INSPIRED BY LIFE

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

A STUDY ON REPRODUCTIVE BEHAVIOUR OF NICOBAR LONG-TAILED MACAQUE (*MACACA FASCICULARIS UMBROSUS*) IN NICOBAR ISLANDS, INDIA

THESIS SUBMITTED TO
MANIPAL ACADEMY OF HIGHER EDUCATION

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

DOCTOR OF PHILOSOPHY
BY

ARIJIT PAL
Reg. No. 139000011

UNDER THE GUIDANCE OF

H. N. KUMARA

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

SÁLIM ALI CENTRE FOR ORNITHOLOGY AND NATURAL HISTORY (SACON)

SACON

APRIL 2018

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

CERTIFICATE

This is to certify that the work incorporated in this thesis **"A study on reproductive behavior of Nicobar long-tailed macaque (*Macaca fascicularis umbrosus*) in Nicobar Islands, India"** submitted by **Mr. Arijit Pal** 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

डॉ. एच एन कुमारा / Dr. HN Kumara
वरिष्ठ वैज्ञानिक / Senior Scientist
सालिम अली पक्षिविज्ञान एवं प्रकृति विज्ञान केन्द्र
Sálim Ali Centre for Ornithology and Natural History
आनाकट्टी, कोयम्बटूर – 641 108
Anaikatty (Post), Coimbatore – 641 108

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

April 2018

ABSTRACT:

Nicobar long-tailed macaques (*Macaca fascicularis umbrosus*) live in three small isolated catastrophic prone Nicobar Islands. This study was conducted to understand the strategies adapted by these macaques to survive on such stressful condition, and compare it with other sub-species distributed in varying environmental conditions. The study suggested a high degree of similarities in demographic traits and social organization between the sub-species, which reflected the high adaptability of these macaques to manage the life-history traits by coping with the stressful condition. Contrasting to other sub-species, the distinct behavioral traits like the variation in age-sex ratio and non-seasonal breeding pattern in these macaques are the adaptive strategies to achieve the conservative life-history traits to maximize the reproductive output. Competition for mate resources was very evident in *M. f. umbrosus*, where individuals of both the sexes were involved in intra and inter-sexual competition to increase their reproductive success. Social hierarchy has a direct impact on the heterogeneous distribution of mate and food resources between individuals with different social status, which ultimately shapes the social organization in *M. f. umbrosus*. Consequently, to balance the disadvantages of living in such hierarchical group, individuals make a trade-off by adopting different behavioral strategies through policing specific inter-individual relationships. These macaques were involved in between-group contest to compete for food and mate resources rather than the territory defense. This study provided first-ever information about demography, social organization, reproductive behaviors, birth seasonality, and intra and inter-group competition in Nicobar long-tailed macaques. It also revealed that in due course of interactions with its environment, a species could become flexible with life history traits and adopt different strategies to increase survivability as well as inclusive fitness.

INSPIRED BY LIFE

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.

Arijit Pal
Signature
Arijit Pal
Reg. No. 139000011

Place : SACON, Coimbatore
Date : 19th April 2018

I, **Dr. H. N. Kumara** certify and attest that the work done by my Ph. D. student **Mr. Arijit Pal** 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.

डॉ. एच एन कुमारा / Dr. HN Kumara
वरिष्ठ वैज्ञानिक / Senior Scientist
सालिम अली पक्षिविज्ञान एवं प्रकृति विज्ञान केन्द्र
Sálim Ali Centre for Ornithology and Natural History
आनैकट्टी, कोयम्बटूर – 641 108
Anaikatty (Post), Coimbatore – 641 108

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

Place : SACON, Coimbatore
Date : 19th April 2018

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

INSPIRED BY LIFE

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

Arijit Pal

Signature
Arijit Pal
Reg. No. 139000011
Conservation Biology Division
Sálim Ali Centre for Ornithology and Natural History (SACON)

April 2018

ACKNOWLEDGEMENTS

Though I am solely responsible for the words filling these pages, it is an evidence of cooperativeness in our society. It would have been impossible for me to accomplish this mammoth task without the cordial help, motivation, and cooperation from a bunch of people. However, acknowledging the efforts of all of my helper-cooperators through this sophisticated linguistic medium is very difficult indeed (a warm hug would have been more appropriate I guess!).

The most central node of my mission Ph.D. network is my guide (also a friend and philosopher) Dr. Honnavalli N. Kumara. Apart from all those insightful, indulgent scientific discussions, he illuminated me about the 'governing dynamics' of the society which has become the greatest lesson to me. Moreover, his approaches towards any obstacle itself have become the 'code of conduct' for me to cross the hurdles I had faced during this tenure. Since the role of 'sex' in the society always fascinates me, I told him about my wish to study reproductive behaviors of Nicobar long-tailed macaque (whom I had not seen though), which made him more excited than me to solve the unsolved puzzle of sexuality. Thereafter, our journey started through study design, proposing objectives and ran along with periodical data analysis, up to articulation of findings in this thesis, and yet to continue. Throughout this period, he was the best audience as well as an editor of my nascent (mostly naïve) scientific thoughts and hypothesis. Despite social courtesy of thanking him (which I am not capable of) or cherishing, I wish to continue my nurturing sessions with him.

I am grateful to Innovation in Science Pursuit for Inspired Research (INSPIRE), Assured Opportunity for Research Careers (AORC), Department of Science and Technology (DST), Ministry of Science and Technology, Government of India for awarding me the prestigious INSPIRE Fellowship (Reg. No. IF130350) which provided the essential financial support for the study.

It gives me pleasure to express my gratitude to Dr. Shyamala Hande, Deputy Registrar, Manipal Academy of Higher Education (MAHE) for her constant support during this study tenure. My warmest thank also extended to all the administrative and financial staff of MAHE, whose quick responses made all the required procedures very ease.

I am indebted to the Principal Chief Conservator of Forest, Andaman and Nicobar Islands for granting the permit (Permit No. CWLW/WL/134/566) to conduct the study. I am grateful to the Deputy Commissioner and Assistant Commissioner, Andaman and Nicobar administration for providing Tribal Pass to carry out the fieldwork on restricted tribal reserves. I express my warm regards and thanks to Agni Da, Divisional Forest Officer, Nicobar Division for his encouragements, suggestions *and support whenever needed. I also thank Divisional Forest Officers Mr. Jabestin A., Mr. A.K. Paul and all the other forest officials especially Mr. Sajan, Mr. Shahid, Mr. Simon, Mr. Alfons, and Mr. Sayeed for their continuous support during the field work.*

I express my warm regards and gratitude to Professor Mewa Singh, another central node of my Ph.D. accomplishment network. I am privileged to be associated with such an inspirational and humble personality who has always been the wizard of puzzle-solving to me.

Another two central-most nodes of my research network are my field-dudes Partha and Avadhoot. During our field-days, we were involved in discussions (often with louder arguments) about serious topics from the selection of study methodology to the selection of fish to be cooked in our field kitchen. I salute my two comrades for what they have done for me to get the work done.

Nature is not for our convenience. This is very true for conducting fieldwork in the remote forests of Nicobar Islands. Therefore, it was impossible to carry out the study without the help of the local people. Firstly, I would like to thank my Nicobari friends Jerund, Rahul, Morris, Safinia, Safrin, Suvas and late Abiho, whose expertise about local forest extremely helped me to study the macaques in such secluded habitats. I also express my gratitude to the inhabitants of Great Nicobar especially RPRS colony, Forest colony, Balu Dera, Babu Lane, Lakshmi Nagar, ALHW colony and Rajiv Nagar for their love, compassion and sharing their information about the macaques, which helped me to facilitate the study. I express my sincere gratitude to K. Krishnamurthy and Pintu of ACC lodge, Mr. Thinakaran of Velavan Stores for providing logistic supports to ease the field work in such limited resources areas. I also thank Balu Prakash (FRNDA), Mr. Kiran, Anna Chi, Lassi anna, Bonda anna, Chai anna for their love and support throughout the study. I also thank A. Simachalam (Amarakirti Foods) for his homely foods, and Sailen da, Dadu and other staffs of Su-Ruchi for serving delicious foods and especially ‘not so good’ gulabjamuns and rosogollas.

I express my heartfelt gratitude to the former director Dr. P.A. Azeez and present Director Dr. K. Sankar of Sálim Ali Centre for Ornithology and Natural History (SACON), for their guidance and supports. I will forever be thankful to Dr. P. Balasubramanian, Research Coordinator, SACON and Dr. Shomita Mukherjee, Head of the Department of Conservation Biology Division and My Doctoral Advisory Committee (DAC) members Dr. Rajah Jayapal and Late Dr. S. Bhupathy for their valuable suggestions for accomplishing the study. I am fortunate to have supports and encouragements from all the Scientists of SACON. Especially, I would like to mention Dr. S. Babu and Dr. R. P. Singh for all the insightful discussions, Dr. Karunakaran and Dr. Goldin Quadros for their constant encouragements and suggestions to complete the study. I am thankful to Mr. Aneesh K Abraham, Finance Officer, Mrs. M. Jayageetha and Mrs. R. Rajalakshmi of Finance Department, SACON for their ingenious help *which smoothened all the necessary financial procedures. I also thank Technical assistant Mr. A. Srinivasan, Librarian in Charge Mr. M. Manoharan, and Lt Col.(Retd) N. Sundararaj and all the Administrative staff of SACON for their timely help. My acknowledgement would not be complete without the special mention of the Akkas and other non-scientific, non-administrative staff of SACON who made my stay in SACON campus enjoyable.*

This study would not be so interesting and entertaining without the support system of the bunch of crazy Saconites. I am fortunate to get such lab-associates like Aditi with whom solving problems was fun and food hunting was always daring for my palates; and Aakriti, Santhosh, and Joydeep for their various help. I wish to mention my beloved friends Jinsa, Sony, Rajan, Anoop, Anup, Akshaya, Madhumita, Lavanya, Piu, Archita, Nambi Ji and Zeeshan who helped me one and another way to conduct the study successfully. I would also like to acknowledge the continuous supports from Srinivas, Nishadh, Prathamesh, Prakash, Kirubha, Divya, Muhil, Niveditha, Suresh, Ramesh, Pankaj, Babu, Gayathri, Mythreyi, Ganesh, Maharajan, Shafeeque and all other friends who motivated me to complete this assignment.

I am also indebted to U.S.R. Sir who is the first one to expose me to the labyrinth of research. I thank Alexandra, Santhala Ma'am and Sayantan for their help and support. I am very much thankful to my childhood friends Tona, Vitu, Heblu, and Suka for their continuous support. Further, I thank all my well-wishers who helped and supported me throughout my journey.

The greatest inspiration which lead me to this field comes from none other than my Maa and Babu. Apart from making me what I am today, Maa was strong enough to let her 'unweaned' infant to go on his quest. Babu the coach of my life, guided me to find myself by exploring. I am fortunate to be parented by such lovely people. Purbi is the one who made the 'frog in the well' me to not only conceive the ocean but also cross the ocean to conquer my dreams. She always poked me to be on the track and now after being together, we have started poking each other to keep ourselves on the track. Last but not the least, I express my love to the Macaques of Nicobar for being the core of my research.

‡ Arijit Pal ‡

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

Introduction

Long-tailed Macaques of Nicobar Islands

“An intellectual is a person who's found one thing that's more interesting than sex.”

‡ Aldous Huxley ‡

1.1. General Overview

In the course of evolution, being in the same order (Primates), non-human primates (hereafter, primates) are the closest relatives of human beings. There are several similarities between primates and humans, including similarities in morphology, physiology, genetics, behavior and cognitive skills. The similarities lead primates to contribute immensely to the mankind by becoming a part of various bio-medical and evolutionary-anthropological studies. Hitherto, about 505 known primate species are majorly distributed in the tropics and sub-tropics of African, South American and Asian continents (Rowe and Myers 2016). However, at present, about 30% of the primate species are endangered, and 27% least concern primate population is in continuous decline (Rowe and Myers 2016).

Phylogenetically, primates are majorly classified into two categories, i.e., ‘Prosimians’ including lemurs, lorises, and tarsiers, and ‘Simians' or anthropoid primates including old-world monkeys, new-world monkeys, and apes. The molecular and fossil evidences suggest that the evolution of primates began approximately 65 million years ago, and the recent living primate societies are the result of periodical evolutions and extinctions (Willoughby 2005, Zhang et al. 2008). The stunning diversity in primate societies is build up with three distinct components, namely social organization, mating system and social structure (Kappeler and van Schaik 2001). The social organization refers to the demographic structure and cohesion in a society; wherein the mating system provides information about the reproductive interactions along with the reproductive consequences and genetics; while the social structure describes social interactions and social relationships between the members of the social unit. The Primates live in three social organizations, namely, *solitary and neighbourhood society* where largely they live and forage alone (e.g., lemurs, lorises, tarsiers); *pair-living society* where one male and one female individual live together after permanent pairing (for e.g. gibbons, owl monkeys and titi monkeys); and *group-living society* where at least more than three adult individuals of both sexes along with different age classes live together as a group (e.g., macaques, baboons, langurs and chimpanzees). The primate societies constitute four basic types of mating systems, i.e., monogamy, polyandry, polygyny and polygynandry (Clutton-Brock 1989). In the monogamy mating system, an individual mate with only one individual of opposite sex (e.g., gibbons). The polyandry society refers to multiple male mating partners of a female individual, wherein each of her mating partners only mates with her (e.g., marmosets and tamarins). In polygyny, one male individual mate with multiple females, where each of his mating partners only mates with him (e.g., gorillas, geladas, and hamadryas baboons). In the polygynandrous mating society, both male and female mate with multiple partners of opposite sex (e.g., macaque, baboon, and chimpanzee). However, it is argued that the availability of food and mating partner in an environment, and the fighting ability of a male ultimately shapes the mating system of a society (Reichard 1995; Fietz et al. 2000; Kappeler and van Schaik 2001; Reichard and Boesch 2003). ‘Social structure,' the last component of primate society, has three elements, i.e., inter-male, inter-female and inter-sex relationships, where the variation in ecological and social factors acts as an ultimate mediator for the variation in social relationships. Therefore, it can be argued that the diversity and evolution of observed variation in primate societies are the consequences of varying socio-ecological factors of the primate societies.

Amongst primates, the macaque (*Macaca* sp.), belonging to the tribe papionini, is one of the most successful monophyletic radiations distributed widely across south and east Asia, trailing only *Homo* sp. Most of the macaque species live in multi-male/multi-female societies, but uni-male/multi-female or all-male groups also exist in some species (Thierry et al. 2004). From the point of social organization, macaques are consistent and conservative, yet, demographic characteristics including group size, age and sex composition of the group, birth rate, mortality, migration frequency of individuals, and intrinsic growth rate change over time with ecological constraints (Dittus 2004). These demographic characteristics are the evolutionary consequences of life history traits, which has often shown plasticity to maximize the reproductive output of a population (Chapman and Rothman 2009; Cords and Chowdhury 2010; Singh et al. 2016).

