

Groves, C. P. (2001). *Primate taxonomy*. Washington, DC: Smithsonian Institution Press.

Grueter, C. C., Li, D., Schaik, C. P., Ren, B., Long, Y., & Wei, F. (2008). Ranging of Rhinopithecus bieti in the Samage Forest, China. I. Characteristics of Range Use. *International Journal of Primatology*, *29*(5), 1121–1145. https://doi.org/10.1007/s10764-008-9299-9

Gumert, M. D., Kluck, M., & Malaivijitnond, S. (2009). The physical characteristics and usage patterns of stone axe and pounding hammers used by long-tailed macaques in the Andaman Sea region of Thailand. *American Journal of Primatology: Official Journal of the American Society of Primatologists*, *71*(7), 594-608.

Gumert, Michael D., Hoong, L. K., & Malaivijitnond, S. (2011). Sex differences in the stone tool-use behavior of a wild population of burmese long-tailed macaques (Macaca fascicularis aurea). *American Journal of Primatology*, *73*(12), 1239–1249.

Gumert, Michael D., & Malaivijitnond, S. (2012). Marine prey processed with stone tools by burmese long-tailed macaques (*Macaca fascicularis aurea*) in intertidal habitats. *American Journal of Physical Anthropology*, *149*(3), 447–457. https://doi.org/10.1002/ajpa.22143

Gumert, Michael David. (2011). The common monkey of Southeast Asia: Longtailed macaque populations, ethnophoresy, and their occurrence in human environments. *Monkeys on the Edge: Ecology and Management of Long-tailed Macaques and their Interface with Humans*, 3–44.

Guo, S., Li, B., & Watanabe, K. (2007). Diet and activity budget of Rhinopithecus roxellana in the Qinling Mountains, China. *Primates*, *48*(4), 268-276.

Hahn, I., Vergara, P. M., Baumeister, J., Soto, G. E., & Römer, U. (2015). Tsunami impact on the population development of a critically endangered hummingbird species of a Pacific island. *Population Ecology*, *57*(1), 143–149.

Hall, K. R. L., & Schaller, G. B. (1964). Tool-using behavior of the California sea otter. *Journal of Mammalogy*, *45*(2), 287-298.

Hambali, K., Ismail, A., & Md-Zain, B. M. (2012). Daily activity budget of long-tailed macaques (Macaca fascicularis) in Kuala Selangor Nature Park. *International Journal of Basic and Applied Sciences*, *12*(4), 47–52.

Haslam, M. (2013). 'Captivity bias' in animal tool use and its implications for the evolution of hominin technology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1630), 20120421.

Hauser, M. D. (1994). The transition to foraging independence in free-ranging vervet monkeys. *Behavioral aspects of feeding. Harwood Academic, Chur, Switzerland*, 165-202.

Hock, L. B., & Sasekumar, A. (1979). A preliminary study on the feeding biology of mangrove forest primates, Kuala Selangor. *Malayan Nature Journal*, *33*(2), 105-112.

Huffman, M. A., & Hirata, S. (2003). Biological and ecological foundations of primate behavioral tradition. *The biology of traditions: Models and evidence*, 267–296.

Isbell, L. A., & Young, T. P. (1993). Social and ecological influences on activity budgets of vervet monkeys, and their implications for group living. *Behavioral ecology and sociobiology*, *32*(6), 377-385.

Jaman, M. F., & Huffman, M. A. (2013). The effect of urban and rural habitats and resource type on activity budgets of commensal rhesus macaques (Macaca mulatta) in Bangladesh. *Primates*, *54*(1), 49-59.

Karr, J. R., & Freemark, K. E. (1985). *Disturbance and vertebrates: an integrative perspective*. Academic Press.

Kavana, T. S., Erinjery, J. J., & Singh, M. (2014). Male takeover and infanticide in Nilgiri langurs Semnopithecus johnii in the Western Ghats, India. *Folia Primatologica*, *85*(3), 164-177.

Kawai, M. (1965). Newly-acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima Islet. *Primates*, *6*(1), 1–30.