In general, the multi-female macaque societies are bound by classical nepotistic hierarchy or classical matrilineal dominance structure (Thierry 2004). In this dominance style, the females are philopatric, where the younger daughter acquires social rank just below her mother and outranks all females that are subordinate to her mother, known as the youngest ascendency (Chapais 2004). Whereas, the males disperse from the natal group and join another group as subordinate or dominant as per their fighting ability. Hence, males and females have a different dominance hierarchy, where males are dominant over females. The dominance style in macaques varies dramatically from despotic to egalitarian (Flack and de Waal 2004). In less tolerant despotic society, the large dynamic asymmetries exist and are reinforced through unidirectional intense aggression between dominants and subordinates. Alternatively, in an egalitarian society, the dyadic asymmetries are uncommon with bidirectional and less severe aggression with a higher level of tolerance and conciliatory tendency.

The social hierarchy has a direct impact on the heterogeneous distribution of limited resources between individuals with different social status (Thierry 2004). For example, by imposing dominance, the high-ranking individuals can access more resources than the low-ranking ones, which ultimately increase their fitness of the former. Therefore, to balance the disadvantages of living in a group, the individuals make a trade-off by adapting different behavioral strategies through policing specific inter-individual relations (Sueur et al. 2011).

While living in a multi male-multi female society with linear dominance hierarchy, the macaque exhibits polygamous and promiscuous mating systems (Soltis 2004). The reproductive success of males increases with siring offspring by accessing the receptive females (Trivers 1972), and reproductive success of females depends on the survival of her infants (Kappeler and van Schaik 2002). Therefore, where the male sexual strategy is to mate more with receptive females by monopolizing mate resources; the females try to incorporate selective mate choice with polyandrous matings, which act as a conflict of interest between sexes. Hence, both the sexes adapt various sexual strategies and counter-strategies to increase their own reproductive success against each other (Clutton-Brock 1974). For example, since copulation requires a high energy, males are more likely to mate females when the chance of insemination is high. In contrast, females adapt various counterstrategies to conceal the fertile phase by making ovulation unpredictable (Engelhardt et al. 2005, 2007).

The dominant rank of an individual has a major role in its reproductive success, which ultimately helps to employ reproductive strategies against intra-sex and inter-sex group members (Kappeler and van Schaik 2002; Wrangham 1980). By involving in intra-sexual context competition for mate resources, the dominant males get more access to receptive females than the subordinates, representing a high correlation between dominance rank and mating success in males (*M. fuscata*: Soltis et al. 2001; *M. fascicularis*: de Ruiter et al. 1994). On the contrary, the subordinate males adapt alternative reproductive strategies like sneak copulation in the absence of dominant male to secure their reproductive success through sperm competition (e.g. *M. fuscata*: Soltis et al. 2001; *M. mulatta*: Manson, 1996; *M. fascicularis*: Gygax 1995). As an alternative reproductive strategy, the dominant females also impose dominance over subordinate females to increase their relative reproductive success. However, the behavioral strategies and counter-strategies vary in each context due to the phylogenetic drift and variation in environmental factors for different species and subspecies (Thierry 2007).

Ten sub-species of long-tailed macaque (*Macaca fascicularis*) are widely distributed across South-East Asia. Most of the sub-species are isolated in small island habitats (Groves 2001), which are susceptible to degradation due to both natural calamities (El Niño, global warming, tsunami and cyclone) and anthropogenic pressures (shrimp farming, ship-building, agriculture and logging) (Carew-Reid 1990; Nelleman 2007). In the varying environmental constraints, the small isolated populations of this sub-species are expected to adapt different behavioral strategies than other sub-species, which might result in variations in their social organization and life-history traits. In the present study, the Nicobar long-tailed macaque (*Macaca fascicularis umbrosus*), endemic to the three-small isolated off-shore Nicobar Islands of India, has thus been considered as one of the suitable model species to understand their flexibility and adaptability of life-history traits and behavioural strategies in such stressful dynamic environmental conditions.

The Nicobar long-tailed macaque is one of the less-studied species in the context of scientific understanding. Prior to this study, there were two short-term studies (Umapathy et al. 2003 and Sivakumar 2010) addressing the population status and group structure of this sub-species. The baseline information on social organization and life-history traits which are essential to understand the behavioural strategies adapted by a species, was unavailable for this sub-species. Therefore, I conducted an exploratory study on reproductive behavior of Nicobar long-tailed macaque to gather that baseline information, and further compared the findings with information available on other well studied sub-species of long-tailed macaque. The ultimate goal of an individual is to survive and maximize its reproductive output, for which individuals adapt various strategies and counter-strategies in their everyday life. Therefore, exploring the social structure and organization of Nicobar long-tailed macaque in respect to their reproductive behavior was considered as an appropriate approach to understand adapted behavioural strategies of this sub-species.

1.2. Importance of the Study

Nicobar long-tailed macaque is restricted within three tropical islands having longer the monsoon period (May-November) with high rainfall (4,200 mm) supporting rich tropical rainforest vegetation (Velankar et al. 2016). This subspecies got isolated from other subspecies in Pleistocene epoch (~11,700 years) and had sustained ever since (Fooden 1995). In December 2004, a devastating tsunami hit the Nicobar Islands which subsequently destroyed most of the coastal habitats (Ramachandran et al. 2005), indeed being one of the primary habitats for the species as well (Umapathy et al. 2003). A post-tsunami survey conducted on 2005 also revealed a sharp decline in the population in coastal areas and alteration of demographic characteristics in these macaques (Sivakumar 2010). In this scenario, the recent population trends of this sub-species, and strategies adapted by them to survive in such stressful condition needs further understanding.

As the habitat parameters influence many of the behavioral strategies of the animal, these macaques may have eventually adapted to or acquired strategies depending on the environmental and ecological conditions during the long period of separation from other population. In this context, understanding of their survivability in a stressful catastrophic prone region might shed light on their adaptive strategies. It would also provide an understanding of any variations or similarities in behavioral aspects between the sub-species occurring in different islands with different degree of isolation and habitat conditions.

1.3. Objectives

After considering the above-mentioned importance of the study, I proposed my doctoral dissertation on the topic entitled "**A study on reproductive behaviors of Nicobar long-tailed macaques (*Macaca fascicularis umbrosus*) in the Nicobar Islands, India**" to addresses the following objectives with specific questions:

1. To study the dominance hierarchy among individuals and its influence on the social relationship in *M. f. umbrosus*
    i. What is the pattern of the dominance hierarchy among males and females in the group?
    ii. How the dominance hierarchy influences the social relationship between males and females?
    iii. How the dominance hierarchy influences mate competition and selection?
2. To study the reproductive behavior and breeding seasonality in *M. f. umbrosus*
    i. What is the pattern of timing of birth (Birth seasonality)?
    ii. What factors influence such timings of birth pattern?
    iii. Do female initiate mating?
    iv. Do females establish courtship with males?
    v. Is male rank and female rank related to mating?

vi. Is post-conception mating present in the subspecies? If yes, what is a frequency of such mating and individual males involved in mating and their role?

vii. Do males migrate?

1.4. Study Animal

1.4.1. Macaques: Macaques, the old-world monkeys of Cercopithecinae subfamily (Tribe: Papionini), are the most successful and widely distributed non-human primate radiation (Thierry et al. 2004). So far, globally 23 macaque species are recognized (Thierry et al. 2004; Li et al. 2015). Among them, the distribution of 22 species is restricted to South and South-east Asia, while a single species Barbary macaque (*Macaca sylvanus*) is distributed in Northern Africa (Thierry et al. 2004). This wide zoogeography of macaques is the result of the dispersal of species in evolutionary time scale (Abegg and Thierry 2002). However, the geographical distribution is ultimately shaped by the species-specific adaptation, inter-specific competition, climatic and eustatic changes along with periodic glaciations (Abegg and Thierry 2002). The paleontological and molecular evidence suggest that 8-7 million years ago, in the late Miocene age, the monophyletic macaque clade evolved in Africa. Later, 5.5 million years ago, they dispersed in Eurasia and had split into several phyletic lineages. Based on the external male genitalia and copulation pattern, Fooden (1976) classified macaques into four broad lineages: *silenus-sylvanus* (*M. silenus*, *M. nemestrina, M. tonkeana, M. maurus, M. ochreata, M. brunnescens, M. hecki, M. nigrescens, M. nigra* and *M. sylvanus*), *fascicularis* (*M. fascicularis, M. mulatta, M. cyclopis* and *M. fuscata*), *arctoides* (*M. arctoides*), and *sinica* (*M. sinica, M. radiata, M. assamensis* and *M. thibetana*). Further, Delson (1980) modified it by placing monophyletic *M. arctoides* into *sinica* group and created another monophyletic group called *sylvanus* for *M. sylvanus*. Once again, Groves (2001) reclassified it into six groups where he removed *M. mulatta, M. fuscata* and *M. cyclopis* from fascicularis group and form new *mulatta* group and put Sulawesi macaques into a different group. However, Zinner et al. (2013) again modified macaque lineage classification into seven groups which includes three monophyletic (*M. sylvanus, M. arctoides* and *M. fascicularis*) and four polyphyletic (*sulawesi*, *mulatta*, *sinica* and *silenus*) groups. Furthermore, recent molecular studies with different genetic markers came up with various distinct results which made evolutionary relationships of macaques more complicated and controversial (Jiang et al. 2016). However, the two recently discovered macaques, Arunachal macaque (*M. munzala*) and White-cheeked macaque (*M. leucogenys*) were not included in any of those studies.

1.4.2. Long-tailed macaque: *Macaca fascicularis*, known as long-tailed or crab-eating macaque is the second widely colonized non-human primates, trailing only *M. mulatta*. According to the divergence time estimation, the *M. fascicularis* had split from *fascicularis/mulatta* lineage between 1.79 and 2.92 million years ago (Jiang et al. 2016). *M. fascicularis* is distributed across South-East Asian countries including Bangladesh, Brunei, Cambodia, India, Indonesia, Lao PDR, Malaysia, Myanmar, Philippines, Singapore, Thailand, Timor-Leste and Vietnam (Fuentes 2011; Gumert 2011). The natural distribution of the species is chiefly confined on the western side of the Wallace line; however, the populations beyond eastern side of the Wallace line are the result of historical introduction by the humans (Gumert 2011). Again, ethnophoresy is the cause behind the population colonization in Mauritius, Ngeaur, Island of Palau, West Papua, Tinjil Island and Kabaena Island of Sulawesi (Gumert 2011). The long-tailed macaques are predominantly found in swamp forests, riverine forests and edge habitats; however, they are also distributed in a wide variety of habitats including bamboo forest, broadleaf forest, coastal regions, evergreen forests, mangroves and secondary forest habitats (Gumert 2011). Being an edge species, the long-tailed macaques successfully inhabit human-induced fragmented forests and have also adapted to explore the edge of various anthropogenic environments (Sha et al. 2009). After considering their wide geographical range and commensal behavior, the IUCN/SSC Red list of threatened species 2008 classified this macaque species as least concern. However, the widespread macaque population is rapidly declining due to the habitat loss, habitat degradation, habitat alterations, uncontrolled trades and conflict with expanding human population (Eudey 2008). Congruent with the wide distribution, the long-tailed macaque varied in their morphology across locations. Based on their morphological variations, Groves (2001) classified them into ten sub-species **(Figure 1.1.)**. Among them, most of the sub-species are geographically isolated and accorded varying conservation status. Wherein, *M. f. fascicularis, M. f. aurea* and *M. f. philippinensis* are widely distributed in the South-east Asian mainland; *M. f. articeps, M. f. condorensis* and *M. f. karimondjiwae* are isolated in small shallow-water fringing islands; and *M. f. umbrosus, M. f. fusca, M. f. lasiae* and *M. f. tua* are restricted in small deep-water fringing islands.

1.4.3. Nicobar long-tailed macaque: The study animal in the present study is the Nicobar long-tailed macaque (hereafter, NLTM) or Nicobar crab-eating macaque (*Macaca* *fascicularis umbrosus*, Miller 1902). This sub-species of long-tailed macaque is endemic to the three small isolated Nicobar group of islands, India, one central (Katchal) and two southern Nicobar group of islands (Great Nicobar and Little Nicobar). Great Nicobar (895.48 km^2), Little Nicobar (138.25 km^2) and Katchal (139.39 km^2) are lying between 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 respectively (**Figure 1.2.**). Due to the unavailability of the population data, NLTM was not evaluated and remained Data Deficient (DD) up to IUCN Red List 2000. However, due to high endemism, this sub-species was accorded the highest protection under 'Schedule-I' of the Indian Wildlife Protection Act (Anonymous, 1972). Based on the first-ever survey on NLTM by Umapathy et al. (2003) and 2003 -SSAP-CAMP report (Molur et al. 2003) the estimated population was 4800 individuals across the three islands and was subsequently evaluated as Near Threatened (NT) in IUCN Red List 2004. In December 2004, devastating tsunamis hit these islands and had destroyed maximum coastal habitats. Therefore, after considering restricted distribution and susceptibility of its habitat to natural calamities, it is accorded Vulnerable (VU) on IUCN Red List 2008. Moreover, after a post-tsunami population survey, Sivakumar (2010) reported a sharp decline of the coastal NLTM populations and alteration of group composition.

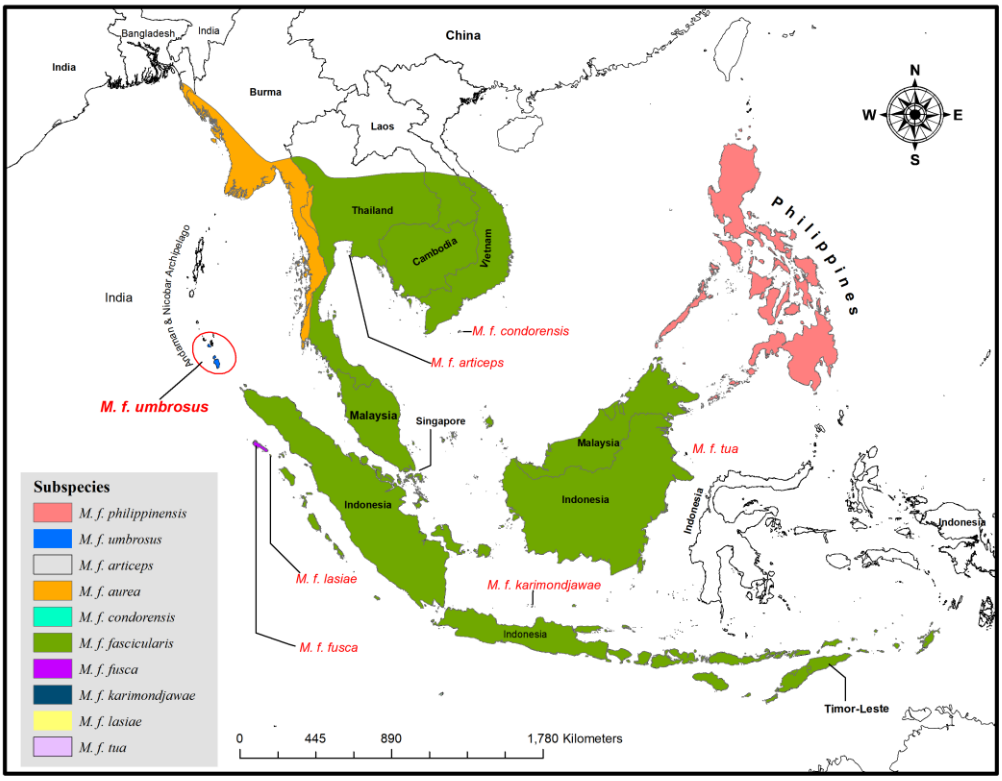

Figure 1.1. Distribution of ten sub-species of long-tailed macaque (*Macaca fascicularis*)

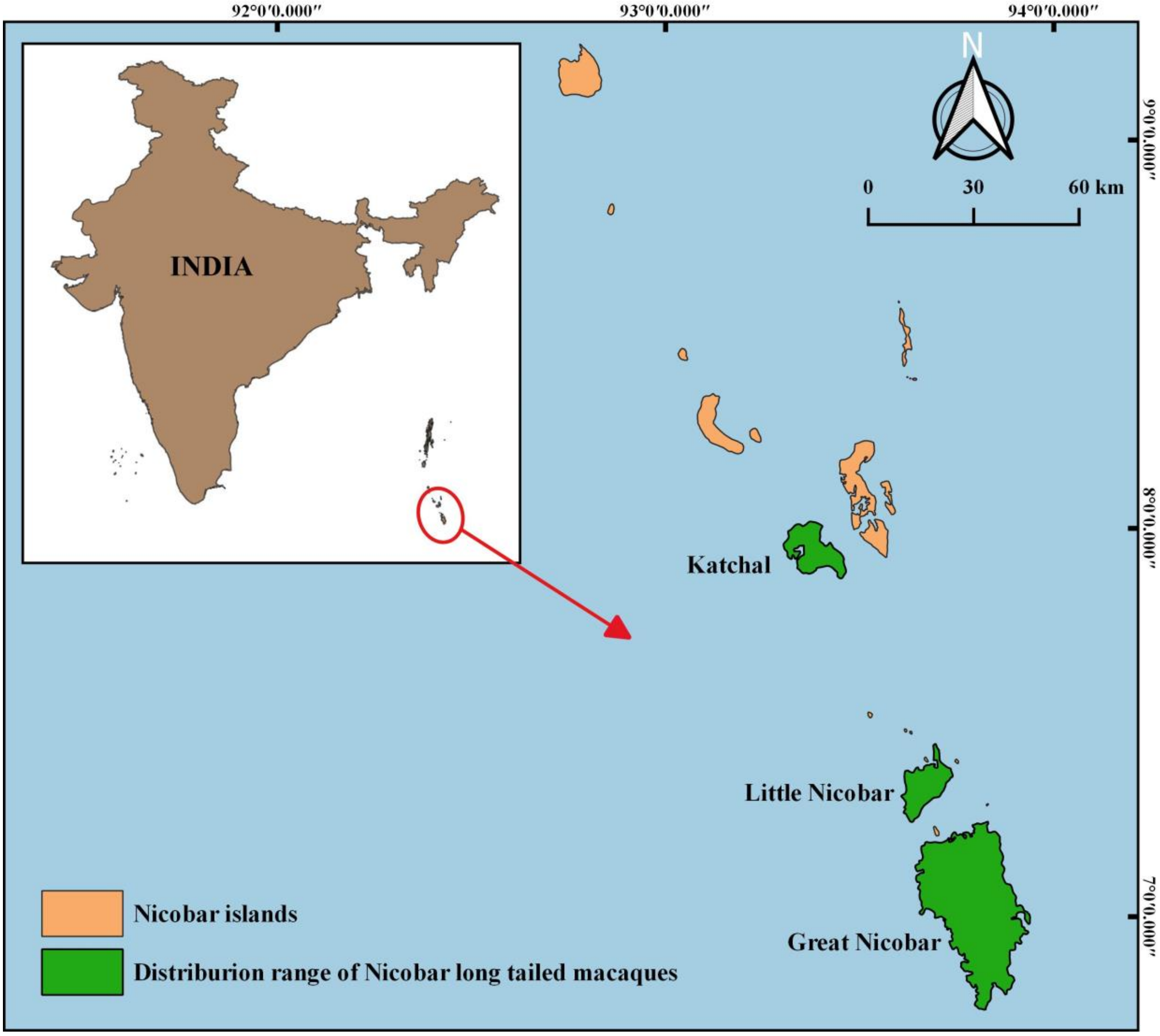

Figure 1.2. Distribution of Nicobar long-tailed macaques (*Macaca fascicularis umbrosus*) in the Nicobar Islands.

1.5. Study Area

1.5.1. Geographical location: Great Nicobar, Little Nicobar and Katchal, where Nicobar long-tailed macaques are distributed, are part of the Andaman Nicobar archipelago. This 800 km long island chain is situated in the Indian Ocean, 1700 km offshore of the mainland India. The Andaman and Nicobar island complex are a conglomeration of 572 islands which lies in the northern tropical hemisphere between 6° 40′ - 14° 45′ N and 92° 8′ - 94° 1′ E. This island complex is broadly divided into two island classes, namely Andaman (6408 km^2) and Nicobar (1841 km^2) group of islands. Among them, a total of 22 Nicobar Islands are geographically categorised into three distinct groups are northern (Car Nicobar group), central (Nancowry group) and southern (Great Nicobar group) Nicobar group of islands.

1.5.2. Origin and geology: The Andaman and Nicobar island arc is situated over the Burma microplate, which is surrounded by the Indian, Eurasian, Sunda and Australian plates. About 100 million years ago, in the late Cretaceous age, the Indian plate had split from the supercontinent Gondwanaland and started moving towards north. Then, in the Eocene era, it collided with the Eurasian plate and started clock-wise rotation which had ultimately torn apart the Eurasian plate and formed the Burma microplate in the late Oligocene age. During the post Oligocene and middle Miocene period, due to seduction of the Indian plate under the overriding Burma micro-plate along with deep Sunda trench, the Andaman Nicobar archipelago was formed as back-arc island chains. Being the outer-arc island, the topography varies from flat coastal to steep creek and undulating inland to hilly mountains. The highest elevation of the Great Nicobar, Little Nicobar and Katchal islands is 642 m, 470 m, and 230 m ASL respectively.

1.5.3. Climate: The Nicobar Islands have a tropical, humid, maritime climate. According to the Planning Commission, Government of India, these islands fall under AN-3 Southern zone of XV agro-climatic zone (Island region). Being closer to the equator these islands has a uniform climate with less variation in maximum (32°C) and minimum (20°C) temperature throughout the year. The humidity ranges between 65% and 89% throughout the year. The Nicobar Islands receives rainfall all through the year due to both south-west and north-east monsoon. The monsoon sets in the month of May, and the islands receive 300 to 500 mm of rain each month till November. In the other months, the rainfall is below 100 mm. The rainfall data of the last six years shows the mean annual rainfall of Great Nicobar to be 3200 mm (Indian Meteorological Department, Andaman Nicobar and Lakshadweep of Islands).

1.5.4. Biodiversity: Although, Nicobar Islands are part of the Indian territory, its biodiversity has an affinity towards the near most sundaic counter-parts particularly that of Sumatra, Indonesia. Due to its rich biodiversity and high endemism, this region also falls under Sundaland Global Biodiversity Hotspot (Chitale et al. 2015). There are two national parks in Great Nicobar Island, namely Campbell Bay National Park and Galathea National Park. Moreover, Great Nicobar Island was included as the 9th Indian Biosphere Reserve by UNESCO in 2013.

1.5.4.1. Flora: The Nicobar group of islands have a forest cover of 74% (1362.9 km^2) of the total geographical area. The vegetation is predominated by the tropical evergreen forest (99.63%) along with relative lesser amounts of moist deciduous forest (0.16%) and coastal mangroves (0.20%) (Reddy et al. 2016). However, about the coastline, the forest of Nicobar Islands is divided into coastal and inland forests. The coastal forest is sub-divided into littoral forest and mangrove forest, and the inland forest is categorized into tropical evergreen forest, mixed evergreen forest, moist deciduous forest, lowland swamp forest and grasslands (Nehru 2013). Apart from the natural vegetation, Nicobar Islands' vegetation also consists of plantation, scrublands and agricultural lands, orchards of cash crops like cotton, rubber, cashew, coconut and betel nut. A total of 390 plant species were recorded from this region, and among them, the evergreen forest type accounted the highest number of plants (214) with 36 endemic and 7 rare species. There are 134, 75 and 33 species along with 22, 14 and 5 endemic species recorded from littoral swamp, lowland swamp and mangrove forests respectively (Porwal et al. 2012). Among the three Nicobar long-tailed macaque inhabiting islands, the tree density is highest in the Great Nicobar (996.9/ha), followed by Little Nicobar (910.3/ha) and Katchal (825.5/ha). The average basal area of the forest of Great Nicobar (91.3 m^2/ha) is also greater than the Little Nicobar (87.3 m^2/ha) and Katchal (75.2 m^2/ha) (Umapathy et al. 2003). When compared to the tropical rainforests of mainland's Western Ghats, the vegetation of these islands is more pristine and robust.

1.5.4.2. Fauna: The rich faunal diversity of the Andaman and Nicobar archipelago is composed of 8386 species (including marine life) with 13.3 % (1117) of endemicity. The geographical separation between the islands is the major factor resulting in rich faunal diversity with high endemism. Among herpetofauna, 15 species of reptiles like Nicobar pit viper (*Trimeresurus labialis*) and Kentor pit viper (*Trimeresurus cantori*); and 2 amphibians (*Lymnonectus shompenorum* and *Polypedates insularis*) are endemic to Nicobar Islands (Andrews 2001). A total of 21 non-marine snakes including world longest reptile namely reticulated python (*Python reticulatus*) are recorded from Nicobar group of islands. All the four endangered sea turtles *viz.* leatherback turtle (*Dermochelys coriacea*), hawksbill turtle (*Eretmochelys imbricata*), green turtle (*Chelonia mydas*) and olive-ridley turtle (*Lepidochelys olivacea*) regularly lay eggs on the beaches of the Nicobar Islands. Sankaran (1998) recorded 73 inland bird species along with 9 endemics in various Nicobar Islands. Among the endemic birds, the Nicobar Megapode (*Megapodius nicobariensis*) is distributed in seven Nicobar Islands, whereas Nicobar bulbul (*Hypsipetes nicobariensis*) and Nicobar parakeet (*Psittacula caniceps*) are restricted respectively in central and southern Nicobar group of islands. The Andaman wild pig (*Sus scrofa andamanensis*) is the only large terrestrial mammal distributed across all the Nicobar Islands. The endangered marine mammals like Dugong (*Dugong *dugon*), Blue whale (*Balaenoptera musculus*) and Sperm whale (*Physeter macrocephalus*) have also been recorded from the surrounding sea of Nicobar Islands. Among other terrestrial endemic mammals, the endangered Nicobar tree shrew (*Tupaia nicobarica*) is restricted only to the Great Nicobar and Little Nicobar Islands, while the Nicobar flying fox (*Pteropus faunulus*) is restricted in eight central Nicobar Islands. The Nicobar long-tailed macaque is the only primate found in the Andaman and Nicobar archipelago and their population is restricted to these three Nicobar Islands.

1.5.3. People: Among the 22 islands of Nicobar, 12 are inhabited by 36,842 humans (Census 2011). There are two indigenous mongoloid tribal groups inhabiting the Nicobar Islands namely, Nicobaris and Shompen. Nicobaris are the predominated local tribe inhabiting in the cost of all islands and comprises 63.66% (23,681) of the total population of Nicobar group of islands. The dialect and culture of essential horticulturists, fisherman-hunter Nicobaris varies across island and island groups (Sankaran 2005). However, about 229 semi-nomadic Shompens inhabit only in the distinct coastal and forest pockets of Great Nicobar Island. Therefore, the major part of the Nicobar group of islands is designated as tribal reserve under the Andaman and Nicobar Tribal Protection of Aboriginal Tribes Regulation (1957). Ever since the late 60s to till date, there have been immigration and colonization of people from mainland India, sharing 35.72% of the total population of the Nicobar Islands. While both aboriginal tribes extract resources from forest and sea by practicing complete sustainable way of living, the mainlanders adapt chemical farming by irreversible transformation of forest land to agricultural fields (Sankaran 2005). For example, in 1969, 1499.65 hectares of forest was cleared to accommodate 337 ex-servicemen on the south-eastern coast of the Great Nicobar, and about 600 hectares of forest land converted to rubber plantations in the Katchal Island (Sankaran 2005). Poachers from Thailand often come to Southern Nicobar group of Island for illegal collection of crocodile, monitor lizard, sea cucumber, fish and may also hunt macaques (Umapathy et al. 2003). Therefore, with the inflow of expanding mainlanders and their anthropocentric activities, the natural habitat is changing rapidly, which becomes a major threat to the biodiversity of this region.

1.5.4. Impact of Tsunami 2004: On 26th December 2004, at 00:58:50 UTC a tsunamigenic earthquake with a magnitude of 9.3 Richter scale originated in the offshore of northern Sumatra and subsequently a devastating tsunami was formed in the Indian Ocean. The Nicobar groups of islands, situated less than 450 km from the epicentre of the earthquake, received a massive hit of the tsunami. Along with the huge loss of human lives, the devastating tsunami caused irreversible damages to the biodiversity and ecosystems. All the three islands inhabited by macaques were highly affected by the tsunami, wherein, 5.48% (51.91 km^2), 6.77% (10.04 km^2), and 13.52% (21.80 km^2) landmass of Great Nicobar, Little Nicobar and Katchal were inundated respectively. The magnitude of the damage was the highest in lowland vegetations of mangroves and littoral forests, wherein 89% and 94.3% mangrove forests of Great Nicobar and Katchal were completely destroyed by the waves and upheaval; 86.3% and 82% littoral forest submerged completely in the respective islands (Porwal et al. 2012). The high losses of coastal lowland and beach forests also affected other faunal inhabitants in those habitats. About 70% of Nicobar megapode population declined due to the loss of their suitable habitats (Sivakumar 2009). Similarly, most of the sea turtle nesting beach were destroyed or inundated which could have also affected the population of several endangered turtles (Andrews et al. 2006). The post-tsunami survey (Sivakumar 2010) reported that, apart from the sharp decline of macaque population in coastal zones, the proportion of juveniles in the groups also declined. Along with the terrestrial ecosystems, the tsunami also caused havoc to the marine ecosystems. In Nicobar Islands, there was extensive tsunami-induced damage (41-100%) to the coral reef, sea-grass and sea-weed ecosystems, which supports food and shelters for a diverse faunal community including whale, dolphin, dugong, turtle, octopus, crab, shrimps, giant clams and various fishes (Ramachandran et al. 2005). Overall, the intensive and irreparable damages of tsunami have pushed various floral and faunal organisms towards their threshold of survival.