Kawamura, S. (1954). A new type of action expressed in feeding behavior of Japanese monkeys in the wild. *Seibutsu Shinka*, *2*(1), 11–13.

Kie, J. G., Matthiopoulos, J., Fieberg, J., Powell, R. A., Cagnacci, F., Mitchell, M. S., et al. (2010). The home-range concept: are traditional estimators still relevant with modern telemetry technology? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1550), 2221–2231. https://doi.org/10.1098/rstb.2010.0093

Kie, John G., Matthiopoulos, J., Fieberg, J., Powell, R. A., Cagnacci, F., Mitchell, M. S., et al. (2010). The home-range concept: are traditional estimators still relevant with modern telemetry technology? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1550), 2221–2231. https://doi.org/10.1098/rstb.2010.0093

King, B. J. (1991). Social information transfer in monkeys, apes, and hominids. *American Journal of Physical Anthropology*, *34*(S13), 97–115. https://doi.org/10.1002/ajpa.1330340607

King, B. J. (1994). Primate infants as skilled information gatherers. *Pre And Perinatal Psychology Journal*, *8*, 287-287.

Kirkpatrick, R. C., Long, Y. C., Zhong, T., & Xiao, L. (1998). Social organization and range use in the Yunnan snub-nosed monkey Rhinopithecus bieti. *International Journal of Primatology*, *19*(1), 13–51.

Koganezawa, M., & Imaki, H. (1999). The effects of food sources on Japanese monkey home range size and location, and population dynamics. *Primates*, *40*(1), 177–185.

Koirala, S., Chalise, M. K., Katuwal, H. B., Gaire, R., Pandey, B., & Ogawa, H. (2017). Diet and activity of Macaca assamensis in wild and semi-provisioned groups in Shivapuri Nagarjun National Park, Nepal. *Folia Primatologica*, *88*(2), 57–74.

Kumar, R. S., Mishra, C., & Sinha, A. (2007). Foraging ecology and time-activity budget of the Arunachal macaque Macaca munzala- A preliminary study. *Current Science*, *93*(4), 532–539.

Kummer, H., & Goodall, J. (1985). Conditions of innovative behaviour in primates. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *308*(1135), 203–214.

Kurup, G. U., & Kumar, A. (1993). Time budget and activity patterns of the lion-tailed macaque (Macaca silenus). *International Journal of Primatology*, *14*(1), 27–39.

Lewis, J. (1990). The vulnerability of small island States to sea level rise: the need for holistic strategies. *Disasters*, *14*(3), 241–249. https://doi.org/10.1111/j.1467-7717.1990.tb01066.x

Liu, Z.-H., & Zhao, Q.-K. (2004). Sleeping sites of Rhinopithecus bieti at Mt. Fuhe, Yunnan. *Primates*, *45*(4), 241–248. Accessed 19 August 2013

Lowe, S., Browne, M., Boudjelas, S., & De Poorter, M. (2000). *100 of the world's worst invasive alien species: a selection from the global invasive species database*. Invasive Species Specialist Group Auckland, New Zealand. http://calendar.k-state.edu/withlab/consbiol/IUCN_invaders.pdf. Accessed 26 October 2012

Macfarlane, N. B. W., & Graziano, M. S. A. (2009). Diversity of grip in Macaca mulatta. *Experimental Brain Research*, *197*(3), 255–268. https://doi.org/10.1007/s00221-009-1909-z

Majolo, B., McFarland, R., Young, C., & Qarro, M. (2013). The effect of climatic factors on the activity budgets of Barbary macaques (Macaca sylvanus). *International Journal of Primatology*, *34*(3), 500-514.

Malaivijitnond, S., Lekprayoon, C., Tandavanittj, N., Panha, S., Cheewatham, C., & Hamada, Y. (2007). Stone-tool usage by Thai long-tailed macaques (Macaca fascicularis). *American journal of primatology*, *69*(2), 227–233.

Malaivijitnond, S., & Hamada, Y. (2008). Current situation and status of long-tailed macaques (Macaca fascicularis) in Thailand. *Tropical Natural History*, *8*(2), 185-204.