1.5.5. Human-macaque interface: The wide distribution and close association of long-tailed macaque with human population helped them to adapt and live in human-modified environments (Wheatley 1999). In several places of human-macaque interface, the synanthropic association between macaques and humans are commensal and the relationship also has mutual and parasitic components (Jones-Engel et al. 2011). Some positive interactions like cultural and religious association of human with macaque have also increased the inter-species cohesion. For example, the proximity of macaques to Hindu and Buddhist temples along with other religious and spiritual beliefs supports mutualistic relations (Gumert 2011). The long-tailed macaque is also the most researched animal in the world, particularly in biomedical and technological science researchers (Kyes et al. 1998). Despite of their extensive contribution to the human society, there are negative impacts of humans on the long-tailed macaque. These include anthropogenic habitat alteration which along with the expanding human population is leading to depredation of the long-tailed macaque’s natural habitats, ultimately pushing them to cohabit with a human in human-dominated landscapes. They are also considered as one of the worlds worst invasive species (IUCN 2000) for their high degree of interface with humans. The macaques have been known to inflict high rate of crop raiding, crop depredation, are considered as urban-pest, and are often involved in aggressive interactions toward humans; thus, the human-macaque conflict is the rising issue in several South-East Asian countries (Gumert 2011). Similarly, the Nicobar long-tailed macaques also raid croplands and coconut orchards in Nicobar Islands, and consequently the farmers use catapult, air-guns and even trained dogs to drive them away (Umapathy et al. 2003). The dog-macaque interaction often goes fatal for either of them. At times the aboriginals also hunt macaques by using fresh *Pandanus* fruit as bait (Umapathy et al. 2003). One of the major negative consequences of macaque-human association is the transmission of infectious diseases (Gumert 2011). Due to the biological similarity between macaques and humans, several infectious agents like *Cercopithecine herpesvirus 1, Simian immunodeficiency virus, Simian foamy virus, Simian type D retrovirus* and *Rabies* can transmit from long-tailed macaques to human; while, *Mycobacterium tuberculosis*, an endemic human respiratory virus is the most significant threat which can be transmitted from humans to macaques (Engel and Jones-Engel 2011). It is thus clear that in human-macaque interface, the human behavior is the major influence of macaque-to-human behaviors, which ultimately develops the platform for human-macaque conflicts (Jones-Engel et al. 2011).

1.6. Study Site

During the initiation phase of the study, a reconnaissance survey was conducted in all three habitat islands of Nicobar long-tailed macaque. After considering accessibility and logistic supports, Campbell Bay of Great Nicobar Biosphere reserve in Great Nicobar Island was selected to carry out the study (**Fig. 1.3**). Campbell Bay is a coastal (4.54 km^2) village situated on the south-eastern coast of Nicobar island, lying between 93˚ 55' 8.417" - 93˚ 56' 51.95" E and 7˚ 1' 39.34" - 6˚ 59' 31.47" N. The study site is a forest fragment isolated from the rest of the forest by an air-defense base. Being a tropical island situated in the Indian Ocean, this area receives a high amount of rainfall (4200 mm) throughout the year, and the temperature through the year varies between 22°C and 32°C. The heterogeneous vegetation cover of this area is chiefly composed of primary hilly tropical evergreen forest, low-land littoral forest, vegetable orchards, and coconut and areca nut plantations. Though there are a few huts and small houses situated in between orchards and plantations, the major human settlements are in the eastern part of this area.

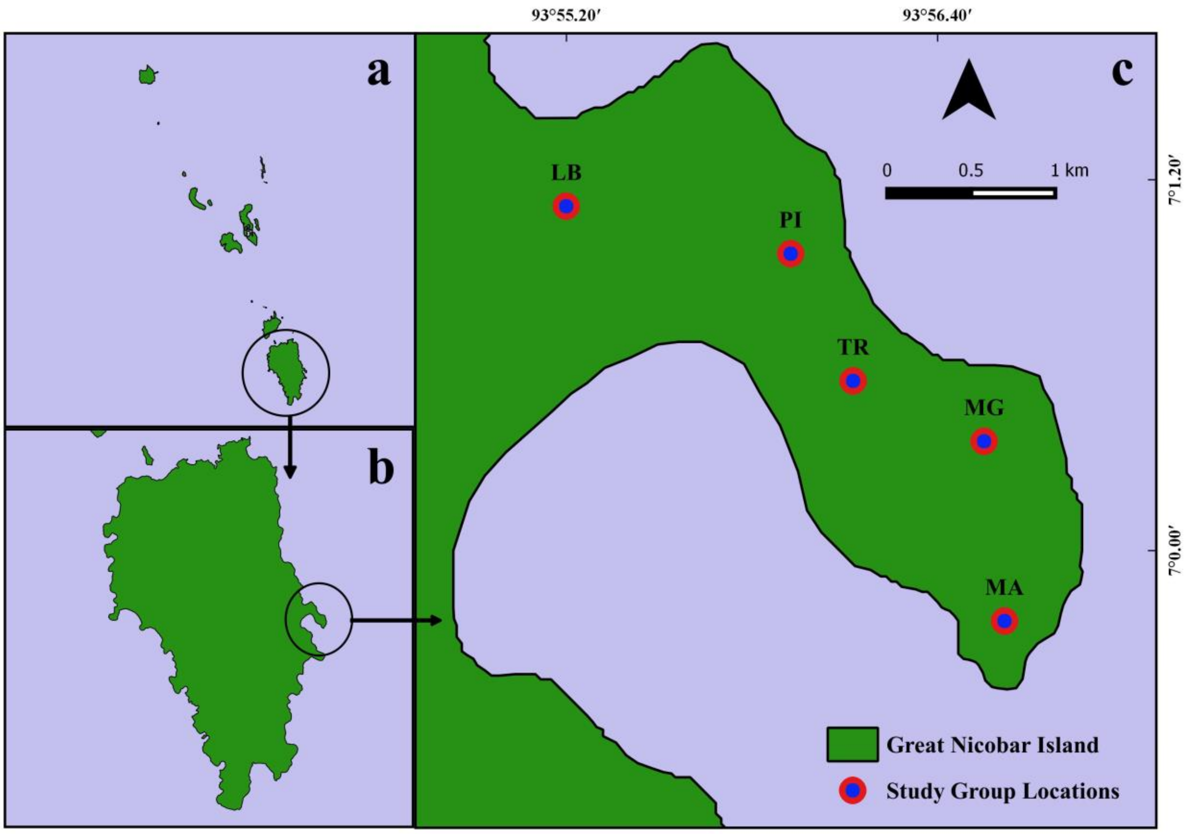

Figure 1.3. Study site: (a) Great Nicobar Island in Nicobar group of Island, (b) Campbell Bay in Great Nicobar Island and (c) locations of study groups in Nicobar Campbell Bay**.**

1.7. Study Groups

The study site was inhabited by five wild groups (LB, PI, TR, MG, MA) of Nicobar long-tailed macaques (**Fig. 1.3**). All the five groups were selected for the study; however, data on different aspects were collected independently from a different group. Whereas all groups were monitored for demography and population dynamics, the TR group, for convenient logistic reasons, was the focal group for a long-term behavioral study. All members of TR group and males of PI and MG groups were individually identified using their facial morphology along with visible wood marks. Based on physical appearance such as body size, canine size of males, nipples size of females, the age of individuals was categorized into four classes: adult (≥ 4 yr), sub-adult (2.5-4 yr), juvenile (6 m-2.5 yr) and infant (≤ 6 m). The fieldwork was conducted between January 2013 and March 2016. The first four months (January 2013 to April 2013) were spent to habituate TR group for behavioral data collection. However, data on each aspect studied during this tenure were collected independently by following different standard methodology (Altmann 1974) and thus effort for each aspect varied.

1.8. Organization of Thesis

My doctoral dissertation is organized into five technical chapters along with the introduction and synthesis of the study. In **Chapter 1** ‘**Introduction: Long-tailed macaques of Nicobar Islands**’ the background of the study has been built up with the baseline information about the macaques, and also discusses the importance of the study. The second part of the first chapter provides general information about the study species and the socio-ecological conditions of its habitat. ‘**Demography and birth seasonality**' (**Chapter 2**) is the first technical chapter explaining the demographic structure and population dynamics of these macaques. **Chapter 3**, ‘**Social organization: Influence of hierarchy on society’** establishes the dominance hierarchy in Nicobar long-tailed macaque, and explores its influence on society. The third technical chapter ‘**Reproductive behaviors: Strategies and counter-strategies**’ (**Chapter 4**), describes in detail the variations of reproductive behaviors in Nicobar long-tailed macaques with reproductive status of females, along with describing the strategies and counter strategies adapted by both sexes. The next chapter (**Chapter 5**), ‘**Rank changeover by challenge: Consequences of a Male Reproductive Strategy on Society'** describes an incident of ‘rank changeover by challenge' and its impact on ranging and reproductive behaviors of a wild group of Nicobar long-tailed macaque. The last technical chapter (**Chapter 6**) ‘**Between-group encounter: When not to fight**’ describes the inter-group relationships of these macaques along with those factors determined the odds of winning of a between-group contest. I conclude the thesis by summarising the findings in **Chapter 7** ‘**Synthesis**’.

CHAPTER 2

Demography and Birth Seasonality

“ The power of population is indefinitely greater
than the power in the earth to produce subsistence for man.”

‡ Thomas Malthus ‡

2.1. Introduction

Demographic characteristics are the evolutionary consequences of life history traits which is fixed in a population as they maximize individual reproductive output (Chapman and Rothman 2009; Cords and Chowdhury 2010; Singh et al. 2016). Demographic characteristics i.e. group size, age and sex composition of the group, birth rate, mortality, migration frequency of individuals, and growth rate, that change over a time due to ecological constraints (Dittus 2004). Predation pressure and intra-group competition over food are the two major factors that determine the upper limit of group size, which directly relates to birth and survival rate of individuals (Wrangham 1980; van Schaik 1983). In the long-tailed macaque, *M. fascicularis*, birth rate and early infant survival decreased with increase in group size due to over-optimal group size (van Schaik et al. 1983). Contrary to this, group size positively correlated with the birth rate but no relationship was found between group size and infant survival in the Japanese macaque, *M. fuscata* (Takahata et al. 1998). Overall, group size influences intra-group resource competition, which in turn affects reproductive output of a group.

Age-sex composition also plays a major role in the reproductive output of a group. In macaques, reproductive success of females increases with the increased proportion of males (adult and sub-adult) in the group due to increased immature survival because of better protection of immatures against infanticide by outer-group males (Ryan et al. 2007). While birth rate decreased with increase in number of females in the group in lion-tailed macaque *M. silenus* (Kumar 1995) and *M. fuscata* (Takahata et al. 1998), both birth rate and infant survival rate decreased in the Taiwanese macaque, *M. cyclopis* (Hsu et al. 2006). Thus, the reproductive success of females is also dependent on intra-group feeding competition.

Birth seasonality refers to the regular fluctuation of births over a year (van Schaik and van Noordwijk 1985). In heterogeneous environmental regimes, seasonality affects behavioral ecology and reproduction in various ways including timing and the narrowness of the breeding peak (Brockman and van Schaik 2005; Janson and Verdolin 2005). Additionally, environmental stress may also affect birth seasonality (Janson and Verdolin 2005). Macaques exhibit various patterns of reproductive seasonality, from sharply discrete matings and births, to complete non-seasonality where matings and births are distributed throughout the year (van

Schaik and Brockman 2005). Whereas Barbary macaque (*M. sylvanus*), Bonnet macaque (*M. radiata*), Rhesus macaque (*M. mulatta*), Japanese macaque (*M. fuscata*), Tibetan macaque (*M. thibetana*) and *M. cyclopis* show discrete reproductive seasonality, *M. fascicularis, M. silenus,* Toque macaque (*M. sinica*), and Celebes macaque (*M. maurus*) give births throughout the year with distinct birth peaks, and black crested macaque (*M. nigra*) and Tonkean macaque (*M. tonkeana*) are completely non-seasonal without any prominent peak (Bercovitch and Harvey 2004).

M. fascicularis is widely distributed in Nicobar, Bali, Java, Kalimantan, Lesser Sunda and Peninsular Malaysia, and is largely confined to islands (Gumert 2011). *M. f. umbrosus,* one of the ten sub-species of *M. fascicularis*, is found on three offshore islands of the southern and central Nicobar archipelago including Great Nicobar, Little Nicobar and Katchal (Umapathy et al. 2003) of India. These islands were hit by a massive earthquake followed by a tsunami in the year 2004, which drastically reduced the population of macaques (Sivakumar 2010). Velankar et al. (2016) reported that the population is in the process of recovering from the crash after ten years. The recovery in population size may be dependent on adjustments or alterations in the life-history traits of the species *viz*. birth rate, survival rate, emigration and immigration, as all these play a major role in regulating population growth. Therefore, exploring the demography and birth seasonality in this macaque, and compare it with other sub-species will provide farther understanding about the survival strategies of these macaques in such stressful condition. Moreover, conservation and population management requires basic data on demographic structures and population dynamics, the first ever data on the demography and birth seasonality of *M. f. umbrosus* in this small, isolated, and environmentally stressed population will set a platform for long term monitoring of population dynamics.

2.2. Materials and Methods

2.2.1. Data collection: The study was carried out on five groups of Nicobar long-tailed macaques (LB, MG, PI, TR and MA) during January 2013 to December 2015 (**Figure 2.1**). Due to remoteness and inaccessibility of the habitat, frequent finding of groups and collecting data on different aspects from all these study groups was difficult. Data on group size and group composition was collected for four groups (LB and MG from March 2014 to March

2015, PI and TR from March 2013 to December 2015), birth data for all the five groups from January 2013 to December 2015, infant survival data for two groups (MG and TR) and inter-birth interval data for one group (TR).