Marsh, C. W. (1981). Time budget of Tana River red colobus. *Folia Primatologica*, *35*(1), 30-50.

Martin, J.-L., Gaston, A. J., & Hitier, S. (1995). The effect of island size and isolation on old growth forest habitat and bird diversity in Gwaii Haanas (Queen Charlotte Islands, Canada). *Oikos*, 115–131.

Maruhashi, T. (1981). Activity patterns of a troop of Japanese monkeys (Macaca fuscata yakui) on Yakushima Island, Japan. *Primates*, *22*(1), 1–14. https://doi.org/10.1007/BF02382552

Maruhashi, T., Saito, C., & Agetsuma, N. (1998). Home range structure and inter-group competition for land of Japanese macaques in evergreen and deciduous forests. *Primates*, *39*(3), 291-301.

McElroy, E. J., McBrayer, L. D., Williams, S. C., Anderson, R. A., & Reilly, S. M. (2012). Sequential analyses of foraging behavior and attack speed in ambush and widely foraging lizards. *Adaptive Behavior*, *20*(1), 16–31. https://doi.org/10.1177/1059712311426800

McFeeters, S. K. (1996). The use of the Normalized Difference Water Index (NDWI) in the delineation of open water features. *International journal of remote sensing*, *17*(7), 1425–1432.

Md-Zain, B. M., Sha'ari, N. A., Mohd-Zaki, M., Ruslin, F., Idris, N. I., Kadderi, M. D., & Idris, W. M. R. (2010). A comprehensive population survey and daily activity budget on long-tailed macaques of Universiti Kebangsaan Malaysia. *Journal of Biological Sciences*, *10*(7), 608–615.

Melin, A. D., Young, H. C., Mosdossy, K. N., & Fedigan, L. M. (2014). Seasonality, extractive foraging and the evolution of primate sensorimotor intelligence. *Journal of Human Evolution*, *71*, 77–86. https://doi.org/10.1016/j.jhevol.2014.02.009

Milton, K. (1981). Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental development. *American Anthropologist*, *83*(3), 534–548.

Milton, K. (1982). Dietary quality and demographic regulation in a howler monkey population. *The ecology of a tropical forest*.

Mishra, P. S., Kumara, H. N., Thiyagesan, K., Singh, M., Velankar, A. D., & Pal, A. (2020a). Chaos in Coexistence: Perceptions of Farmers towards Long-tailed Macaques (Macaca fascicularis umbrosus) Related to Crop Loss on Great Nicobar Island. *Primate Conservation*, *34*, 175-183.

Mishra, P. S., Pal, A., Velankar, A. D., Kumara, H. N., & Singh, M. (2020b). Do males bond? A study of male-male relationships in Nicobar long-tailed macaques Macaca fascicularis umbrosus. *Journal of Biosciences*, *45*(1), 22.

Mishra, P. S., Pal, A., Velankar, A. D., Kumara, H. N., Singh, M., & Cooper, M. (2020c). Does rank rule? Rank-related grooming patterns in Nicobar long-tailed macaques Macaca fascicularis umbrosus. *Primates*, 1–11.

Molur, S., D. Brandon-Jones, W. Dittus, A. Eudey, A. Kumar, M. Singh, M. M. Feeroz, M. Chalise, P. Priya and S. Walker (eds.) (2003). Status of South Asian Primates: Conservation and Management Plan (C.A.M.P.) Workshop Report. Zoo Outreach Organisation/CBSG-South Asia, Coimbatore, India

Moura, A. D. A., & Lee, P. C. (2004). Capuchin stone tool use in Caatinga dry forest. *Science*, *306*(5703), 1909-1909.

Nellemann, C. (Ed.). (2007). *The last stand of the orangutan: state of emergency: illegal logging, fire and palm oil in Indonesia's national parks*. UNEP/Earthprint.

Newton, A. C. (2007). *Forest Ecology and Conservation*. Oxford University Press, USA.

O'brien, T. G., & Kinnaird, M. F. (1997). Behavior, diet, and movements of the Sulawesi crested black macaque (Macaca nigra). *International Journal of Primatology*, *18*(3), 321–351.

Pal, A., Kumara, H. N., Mishra, P. S., Velankar, A. D., & Singh, M. (2018a). Extractive foraging and tool-aided behaviors in the wild Nicobar long-tailed macaque (Macaca fascicularis umbrosus). *Primates*, *59*(2), 173–183. https://doi.org/10.1007/s10329-017-0635-6

Pal, A., Kumara, H. N., Mishra, P. S., Velankar, A. D., & Singh, M. (2018b). Between-group encounters in Nicobar long-tailed macaque (*Macaca fascicularis umbrosus*). *Ethology Ecology & Evolution*, *30*(6), 582–599. https://doi.org/10.1080/03949370.2018.1459866

Pal, A., Kumara, H. N., Mishra, P. S., Velankar, A. D., & Singh, M. (2018c). Between-group encounters in Nicobar long-tailed macaque (Macaca fascicularis umbrosus). *Ethology Ecology & Evolution*, *30*(6), 582–599.

Palacios, E., & Rodriguez, A. (2001). Ranging pattern and use of space in a group of red howler monkeys (Alouatta seniculus) in a southeastern Colombian rainforest. *American Journal of Primatology*, *55*(4), 233–251.

Parker, S. T., & Gibson, K. R. (1977). Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in Cebus monkeys and great apes. *Journal of Human Evolution*, *6*(7), 623-641.

Patzelt, A., Kopp, G. H., Ndao, I., Kalbitzer, U., Zinner, D., & Fischer, J. (2014). Male tolerance and male–male bonds in a multilevel primate society. *Proceedings of the National Academy of Sciences*, *111*(41), 14740–14745.

Pimley, E. R., Bearder, S. K., & Dixson, A. F. (2005). Home Range Analysis of Perodicticus potto edwardsi and Sciurocheirus cameronensis. *International Journal of Primatology*, *26*(1), 191–206. https://doi.org/10.1007/s10764-005-0730-1

Porwal, M. C., Padalia, H., & Roy, P. S. (2012). Impact of tsunami on the forest and biodiversity richness in Nicobar Islands (Andaman and Nicobar Islands), India. *Biodiversity and Conservation*, *21*(5), 1267-1287.

Pouydebat, E., Reghem, E., Borel, A., & Gorce, P. (2011). Diversity of grip in adults and young humans and chimpanzees (Pan troglodytes). *Behavioural Brain Research*, *218*(1), 21–28. https://doi.org/10.1016/j.bbr.2010.11.021

Powell, R. A. (2000). Animal home ranges and territories and home range estimators. *Research techniques in animal ecology: controversies and consequences*, *442*.

Queen, J. P., Quinn, G. P., & Keough, M. J. (2002). *Experimental design and data analysis for biologists*. Cambridge university press.

Ramachandran, S., Anitha, S., Balamurugan, V., Dharanirajan, K., Vendhan, K. E., Divien, M. I. P., ... & Udayaraj, A. (2005). Ecological impact of tsunami on Nicobar islands (Camorta, Katchal, Nancowry and Trinkat). *Current Science*, 195-200.

Rao, M. V. (1986). A preliminary report on the angiosperms of Andaman and Nicobar Islands. *Journal of Economic and Taxonomic Botany*, *8*(1), 107-184.

Rapaport, L. G., & Brown, G. R. (2008). Social influences on foraging behavior in young nonhuman primates: learning what, where, and how to eat. *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews*, *17*(4), 189–201.

Riley, E. P. (2008). Ranging patterns and habitat use of Sulawesi Tonkean macaques (Macaca tonkeana) in a human-modified habitat. *American Journal of Primatology*, *70*(7), 670–679. https://doi.org/10.1002/ajp.20543

Rodgers, A. R., & Carr, A. P. (1998). HRE: the home range extension for ArcView. *Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada*. http://planet.botany.uwc.ac.za/nisl/computing/HRE/Users%20Manual.pdf. Accessed 7 October 2015

Rosati, A. G. (2017). Foraging cognition: reviving the ecological intelligence hypothesis. *Trends in cognitive sciences*, *21*(9), 691–702.