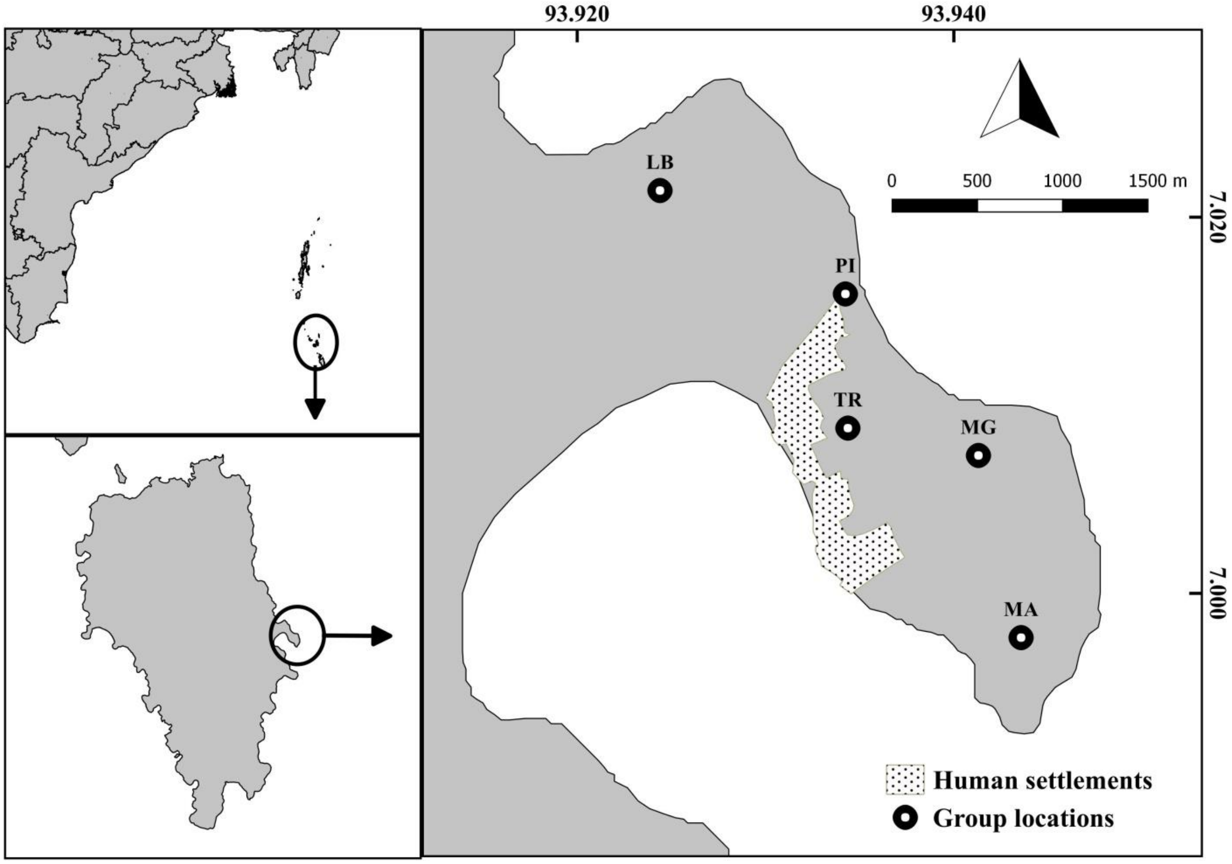

Figure 2.1. Group locations in the study site, Campbell Bay, Great Nicobar Island.

The data on group size and group composition was collected fortnightly for each group for two years for LB and MG groups, and for three years for PI and TR groups. A group count was conducted while all individuals were crossing a road or moving for roosting, usually in a single file. Based on physical appearance such as body size, canine size of males, nipples size of females, the age of individuals was categorized into four classes: adult (≥ 4 yr), sub-adult (2.5-4 yr), juvenile (6 m-2.5 yr) and infant (≤ 6 m). Birth data was recorded fortnightly in two groups (PI and TR) for three years and two other groups (LB and MG) for two years.

The group TR was selected for a detailed study on demography and it was followed for at least 10 days in a month across the entire study period. All individuals in the group were identified using their facial morphology, and wounds and marks on the body. The birth data was collected along with the identity of the mother.

Monthly rainfall data of the last six years from 2010 to 2015 of Nicobar Islands was obtained from the Indian Meteorological Department, Andaman Nicobar and Lakshadweep group of Islands, Ministry of Earth Science, Government of India.

2.2.2. Data analysis: The classes of sub-adult males, juveniles and infants were combined into one category as immature, while, for some analyses, adult males and adult females were put together as adult individuals. The age-sex ratio was computed and analyzed for four categories: adult male (ADM), adult female (ADF), adult individual (AD), immature (IMM) and infant (INF). In a fission-fusion macaque society, temporary absence from the main group is a very common phenomenon (Kumar et al. 2001), and hence, for group dynamics, an individual was considered to be part of a group only (or not) if it was present (or absent) for a continuous stretch of at least 15 days.

Mean group size, number of individuals in each age-sex class (ADM, ADF and IMM) and age-sex ratio (ADM:ADF, AD:IMM, ADF:IMM and ADF:INF) for each group were calculated using the data collected in the month of March in each year.

The births recorded for all adult females of the four study groups (LB, MG, PI and TR) were used to calculate the birth rate. The birth rate was computed as the number of births divided by the number of adult females in each group in each year, and the mean birth rate of each group was calculated from the yearly birth rate. The total number of births was also recorded for these four groups as well as group MA where females were not individually identified. To test whether birth rate was associated with the number of adult females in the group or with the group size, birth rate was correlated with number of adult females and group size.

Immature survival data was collected only for two study groups viz. MG and TR. Immature survival rate was estimated as the proportion of immatures surviving annually till the end of the study out of the total number of immatures present in each year in each group. The inter-birth interval was calculated from data on eight births in four females after directly recording their previous parturition date.

Birth data collected from all the five groups were arranged month wise. Mean monthly rainfall of each month was calculated from the rainfall data of the last six years (2010-2015). Pearson's product-moment correlation test was applied to check the relationship between monthly births and mean rainfall data. All statistical analysis was done using SPSS 20 statistical software.

2.3. Results

The mean group size of LB, MG, PI and TR were 39, 40, 79 and 16.67 respectively (**Table 2.1**) differed significantly (Kruskal-Wallis H= 246.07, p= 0.01 indicating that group size varied more across groups than within groups across years.). However, the size in the case of each group did not differ over the years (**Table 2.1**). Similarly, the number of adult males, adult females and immature individuals also did not change over the years. The overall adult male to adult female ratio in the population over the years was 1:2.05. Although this ratio did not vary significantly over the years in either of the groups, the smallest TR group showed more variation than the other groups over the years (**Table 2.2**). The age-sex ratios for other classes were almost similar in all groups over the years (**Table 2.2**).

Table 2.1. Variation in group size and age-sex individuals between group years (N= 10) in the study groups (N= 4)

Group ID	Year	Group Size	ADM	ADF	IMM*
LB	2014	34	5	12	17
	2015	44	5	14	25
MG	2014	35	6	10	19
	2015	45	8	13	24
PI	2013	73	12	28	33
	2014	86	14	26	46
	2015	78	13	23	42
TR	2013	16	3	6	7
	2014	19	4	8	7
	2015	15	1	6	8

ADM: Adult male, ADF: Adult female, IMM: Immature.; *Immature includes sub-adults, juveniles and infants.

A total of 69 births were recorded in the four main study groups, of which 25 were males and 44 were females. The mean birth rate was 0.49 per adult female per year (range: 0.32 - 0.70) with maximum in group MG (0.70) in 2014 and minimum in group PI (0.32) in the year 2013

(**Table 2.3**). Each group-year was treated as an independent data point for further calculations. The birth rate (**Table 2.3**) was neither associated with the number of adult females in the group (r= 0.33, N= 10, p= 0.94) nor with the group size (r= 0.15, N= 10, p= 0.68). The mean annual survival rate of immatures was 0.79 (N= 65 animal-years) (**Table 2.4**). The mean inter-birth interval in TR group females was 14.75 months with a considerable variation ranging from 9 to 23 between individuals (N= 8 females) (**Table 2.5**).

Table 2.2. Age-sex ratio of study groups (N= 4) between group-years (N= 10)

Group ID	Year	ADM:ADF	AD:IMM	ADF:IMM	ADF:INF
LB	2014	2.40	1.00	1.42	0.33
	2015	2.80	1.32	1.79	0.50
MG	2014	1.67	1.19	1.90	0.40
	2015	1.63	1.14	1.85	0.62
PI	2013	2.33	0.83	1.18	0.36
	2014	1.86	1.15	1.78	0.58
	2015	1.77	1.17	1.83	0.48
TR	2013	1.99	0.78	1.17	0.50
	2014	2.00	0.58	0.89	0.25
	2015	6.00	0.89	1.33	0.67

ADM: Adult male, ADF: Adult female, IMM: Immature, INF: Infant.

Table 2.3. Births (N= 69) observed and the calculated birth rate in four study groups

Group ID	Year	No. of Adult females	No. of births	Birth rate (per female)	Birth rate (per group size)
LB	2014	12	5	0.42	0.15
	2015	14	8	0.57	0.18
MG	2014	10	7	0.70	0.20
	2015	13	6	0.46	0.13
PI	2013	28	9	0.32	0.12
	2014	26	13	0.50	0.15
	2015	23	13	0.57	0.17
TR	2013	6	3	0.50	0.19
	2014	8	3	0.38	0.16
	2015	6	2	0.33	0.13
Average		14.60	6.90	0.49	0.16

A total of 92 births were recorded in all the five study groups, which comprised 33 males and 59 females (**Figure 2.2**). Births were distributed throughout the year, though, 13.04% of births were recorded in July and November, whereas 3.26 % were recorded in February and April. About 70.65% of the total births were recorded in the wet season (May to November). The number of adult females and the number of births did not vary systematically over the months (χ^2= 0.56, df= 11, p= 0.99 and χ^2= 7.65, df= 11, p= 0.75 respectively). The number of births in a month was positively correlated with total rainfall in that month (r= 0.621, N= 12, p= 0.03) (**Figure 2.3**).

Table 2.4. Immature survival rate in each group (N= 2)

Group ID	Years monitored	Total animal years	Deaths or disappearances	Annual survival
MG	2	43	8	0.81
TR	3	22	5	0.77
Average				0.79

Table 2.5. Inter-birth Interval for TR group females

Sl. No.	Female ID	Inter-birth interval (months)
1	AU 1	17
2	AU 2	9
3	AU 3	12
4	BY 1	18
5	BY 2	15
6	BY 3	10
7	PM 1	23
8	RE 1	14
Mean (±SD)		14.75 (±4.59)

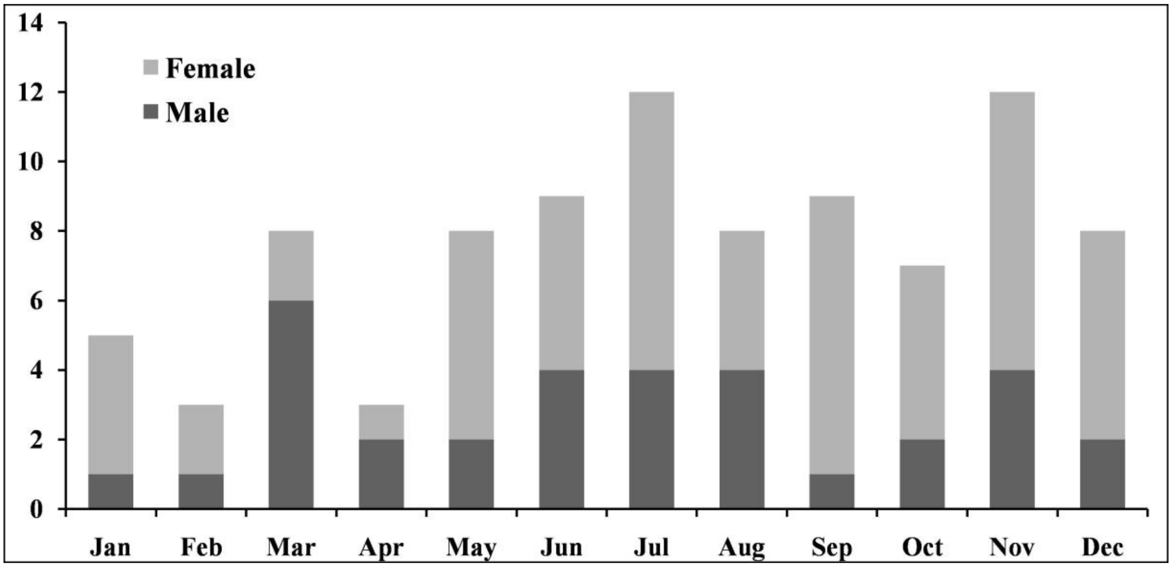

Figure 2.2. Distribution of births in each month in all groups
(N= 92, males= 33, females= 59).

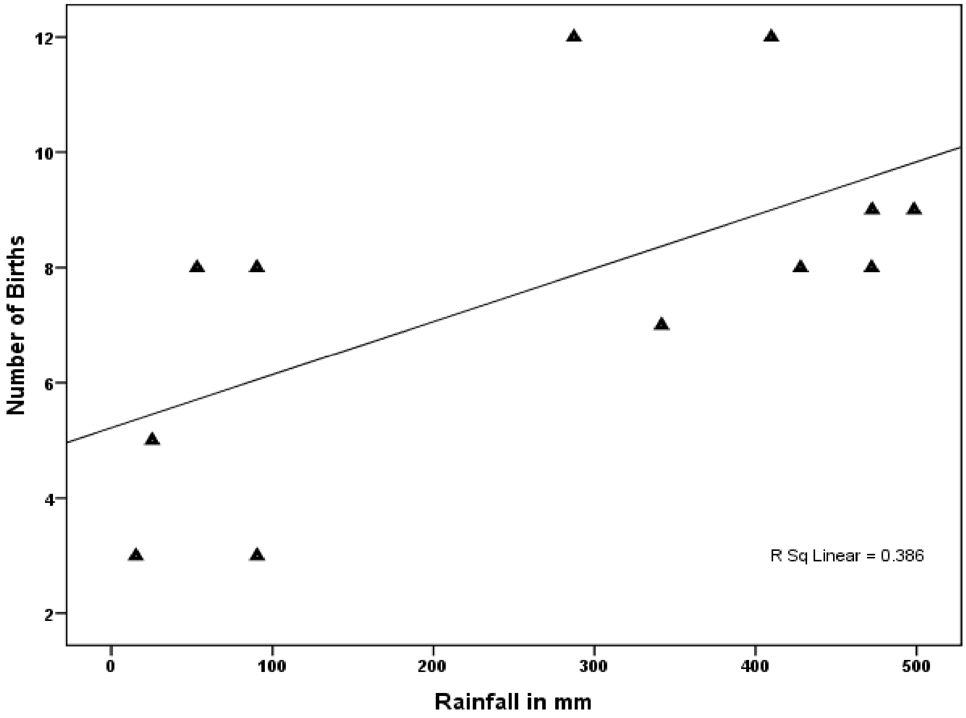

Figure 2.3. The relationship between number of births in a month and mean monthly rainfall.