Santhosh, K., Kumara, H. N., Velankar, A. D., & Sinha, A. (2015). Ranging behavior and resource use by lion-tailed macaques (Macaca silenus) in selectively logged forests. *International Journal of Primatology*, *36*(2), 288–310.

Sankaran, R. (2005). Impact of the earthquake and the tsunami on the Nicobar Islands. *The ground beneath the waves: post-tsunami impact assessment of wildlife and their habitats in India*, *2*, 10-77.

Seaman, D. E., & Powell, R. A. (1996). An Evaluation of Kernel Density Estimators for Home Range Analysis. *Ecology*, *77*(7), 2075–2085.

Sekhsaria, P. (2009). When Chanos Chanos became Tsunami Macchi: The Post-December 2004 Scenario in the Andaman & Nicobar Islands. *Journal of the Bombay Natural History Society*, *106*(3), 256.

Salter, R. E., MacKenzie, N. A., Nightingale, N., Aken, K. M., & Chai PK, P. (1985). Habitat use, ranging behaviour, and food habits of the proboscis monkey, Nasalis larvatus (van Wurmb), in Sarawak. *Primates*, *26*(4), 436-451.

Sha, J. C. M., & Hanya, G. (2013). Diet, Activity, Habitat Use, and Ranging of Two Neighboring Groups of Food-Enhanced Long-Tailed Macaques (*Macaca fascicularis*): Long-Tailed Macaques. *American Journal of Primatology*, *75*(6), 581–592. https://doi.org/10.1002/ajp.22137

Shaffer, M. (1987). *Minimum viable populations: coping with uncertainty In Soule ME ed. Viable Populations for Conservation, Great Britain*. Cambridge University Press.

Shilova, S. A., & Shatunovskii, M. I. (2005). Ecophysiological indicators of the state of animal populations exposed to damaging factors. *Russian Journal of Ecology*, *36*(1), 27–32.

Sinha, B. (1999). *Flora of Great Nicobar Island*. (P. Hajra & P. S. N. Rao, Eds.). Botanical Survey of India, Kolkata. http://scholar.google.com/scholar?q=Flora of Great Nicobar Island&btnG=&hl=en&num=20&as_sdt=0%2C22

Sivakumar, K. (2010a). Impact of the tsunami (December, 2004) on the long tailed macaque of Nicobar Islands, India. *Hystrix-the Italian Journal of Mammalogy*, *21*(1).

Sivakumar, K. (2010b). Impact of the 2004 tsunami on the Vulnerable Nicobar megapode Megapodius nicobariensis. *Oryx*, *44*(1), 71–78.

Son, V. D. (2003). Morphology of Macaca fascicularis in a mangrove forest, Vietnam. *Laboratory Primate Newsletter*, *42*(2), 9-11.

Spedicato, G. A. (2017). Discrete Time Markov Chains with R. *R J.*, *9*(2), 84.

Stephens, P. A., Sutherland, W. J., & Freckleton, R. P. (1999). What is the Allee effect? *Oikos*, 185–190.

Sugiyama, Y., & Koman, J. (1979). Tool-using and-making behavior in wild chimpanzees at Bossou, Guinea. *Primates*, *20*(4), 513-524.

Tan, A. W. (2017). From play to proficiency: The ontogeny of stone-tool use in coastal-foraging long-tailed macaques (Macaca fascicularis) from a comparative perception-action perspective. *Journal of comparative psychology*, *131*(2), 89.

Tan, A. W., Luncz, L., Haslam, M., Malaivijitnond, S., & Gumert, M. D. (2016). Complex processing of prickly pear cactus (Opuntia sp.) by free-ranging long-tailed macaques: preliminary analysis for hierarchical organisation. *Primates*, *57*(2), 141-147.

Thieler, E. R., Himmelstoss, E. A., Zichichi, J. L., & Ergul, A. (2009). *The Digital Shoreline Analysis System (DSAS) version 4.0-an ArcGIS extension for calculating shoreline change*. US Geological Survey.

Teichroeb, J. A., Saj, T. L., Paterson, J. D., & Sicotte, P. (2003). Effect of group size on activity budgets of Colobus vellerosus in Ghana. *International Journal of Primatology*, *24*(4), 743-758.

Troscianko, J., Bluff, L. A., & Rutz, C. (2008). Grass-stem tool use in New Caledonian crows Corvus moneduloides. *Ardea*, *96*(2), 283-285.

Umapathy, G., Singh, M., & Mohnot, S. M. (2003). Status and distribution of Macaca fascicularis umbrosa in the Nicobar Islands, India. *International Journal of Primatology*, *24*(2), 281–293.

van Lawick-Goodall, J., & van Lawick-Goodall, H. (1966). Use of tools by the Egyptian vulture, Neophron percnopterus. *Nature*, *212*(5069), 1468-1469.

van Schaik, C. P., Netto, W. J., van Amerongen, A. J. J., & Westland, H. (1989). Social rank and sex ratio of captive long-tailed macaque females (Macaca fascicularis). *American Journal of Primatology*, *19*(3), 147-161.

van Schaik, C. P., van Noordwijk, M. A., de Boer, R. J., & den Tonkelaar, I. (1983). The effect of group size on time budgets and social behaviour in wild long-tailed macaques (Macaca fascicularis). *Behavioral ecology and sociobiology*, *13*(3), 173-181.

van Schaik, C. P. (1996). Riverine refuging by wild Sumatran long-tailed macaques. *Evolution and ecology of macaque societies*, 160-181.

van Schaik, C., Deaner, R., & Merrill, M. (1999). The conditions for tool use in primates: implications for the evolution of material culture. *The conditions for tool use in primates: implications for the evolution of material culture*, *36*(6).

Velankar, A. D., Kumara, H. N., Pal, A., Mishra, P. S., & Singh, M. (2016). Population recovery of Nicobar long-tailed macaque Macaca fascicularis umbrosus following a tsunami in the Nicobar Islands, India. *PloS one*, *11*(2), e0148205.

Viera, V. M., Le Bohec, C., Côté, S. D., & Groscolas, R. (2006). Massive breeding failures following a tsunami in a colonial seabird. *Polar Biology*, *29*(8), 713–716.

Visalberghi, E. (1993). Capuchin monkeys: A window into tool use in apes and humans. *Tools, language and cognition in human evolution*, 138–150.

Visalberghi, E., & Fragaszy, D. M. (1990). Food-washing behaviour in tufted capuchin monkeys, Cebus apella, and crabeating macaques, Macaca fascicularis. *Animal Behaviour*, *40*(5), 829–836.

Visalberghi, E., & Fragaszy, D. M. (1994). Do monkeys ape? In S. T. Parker & K. R. Gibson (Eds.), *"Language" and Intelligence in Monkeys and Apes: Comparative Developmental Perspectives* (pp. 247–273). Cambridge University Press.

Watts, D. P. (2008). Scavenging by chimpanzees at Ngogo and the relevance of chimpanzee scavenging to early hominin behavioral ecology. *Journal of Human Evolution*, *54*(1), 125-133.

Wheatley, B. P. (1988). Cultural Behavior and Extractive Foraging in Macaca Fascicularis. *Current Anthropology*, *29*(3), 516–519. https://doi.org/10.1086/203670

Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, *70*(1), 164–168.

Yamakoshi, G. (2004). Evolution of complex feeding techniques in primates: is this the origin of greatape intelligence?. *The evolution of thought: Evolutionary origins of great ape intelligence*, 140-171.

Yeager, C. (1996). Feeding ecology of the long-tailed macaque(Macaca fascicularis) in Kalimantan Tengah, Indonesia. *International Journal of Primatology*, *17*(1), 51–62. https://doi.org/10.1007/BF02696158

Zinner, D., Fickenscher, G. H., Roos, C., Anandam, M. V., Bennett, E. L., Davenport, T. R., et al. (2013). Family Cercopithecidae (old world monkeys). In *Handbook of the mammals of the world-Primates*. Lynx.

Zuberbühler, K., Gygax, L., Harley, N., & Kummer, H. (1996). Stimulus enhancement and spread of a spontaneous tool use in a colony of long-tailed macaques. *Primates*, *37*(1), 1–12.