2.4. Discussion

This is the first ever study to document and describe the group structure, demography and birth seasonality in the Nicobar long-tailed macaque. The groups differed in size but the size of each group and the number of individuals in various age-sex classes remained largely similar over the years. The mean birth rate and infant survival rate was 0.49 and 0.79 respectively, and the inter-birth interval was 14.75 months. Although births occurred throughout the year, ~71% of births were recorded in the wet season, and the number of births in each month was positively correlated with the mean monthly rainfall.

Macaques live in a largely female philopatric society where females stay in their natal groups and males migrate (Thierry 2004). Frequent inter-group male migration makes the demographic structure very dynamic (Dittus 2004). Although adult females do migrate, such instances are rare; and minimum changes in the number of adult females in study groups between years may reflect female philopatry in macaques. Conversely, variation in the number of immatures than other age-sex individuals causes the maximum observed variation in the macaque groups. This may be due to the variation in birth rate, high rate of immature mortality and non-natal migration of sub-adult males in macaques (Kumar 1995).

There are optimal demographic sex ratios in each macaque species, which support maximum reproductive output, growth and stability in the population (van Schaik and van Noordwijk 1983). Although, the number of adult females to males in *M. f. umbrosus* (1:2.05) is similar to that in *M. f. fascicularis* (1:2.10), the immature to adult female ratio was higher in *M. f. umbrosus* (1:1.55) than in *M. f. fascicularis* (1:1.25) (van Noordwijk 1985). The variation in age-sex ratio between these sub-species may be the result of variation in the local ecological conditions and recent histories.

Neither the per capita group size, nor the per capita number of females was related to birth rate and the birth rate did not differ between the groups suggesting that the reproductive output of female Nicobar long-tailed macaques did not vary across groups. However, the birth rate in *M. f. umbrosus* (0.49) was lower than that in *M. f. fascicularis* (0.63) (van Noordwijk and van Schaik 1987), though the inter-birth interval and infant survival rate were similar in the two subspecies (van Schaik et al. 1985). The preliminary findings on demographic parameters of long-tailed macaques show a large consistency between the subspecies, which may be signifying the species-specific conservative nature of traits (Dittus 1989).

Births occurred throughout the year suggesting a non-seasonal breeding pattern in *M. f. umbrosus*, though larger number of births occurred in the wet season than in the dry season. *M. f. fascicularis* shows a May-July birth peak in peninsular Malaysia (Kavanagh and Laursen 1984), while the population in northern Sumatra shows two birth peaks in July, and September-October (van Schaik and van Noordwijk 1985). The introduced *M. f. fascicularis* population in Anguar Island, Micronesia, shows marked birth peak in January-April (Poirier and Smith 1974). In frugivorous macaques, breeding pattern strongly depends on seasonal fruit peak which is directly dependent on seasonal rainfall (van Schaik and van Noordwijk 1985). Hence, phenology of fruiting trees (timing of fruit) of different geographical regions with even similar vegetal characteristics may differ with rainfall variation of that region (Kavanagh and Laursen 1984), which can explain the variation in birth pattern in long-tailed macaques. The relatively higher number of births in *M. f. umbrosus* during the rainy months may be due to the high availability of food resources (Brockmann and van Schaik 2005), which may support lactating females and provide food to the weaned infants.

Birth rate in most macaque species ranges between 0.29 (*M. silenus*) (Krishna et al. 2006) and 0.78 (*M. cyclopis*) (Hsu et al. 2006), and the birth rate of *M. f. umbrosus* (0.49) falls in middle of the range (**Table 2.6**). Immature survival rate of many of the macaque species ranges between 0.52 (*M. sinica*) (Dittus 1975) and 0.96 (*M. silenus*) (Kumar 1995) and *M. f. umbrosus* (0.79) showed an intermediate immature survival rate. However, inter-birth intervals of these macaques can be grouped under two ranges, one is between 13.85 (*M. cyclopis*) (Hsu et al. 2001) and 15.60 (*M. fuscata*) (Fooden and Aimi 2005) months where the *M. f. umbrosus* (14.75) falls, and the second is between 19.30 (*M. sinica*) (Bercovitch and Harvey 2004) and 30.00 (*M. silenus*) (Kumar 1987) months. Although, many of the macaque species inhabit evergreen forests, life history traits of them vary highly, especially birth rate and inter-birth interval. Phylogenetic background and current ecological factors of a species determine the life history traits which in turn influence the demographic characteristics (Chapman and Rothman 2009), including the reproductive output (Kamilar and Cooper 2013).

Table 2.6. Reproductive life-history traits in macaques

Species	**Birth seasonality**	**Birth rate (births/female/year)**	**Infant survival survivability/ infant/year)**	**Inter-birth interval (months)**	**Habitat**	**Conditions**
M. sylvanus	Discrete[1]	0.58[1]	0.78[1]	22.00[1]	Conifer-Disturbed	Wild
M. silenus	Peak February-March[2]	0.50[2]	0.93[2]	23.18[2]	Evergreen-fragmented	Wild
M. silenus	Peak January-April[3]	0.29[4]	0.96[4]	30.00[5]	Evergreen	Wild
M. sinica	Peak December-May[6]	0.69[6]	0.52[6]	19.30[7]	Dry deciduous -disturbed	Wild
M. fuscata	Discrete[8]	0.36[8]	0.77[8]	29.76[8]	Evergreen	Wild
M. fuscata	Discrete[8]	0.62[8]	0.90[8]	15.60[8]	Evergreen	Free ranging, provisioned
M. cyclopis	Discrete[9]	0.78[9]	0.84[9]	13.85[10]	Evergreen-Fragmented	Wild, partly provisioned
M. f. fascicularis	Birth peak July-November[11]	0.63[12]	0.79[12]	15.00[13]*	Evergreen or *Captive	Wild or *Provisioned
M. f. umbrosus	Throughout year	0.49	0.79	14.75	Evergreen	Wild, partly village

1:Mehlman 1989; 2:Krishna et al. 2006; 3:Singh et al. 2006; 4:Kumar 1995; 5:Kumar 1987; 6:Dittus 1975; 7:Bercovitch and Hervey 2004; 8:Fooden and Aimi 2005 ; 9:Hus et al. 2006; 10:Hus et al. 2001; 11:van Schaik and van Noordwijk 1985; 12:van Noordwijk and van Schaik 1987; 13:van Schaik et al. 1989.

M. f. umbrosus is facing both anthropogenic pressures like habitat fragmentation, habitat loss and natural disturbances like tsunami, cyclones, El Niño events, all of which have a negative impact on these macaques (Velankar et al. 2016). High degree of similarity of demographic traits of *M. f. umbrosus* with other sub species shows that these traits are quite conservative, though a few traits appear to be influenced by local conditions and recent history.

CHAPTER 3

Social Organization

Influence of Hierarchy on Society

“*Society does not consist of individuals but expresses the sum of interrelations, the relations within which these individuals stand.****”***

‡Karl Marx‡

3.1. Introduction

In the heterogeneous environmental regime, inter-individual competition for limited resources is evident in macaque society (van Schaik 1989). The inter-individual competition often leads to aggressive interactions between group members (Thierry 2004, 2007). The asymmetry in those aggressive interactions between members shapes the dominance style in the members, which shows an extent of conservative species -specific variation in social organization (de Waal and Luttrell 1989, Thierry 2004). The dominance style is represented as linear hierarchical relationship between group members, which is broadly classified into two categories viz. despotic and egalitarian (Flack and de Waal 2004). In a despotic society, individuals follow a highly linear dominance hierarchy with less tolerance towards each other, where the egalitarian society members are more tolerant to each other. However, based on interspecific variation of fourteen behavioral approaches (e.g. conflict asymmetry, conciliatory tendency, intensity of aggression, dominance gradient, degree of nepotism), Thierry (2004) categorized the social style of macaques into four-graded scale ranging from highly despotic nepotistic society (Grade 1) to more tolerant less kin-biased societies (Grade 4). The rate of aggressive interactions between group member decreases, and the intensity of aggression, conflict asymmetry and conciliatory tendency increases with the higher grades (Thierry 2007).

The hierarchical status has direct impact on heterogeneous distribution of limited resources in a society; which ultimately governs the inclusive fitness of an individual (van Noordwijk and van Schaik 1999). The resource holding potential of an individual depends on the difference in the hierarchical power with the adjacent ranking individuals, which is denoted by steepness (de Vries et al. 2006). In a society with high steepness, there is a biased resource allocation towards the high-ranking individuals. In order to balance this skewed disadvantage, low ranking individuals make trade-off by adopting different behavioral strategies by policing specific inter-individual interactions (Sueur et al. 2011).

Among the affiliative interactions, grooming is the most common and perhaps the most important interaction where macaques spend up to 20% of their daily activity (Lehmann et al. 2007). The fundamental aspect of grooming is to clean dirt and ectoparasites by manual brushing from own (self-grooming) or other individuals' (allogrooming, grooming henceforth) body fur (Schino et al. 1988). However, grooming also has a hedonistic benefit which helps to reduce stress level by releasing β-endorphins which stabilizes the heart rate (Keverne et al. 1989). Apart from its hygienic and physiological benefits, grooming also offers a set of reciprocal benefits to the groomer (Gumert 2007).

According to Biological Market Theory (Noë and Hammerstein 1994) grooming is used as currency for stable and equitable trade of social commodity, and the selection of groomee is dependent on the most even-handed benefits one can get by serving as a groomer (Henzi and Barrett 1999). For example, grooming can be traded as a currency to obtain various goods (food, shelter, gametes) and services (alarm call, coalitionary support) (Wrangham 1980). However, the grooming pattern within and between sex depends on the philopatry of the society. For example, in female philopatric societies, where female stay in stable, close knit kin-based group, females groom more than the males to maintain their social bonding (*M. assamensis*: Cooper and Bernstein 2000; *M. fascicularis*: Gumert 2010; *M. fuscata*: Tsukahara 1990; *M. radiata*: Kurup 1988). There are various socio-ecological models used to explain the adaptive significance of low-cost grooming to coordinate cooperation between females of asymmetric social status. Seyfarth (1977) proposed that the directionality and reciprocity of grooming between females is directly related to dominance hierarchy and kinship. He argued that grooming will be directed from subordinate (low ranking) females to dominant (high ranking) females to get benefits like infant handling, coalitionary support, and tolerance against contestable food resource. Grooming has been directed towards high ranking individuals in exchange for agonistic support e.g. *M. sylvanus* (Carne et al. 2011), exchange with reduced aggression and infant handling e.g. *M. fascicularis* (Gumert 2007; Gumert and Ho 2008), access to drinking sites e.g. *M. mulatta* (Kapsalis and Berman 1996) and tolerance near food e.g. *M. arctoides* (Richter et al. 2009). Schino and Aureli (2008) also argue that rank-related benefits are dependent on the steepness of hierarchy (power differential between adjacent ranks) and not on the rank position itself. Thus the duration, directionality and reciprocity of grooming help to build and maintain the social relationships between individuals.

Social hierarchy is the stepping stone to understand social organization as well as association in a society. Moreover, variation in social organization between subspecies along with its influence on social relationships would also enrich the scientific understanding of a species. Therefore, the study was conducted to explore social organization of Nicobar long-tailed macaque (*Macaca fascicularis umbrosus*) where grooming was used as a proxy of social interactions between individuals to explore the relation between them along with the influence of social hierarchy on the grooming pattern.

3.2. Methodology

3.2.1. Data collection: The study was conducted on TR group during October 2013 to November 2015, while the group was followed from 0600 to 1800 h. Due to the terrain and restriction in using some of the private or government area, these part of the range of the group was inaccessible thus it was difficult to continuously follow an individual for a long time. Therefore, 5 minutes focal animal sampling was followed to collect the data on individual activity (Altmann 1974). Focal sampling was evenly allocated in 6 two-hour blocks from 0600 to 1800 where focal animal was selected randomly and one individual was not sampled more than once in a single slot. If the focal individual was lost, the sampling was resumed for the next randomly selected individual. If an individual could not be followed or disappeared, an attempt was made to track it for the next 5 min, and the duration of disappearance was recorded. Data on frequency (silent bared-teeth display, call, charge, chase, flee, genital scratch, muzzle contact, single touch, touch, yawn) and duration (exploring, feeding, grooming, infant care, mating, play (social and solitary), rest, vigilance) of behaviors were collected. For each grooming bouts, identity of groomee and groomer, duration and direction of bout were recorded. Bouts 30s apart were considered separate. Ad libitum sampling method was used to collect data on above mention affiliative and agonistic interaction along with the identity of individuals, direction and the ultimate outcome of the interactions (Altmann 1974). Total of 1660 hours of observation were employed to collect social behavioral data of TR group individuals.

3.2.2. Data analysis

Dominance hierarchy: The dominance hierarchy was determined by assessing the consequences of aggressive encounters among the individuals. Aggressive interaction data along with direction and win loose information were used to calculate the dominance hierarchy of males, females and overall members of TR group. DomiCalc (Schmid and de Vries 2013) software was used to calculate the dominance hierarchy along with normalize David's score (NDS), linearity (h') and steepness (r^2) indices. The NDS is the unique value calculated for each individual after calculation of the result of direct relationships as well as secondary interactions between individuals. The measure of dominance are used to explain the hierarchical order, where, the strength in linearity is a direct measure of strength of dominance (Singh et al. 2003); and the steepness measures absolute difference between adjacent ranks in terms of winning (Schmid and de Vries 2013).

Grooming distribution: Only adult-adult allogrooming data were used to analyze the distribution of grooming. The total grooming bouts, total bout duration and average bout duration was calculated to explore the grooming pattern in the study group. The variation in grooming bouts between males and females were determined through "N-1" Chi-square test (Campbell 2007), and confidence intervals were calculated based on the recommendations by Altmann et al. (2000).

Influence of hierarchy on grooming: Spearman ρ correlation test were employed to check the relation between rank and grooming within both sex, where NDS of each individual were correlated with total number of grooming bouts, total duration of grooming and average duration of grooming given as well as received in both males and females to scrutinize the relation between rank and grooming. Similarly, Spearman's ρ were used to check the relation between social rank and allocation of grooming in males and females.

3.3. Results

A total of 155 aggressive interactions were recorded during the 1660 hours of observation that was used to calculate the dominance hierarchy in the TR group. There was a sharp decline of NDS value after top most ranked individuals. The linearity and steepness of males and females were 0.65 and 0.40 respectively, and 0.79 and 0.52 respectively (**Table 3.1**).

Of the total 1047 grooming bouts recorded, 953 bouts were considered in analysis which was recorded from initiation to end. Of the 146 intra-sexual bouts, 120 and 26 bouts were occurred among females and males respectively, where frequency of grooming among females were significantly higher than among males ($\chi^2 = 12.47$, df= 1, $p < 0.01$). The average duration of grooming bouts among females and males were $1.80 \pm 7.55_{SD}$ min and $2.55 \pm 2.68_{SD}$ min respectively (**Table 3.2**).

Table 3.1. Social hierarchy in TR group

Sex	ID	NDS	Rank	Linearity (h′)	Steepness (r^2)		ID	David's score	Rank	Linearity (h′)	Steepness (r^2)
Male	FY	3.00	1	0.65	0.79	**Overall**	NI	14.38	1	0.36	0.96
	KU	0.98	2				FY	12.16	2		
	BA	-0.31	3				BA	4.85	3		
	HK	-0.94	4				BY	3.85	4		
	AI	-2.73	5				AU	3.22	5		
Female	NI	3.73	1	0.40	0.52		RE	-1.53	6		
	TE	1.10	2				TE	-4.35	7		
	AU	0.03	3				KU	-6.37	8		
	BY	-0.74	4				HK	-6.92	9		
	RE	-1.3	5				SC	-8.24	10		
	ST	-2.82	6				AI	-11.05	11		

Table 3.2. Distribution of grooming between males and females of TR group

Sex	ID	Total number of grooming bouts given	Total grooming given duration (min)	Average duration of grooming given (min)	Total number of grooming bouts received	Total grooming received duration (min)	Average duration of grooming received (min)
Female	Ni	19	26.37	1.39	26	37.28	1.43
	Te	21	38.25	1.82	17	28.6	1.68
	Au	15	19.02	1.27	34	66.58	1.96
	By	26	51.97	2	20	36.88	1.84
	Re	19	31.45	1.66	11	23.4	2.12
	St	20	50.08	2.50	12	24.35	2.03
Male	Fy	2	6.20	3.1	6	27.57	4.59
	Ku	10	22.95	2.30	3	4.38	1.46
	Be	3	13.27	4.42	7	14.11	2.02
	Hk	1	1.38	1.38	0	0	0
	Ai	9	24.78	2.75	7	21.6	3.09

In females, grooming given did not correlate with the rank (**Table 3.3**). Though, there was no relation found for social rank and total grooming bouts and duration of grooming received, strong negative correlation for average grooming duration showed that low ranking females received higher amount of grooming than higher ranking ones (**Table 3.3**). In males, where grooming was given towards high-ranking individuals, there was no relation found between rank and grooming given (**Table 3.3**). However, in case of grooming received, strong negative relation found between rank and average grooming duration, however, rank did not correlated with total bouts of grooming and total grooming duration (**Table 3.3**).In both males and females, there was no difference in grooming allocation found between high and low ranking individuals (**Table 3.4**).

Table 3.3. Relations between social rank and grooming distribution (Spearman's ρ correlation)

Sex	**Grooming direction**	**Parameter**	**Spearman's ρ**	**p**	**N**
Female	Grooming given	Total grooming bouts	-0.15	0.78	6
		Total grooming duration	0.49	0.33	6
		Average grooming duration	-0.60	0.21	6
	Received	Total grooming bouts	0.66	0.16	6
		Total grooming duration	0.66	0.16	6
		Average grooming duration	0.89	<0.01	6
Male	Grooming given	Total grooming bouts	0.00	1.00	5
		Total grooming duration	0.30	0.62	5
		Average grooming duration	0.70	0.80	5
	Received	Total grooming bouts	-0.30	<0.01	5
		Total grooming duration	0.21	0.74	5
		Average grooming duration	-0.30	0.62	5

Table 3.4. Relation between social rank and grooming allocation (Spearman's ρ correlation)

Sex	**Parameter**	**Spearman's ρ**	**p**	**N**
Female	Total grooming bouts	0.43	0.42	6
	Total grooming duration	0.49	0.35	6
	Average grooming duration	-0.14	0.80	6
Male	Total grooming bouts	-0.70	0.19	5
	Total grooming duration	-0.70	0.19	5
	Average grooming duration	0.70	0.19	5

3.4. Discussion

Like other macaques, Nicobar long-tailed macaques live in a linear hierarchical society. The linearity of social hierarchy is low, where male linearity of dominance is higher than females. However, steepness or the asymmetric distribution of hierarchy is moderately high among both male and overall group members. There was no relation between ranks and grooming given was observed in males or females of the study group. The average duration of grooming received by females is correlated with the ranks, and number of total grooming bout negatively correlated with rank. Moreover, no grooming preferences for adjacent ranks were observed in males or female.

After one/two top most dominant individuals of males, females and overall group members, NDS index decline sharply, which describes hierarchical asymmetry in *M. f. umbrosus* (Schmid and de Vries 2013). The data from captive population of *M. f. fascicularis* also showed a high steepness value (0.79-0.94) (Balasubramaniam et al. 2012). Since, the higher value of this hierarchical steepness is the absolute index for winning asymmetry between adjacent ranked individuals suggesting higher resource monopolizability in the society. After collecting data from captive populations of other sub-species (*M. f. fascicularis*) long-tailed macaque was put in 'Grade-2' social scale which represents highly linear despotic, less-tolerant social style with less steep dominance hierarchy (Thierry 2004, 2007). In contrast to this, low linearity in males, females and overall group in *M. f. umbrosus* suggests less despotic and more tolerant social organization. Though, macaques exhibit species specific dominance style, local ecological factors like climatic condition and food availability act as influential factors which ultimately lead to variation in dominance hierarchy (Thierry 2007). Moreover, *M. f. umbrosus* lives in three isolated islands which are highly susceptible to natural catastrophes like earthquakes, tsunami and El Niño. Therefore, these macaques may become flexible with their life history traits to survive in such stressful environment which ultimately leads to the variation in social organization.

The relation between grooming and social rank in *M. f. umbrosus* is partially congruence with previous study conducted on *M. f. fascicularis* in captive (Butovskaya 1995) and wild conditions (Gumert 2010). Where, two captive populations of *M. f. fascicularis* reared in similar conditions showed significant variation in rank related grooming patterns (Butovskaya 1995). In wild population of *M. f. fascicularis* of Bali, Indonesia, the grooming was directed towards high ranking individuals (Wheatley 1999) which corresponds to the Seyfarth's model (1977). Where in Kalimantan, grooming distribution in free ranging populationwas not influenced by the rank (Gumert 2010), which suggests that the high inconsistency in grooming pattern and rank of the individuals. Moreover, other macaque species grouped in the same grade with also showed variation in relationships between hierarchical rank and grooming pattern, for example, where higher rank directed grooming was observed in *M. thibetana* (Xia et al. 2012), *M. assamensis* showed absence of such grooming patterns (Cooper and Bernstein 2000; Macdonald et al. 2013). After a meta-analysis of 38 social groups of 16 primate species, Schino and Aureli (2008) argued that steepness of dominance has an influence on rank related grooming, which results in variation of grooming pattern within and between the species. In a hierarchical society with higher asymmetry, subordinate individuals avoid interaction with high ranking individuals, which results in non-linear relationships between rank and grooming patterns (Thierry et al.

1990). However, in a competitive environment where long-term bonding or affiliative interaction did not exclude the condition, between individuals grooming would only be used as a commodity to access immediate success by an individual (Gumert 2010), which may have resulted absence of rank-related grooming in this macaque.

Though the drifts of phylogenetic inertia keep social organization pattern consistent and conservative for similar lineages, variation in local ecological conditions and environmental constrains affect the trade-off between group members which results in the variation in social organizations between species or populations (Thierry 2007). Moreover, immediate needs of an individual also induce individual-specific interactions (Gumert 2010). Similarly, *Macaca fascicularis umbrosus* also showed such conservative species-specific social organizational traits with some distinct characteristics in the social styles.

CHAPTER 4

Reproductive Behaviors

Strategies & Counter-strategies

"Ethics, like natural selection, make existence possible. Aesthetics, like sexual selection, make life lovely and wonderful, fill it with new forms, and give it progress, and variety and change."

‡ Oscar Wilde ‡

4.1. Introduction

In group-living macaques, birth takes place after a long gestation period and a prolonged lactation period where intensive parental care is required to wean the dependent infant. In this scenario, the parental investment is highly skewed towards females, where males only contribute by fertilizing ova with relatively low-cost sperm and involve in little or no parental care (Trivers 1972). Consequently, the reproductive success of males increases with siring offspring by accessing the receptive females, while the reproductive success in females depends on the fecundity as well as the survival of the infants (Kappeler and van Schaik 2004; Soltis 2004). Therefore, the male sexual strategy is to mate more with receptive females by monopolizing mate resources, where females try to incorporate selective mate choice with polyandrous matings, which ultimately act as a conflict of interest between sexes and leads to inter-sexual competition (Trivers 1972). This inter-sexual competition is one of the major governing factors which finally contribute to the reproductive success of both sexes (Paul 2004; Soltis 2004).

Through inter-sexual competition, both the sexes adopt different sexual strategies and counter-strategies to increase their reproductive success against each other (Clutton-Brock 1974; de Waal and Luttrell 1989). Since, female's reproductive success lies on the survivability of her infants, females often show cryptic mate choice behaviors which increases the likelihood of insemination by particular male (e.g. *M. mulatta*: Manson 1992; *M. fuscata*: Soltis 1997; *M. fascicularis*: Engelhardt et al. 2006), which provides direct benefit like positive effect on fecundity by acquiring high quality genotype and indirect benefits like avoidance of inbreeding by increasing genetic heterozygosity in offspring (Waser et al. 1986; Kappeler and van Schaik 2004). Selective mating also used as a strategy to prevent inbreeding from intra group individuals e.g. both captive and wild societies of *M. fuscata* (Inoue et al. 1990; Soltis et al. 1999) and *M. mulatta* (Smith 1986; Manson and Perry 1993) showed mating avoidance with matrilineal relatives, while *M. sylvanus* avoided breeding from both matrilineal and paternal relatives (Kuester and Paul 1994). Apart from cryptic mate choice, females also shows polyandrous and promiscuous mating (e.g., *M. fuscata*: Soltis *et al*. 1999; *M. mulatta*: Bercovitch 1997; *M. nemestrina*: Oi 1996; *M. sylvanus*: Small 1990), where they mate with multiple males in pre and post conception period to increase the paternity confusion (van

Schaik et al. 2000, 2004; Hestermann et al. 2001). Females can secure infant survival by reducing the chance of infanticide and also gain protection from outsider males through manipulating paternity assessment of males (Kappeler and van Schaik 2004; Soltis 2004). Further, an increasing number of male mating partner (probable sire of an infant) also increase the access to valuable resources to female and her offspring and ultimately increase the survivability of infants (Hrdy 1986).

On the other hand, males are more likely to mate females when the chance of fertilizing her egg is high since the copulation requires high energy (Bercovitch 1987). In contrast, females adopt various counterstrategies to conceal the fertile phase by making ovulation unpredictable (Soltis 2004). The females of seasonal breeders become receptive only in a distinct period, where males may get a clue of female receptiveness from socio-sexual behaviors of females. However, females of non-seasonal breeders may become receptive in any time of the year thus the females develop sexual swelling which is controlled by estradiol and progesterone hormone levels (Michael and Zumpe 1993). The swelling size was considered as a ‘graded signal’ of receptivity of female, which helps the males to assess the time of ovulation by providing information about their reproductive status (Nunn 1990). Though male mating frequency increases with the swelling size (e.g., *M. fascicularis*: Engelhardt et al. 2005; *M. nigra*: Thomson et al. 1992 and *M. tonkena:* Aujard et al. 1998), the duration of maximum swelling is longer than the female fertile phase e.g., long cycling post-partum swelling is showed in *M. silenus* (Clarke and Harvey 1993); which makes swelling not so reliable predictor of female fertility. Therefore, it can be argued that females make ovulation further unpredictable to males by deceptive swelling status. Apart from the pre-conception period, females also observed to engage in post-conception mating which is considered as a reproductive strategy of females to confuse paternity to increasing paternal investment and reducing infanticidal risks (Engelhardt et al. 2007). However, the duration and intensity of sexual swelling vary, wherein *M. fascicularis* post-conception mating continue up to 80 days of pregnancy with a peak at 40-60 days of gestation (Engelhardt et al. 2007), *M. arctoides* mate first trimester of pregnancy without showing any peak (Nieuwenhuijsen et al. 1986). Further, females also engage in post-parturition mating, for example, sexual present followed by brief mating also recorded in *M. arctoides* (Nieuwenhuijsen et al. 1986), and *M. nemestrina* (Hadidian and Bernstein 1979) were observed to start post-partum cycling just after nine days from parturition. van Schaik (2000) argued that the risk of infanticide is high in non-communal infant-carrying primates, where females may adopt alternative reproductive strategies like post-parturition mating to reduce the infanticidal risk. Moreover, receptive behavior like post-parturition presentation or cycling may be used by females as an adaptive strategy to monopolize male resources by reducing the chance of mating with other ovulating females (Engelhardt et al. 2007).

In a hierarchical society, the dominant rank of an individual has the major role on its reproductive success, which ultimately helps in employing the reproductive strategies against intra-sex and inter-sex group members (Kappeler and van Schaik 2002; Wrangham 1980). The high correlation between dominance rank and mating success in males indicate that the dominant males get more access to receptive females than the subordinates by involving in intra-sexual competition for mate resources (e.g. *M. fuscata*: Soltis et al. 2001; *M. mulatta*: Melnick 1987; *M. fascicularis*: de Ruiter et al. 1994). Meanwhile, the subordinate males adopt alternative reproductive strategies like sneak copulation in the absence of dominant males to secure their reproductive success through sperm competition, which is often observed in macaque society (e.g. *M. fuscata*: Soltis et al. 2001; *M. mulatta*: Manson, 1996; *M. fascicularis*: Gygax, 1995; *M. arctoides*: Nieuwenhuijsen *et al*., 1988; *M. sylvanus*: Paul and Kuester, 1996; *M. maurus*: Matsumura, 1993). The dominant males often guard females to reduce the chance of sneak copulation by subordinates (e.g., *M. fascicularis*: Girard-Buttoz et al. 2014; *M. fuscata*: Matsubara 2003; *M. mulatta*: Bercovitch 1997; Soltis 2004). For example, dominant male involves in longer mount series with receptive females when females were less likely to break the consort in Japanese macaque (Soltis 1999) and rhesus macaque (Manson 1996), which ultimately increases the paternity concentration of the dominant male.

In a female philopatry society where females stay in a natal group with their close kin and the youngest infant acquires a social rank just below her mother, competition between females become higher. In such condition, high ranking females impose their dominance over subordinate females to monopolize food and mate resources as alternative reproductive strategies to increase their relative reproductive success (Soltis 2004). By monopolizing the high-value food resources females increase their health which ultimately increases their fecundity (Wrangham 1980). Moreover, females also monopolize mate resources by making males engage with prospective approaches, wherein the dominant female successfully monopolized male mate resource by preventing subordinate females from copulation in *M. mulatta* (Zumpe and Michael 1987). In the early post-parturition period when females are in lactating amenorrhoea, females of *M. silenus* developed deceptive swelling (Clarke et al. 1993), and females approached male pro-receptively (Nieuwenhuijsen et al. 1986) to decrease the sperm availability for other females of the group in *M. arctoides*. On the other hand, a female also increases her relative reproductive success by interfering in matings of other females. For example, females of *M. fuscata* (Rendall and Taylor 1991), *M. fascicularis* (Kumar 1987) and *M. arctoides* (Niemeyer and Chamove 1983) harassed other females during copulation.

The macaques are quite conservative in social organizations (Dittus 2004) which ultimately governed by the phylogenetic inertia, yet local ecological conditions along with recent histories influence the reproductive output of a population (Thierry 2004). Macaques become flexible with their behavioral traits to balance the trade-off for certain environmental constraints that might results in behavioral variation (Thierry 2007). Therefore, understanding a species across different ecological conditions reveals the adaptability of a species. The long-tailed macaque (*Macaca fascicularis*) is one such model species having 10 subspecies, most of them inhabiting isolated islands in South East Asia (Gumert 2011). Nicobar long-tailed macaque (*M. f. umbrosus*) is one of the sub-species long-isolated and live in three offshore tropical islands of Nicobar archipelago (Umapathy et al. 2003), which are highly susceptible for natural catastrophes. They live in a multi male-multi female society with female philopatry and give births throughout the year. The *M. f. umbrosus* faced a sharp decline in their population due to a 2004-tsunami and also that resulted in less immature to adult female ratio (Sivakumar 2010). However, currently, the population is being recovering including the immature to the adult female ratio (Velankar et al. 2015). It is a unique opportunity to understand the reproductive profile of *M. f. umbrosus* in a highly dynamic island. A study on reproductive behavior was carried out to explore and document the first ever baseline data on reproductive traits of the Nicobar long-tailed macaques on Great Nicobar Island.

4.2. Materials and Methods:

4.2.1. Data collection: The study was conducted on TR group during May 2013 to December 2015. During the study period 24 individuals were recorded in the group i.e. adult males (FY, GP, HK, MA and RY), adult females (AU, BY, NI, PM, RE, SC and TE), sub-adult males (AI, BA and KA), juvenile males (BN, NL, PT), juvenile females (LA), and infants (AK, BO, PI, RT and SO).

First three months of the study period was spent to habituate the group. Three observers followed the group for the entire day from 0600 to 1800 hours or until the group moved to the inaccessible area. When the group is in not sight, that period was not included in observation hours. Group count and demography data were collected weekly while all individuals were crossing roads or moving in a single file.

Reproductive behaviors: Reproductive behavioral data were collected with all-occurrence sampling (Altmann 1974). Three observers were following the group by keeping adult males as a focal animal. Furthermore, data were collecting from two different halves of group's range. Therefore, both groups centered and peripheral individuals were monitored at the same time. All pre-copulatory, copulatory and post-copulatory behaviors of each individual with their identity were recorded in a structured data sheet (**Table 4.1**). The identity of interacting individuals along with the occurrence and frequency of reproductive behaviors like mating approach or mating initiation by male and female, the occurrence of mating, duration of mating, the total number of thrust in mating, mating with ejaculation, copulation call and post-copulatory behavior of male and female were recorded (Kowalewski and Garber 2010). A mating was considered when there was a mounting with intromission and sequence of pelvic thrusts (Jones 1985). The genital inspection by a male, and anogenital presentation and reaching back by a female were considered as a mating initiation approaches (Soltis et al. 1997). Ejaculatory mating was determined by observing the presence of ejaculation pause (Engelhardt et al. 2005). Mate guarding or consortship, sexual swelling, individual migrations and data on other infrequent behaviors were collected by *ad libitum* sampling method (Altmann 1974). The sexual swelling was classified into five grades (**Fig. 4.1**) from no swelling (grade 0) to maximum swelling (grade 4) and collected on each observation day (Engelhardt et al. 2005). In this fission-fusion macaque society, more than 30 consecutive days present of a new individual and absent of a resident individual were considered as immigration and emigration respectively.

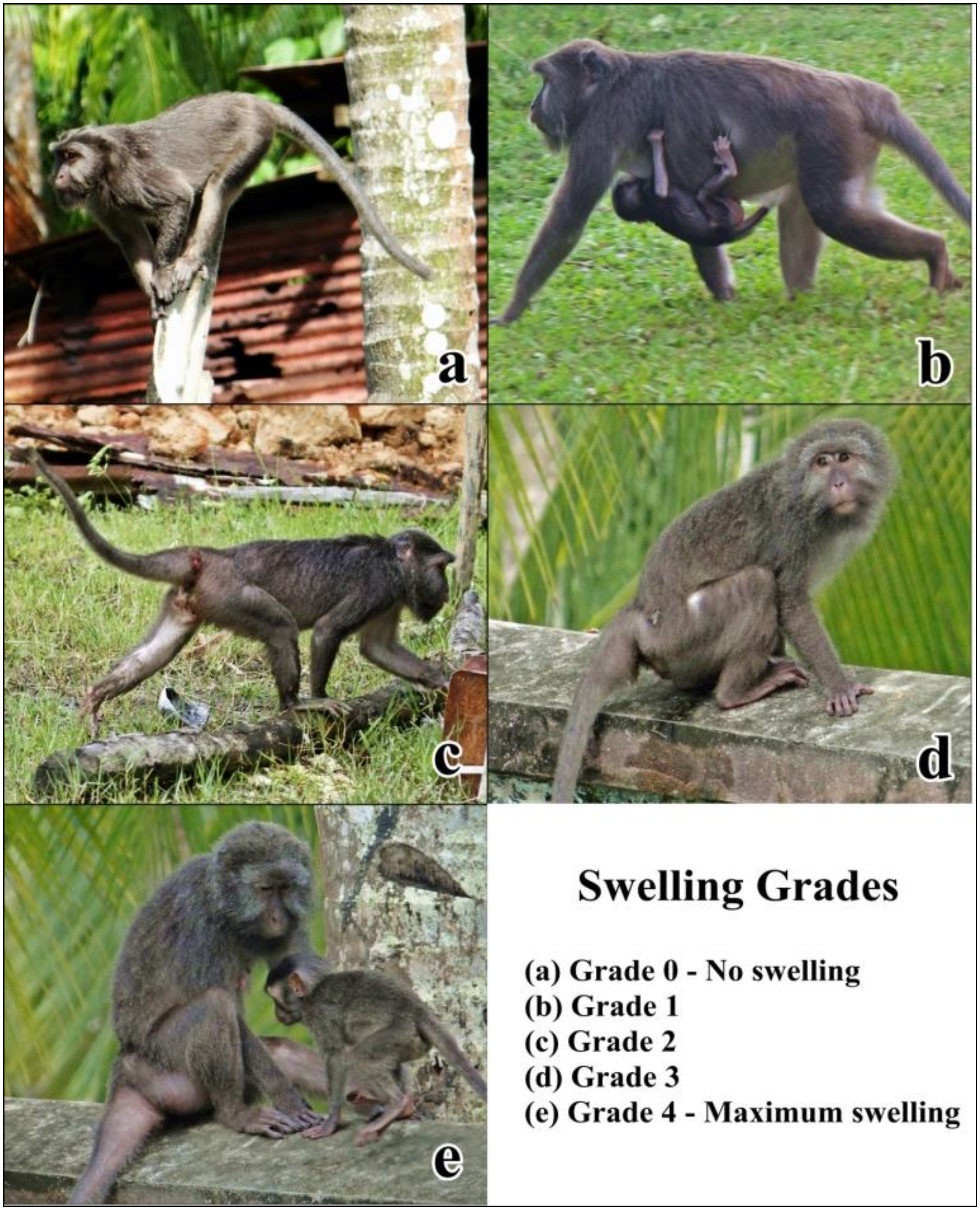

Figure 4.1. Grades of sexual swelling in females of Nicobar long-tailed macaque

Table 4.1. Ethogram of reproductive behaviors of Nicobar long-tailed macaque

Behavior	Description	Reference
Mating initiation by male	Behavioral approaches by a male to show motivation for mating towards specific female, i.e. inspection: examine anogenital region of female by sniffing, touching and licking; solicitation: increase proximity to a distinct female by touching, grooming and following, and aggressive and non-aggressive approaches for mating by coercion and grasping the back of the female.	Soltis et al. 1997; Kowalewski and Garber 2010; Engelhardt et al. 2005
Mating initiation by female	Behavioral approaches by a female to show motivation for mating towards specific female, i.e. present: present anogenital region to male with close proximity, reaching back: reaches back for the male and solicitation: Increase proximity to distinct male by touching, grooming and following him.	Soltis et al. 1997; Kowalewski and Garber 2010; Engelhardt et al. 2005
Mating / copulation	A heterosexual mount with intromission with continuous series of pelvic thrusts.	Jones 1985; Kowalewski and Garber 2010;
Mating duration	Duration from the first to the last pelvic thrust in a mating event.	Kowalewski and Garber 2010;
Thrust	Sequential pelvic movement in a mating event.	Kowalewski and Garber 2010;
Ejaculatory mating	A mating event with sperm ejaculation, which is determined by the ejaculation pause along with visible semen in the females' anogenital region.	Engelhardt et al. 2005
Copulation call	Vocalization (continuous short call) by either sex of macaque just before, during and after copulation.	Engelhardt et al. 2012

Social behaviors: The *ad libitum* sampling methods were used to collect the social interaction data like agonistic and affiliative approaches between individuals. In case of agonistic approaches, all information like the identity of aggressor and receiver, aggressor behavior, receiver response, the degree of aggression, retreat behavior, the identity of winner and looser were recorded (Beisner et al. 2011).

4.2.2. Data analysis: A total of 2160 h of observation was made to collect the data on reproductive behavior on TR group. An observation period of each day was considered as one sample. The frequency or rate of reproductive behaviors like mating initiation by males, mating initiation by females, mating by individual males and females were calculated as the number of each behavior recorded divided by the number of observation hours in each day and presented as number per observation hour. Mating success of males, females and overall was computed as the number of successful mating events in each sampling day divided by the total number of mating initiations on that day by males, females and overall respectively. The ejaculation rate was estimated as the number of ejaculatory matings in each observation day against the total number of successful matings on that day.

By back calculation, estimated the different reproductive stages of females from the date of parturition, where the gestation period was kept as 164 days (Fooden 2006). Reproductive stages of females were divided into three classes with six 30 days (month) interval for each class, i.e. pre-conception, post-conception and post-parturition periods. From 180 days (six months) before the birth up to the parturition day was considered as post-conception period, where conception occurred in the middle of the first month of the post-conception period. Six months before the post-conception period was considered as pre-conception period and six months after the date of parturition was projected as a post-parturition period.

Dominance hierarchy of group individuals was determined by assessing the consequences (win/loose) of aggressive encounters. DomiCalc (Schmid and de Vries 2013) software was used on aggressive interaction data along with direction and win loose information to calculate dominance hierarchy of group males.

In macaque society, where male migrates, social rank of a male between groups changes with emigration and immigration of males. I examined the influence of social rank of males on reproductive behaviors by considering mating data of a period of six months (from 1/11/13 to 30/5/14) while there was no male migration in the TR group.

Statistical analysis: Chi-square test was used to examine the differences in copulatory behaviors (mating duration, thrust rate, the interval between ejaculatory matings and ejaculation rate) between males. The intensity of swelling during pre and post-conception period were tested using Kruskal-Wallis test, where the variations of swelling between females were checked with Friedman test. Chi-square test was employed to check the variation of the inter-birth interval between females. Similarly, Kruskal-Wallis test was employed to compare the distribution of reproductive behaviors (mating initiation by a male, mating initiation by a female, mating success by a male, mating success by a female, overall mating success, mating rate and ejaculation rate) between pre-conception, post-conception and post-parturition periods of females. The Friedman test was used to compare the reproductive behaviors between females in all three reproductive stages. Pearson product-moment correlation test was employed to check the relationship between different reproductive behaviors in different reproductive stages of females. Variation in mating rate between males was analyzed with chi-square test and relation of mating with Kendall's tub correlation test. I used Wilcox rank-sum test to examine the involvement of alpha male and other males during pre- and post-conception periods.

4.3. Results

Initially, the TR group had 16 individuals with three adult males, six adult females and seven immature individuals. During the study period, two females matured and later gave births. A total of 12 births, two deaths (one adult male and one sub-adult male) occurred in the study group. Further, two adult males immigrated, and three adult males, two adult females and two sub-adult males were missing from the group. This has resulted in the variation in demography of the group.

A total of 1412 mating initiation were recorded with 11 individuals, i.e. four males (FY, GP, MA, and RY) and seven females (AU, BY, NI, PM, RE, ST, and TE), of that 838 initiations were resulted in successful matings. The rate of overall mean mating initiation was $0.21\pm0.09_{SD}$/h, where the rate of mean mating initiation by male and female were $0.26\pm0.12_{SD}$/h (68.41%, N = 966) and $0.18\pm0.07_{SD}$ /h (31.59%, N = 446) respectively. The mating success of males, females and overall was, $0.45\pm0.22_{SD}$, $0.71\pm0.30_{SD,}$ and $0.57\pm0.26_{SD}$ respectively. The mean mating rate was $0.16\pm0.14_{SD}$/h.

4.3.1. Reproductive behavior of males:

Of the 838 matings recorded, the number of matings by FY (80.79%, N= 677) was higher than other males (**Table 4.2**). The mean duration of mating by all the males was $4.60\pm0.65_{SD}$ seconds which ranged between 3.89 seconds by MA and 5.34 seconds by FY, however, the variation was not significant (χ^2= 0.28, df= 3, p= 0.96). During the mating, the mean rate of pelvic thrust was $2.12\pm0.43_{SD}$/seconds, which did not differ between the males (χ^2= 0.26, df= 3, p= 0.97). All the males showed multiple mating ejaculations (MME). The mean ejaculation rate ($0.55\pm0.14_{SD}$/mating) did not vary between the males (χ^2= 0.11, df= 3, p= 0.99).

Table 4.2. Reproductive behaviors of males

Male ID	Days of observation (N)	Observation period (hour)	No. of mating (N)	Average mating duration in second (±SD)	Average no. of thrust per second (±SD)	Average ejaculation rate (±SD)
FY	220	1774	677	5.34(±2.16)	2.22(±0.88)	0.49(±0.38)
GP	61	492	44	4.25(±2.12)	2.55(±0.66)	0.61(±0.46)
MA	166	1086	48	3.89(±2.39)	1.53(±1.23)	0.38(±0.47)
RY	83	670	69	4.93(±1.47)	2.19(±0.79)	0.71(±0.35)
Overall	530	4022	838	4.60(±0.65)	2.12(±0.43)	0.55(±0.14)

4.3.2. Reproductive behaviors of females:

All adult females showed sexual swelling which was characterized by inflation of the tail root with reddening in appending skins. The intensity of maximum swelling varied between females. Where the nulliparous and primiparous (RE and TE) females showed more intense sexual swelling than the multiparous (AU, BY and PM) females whose swelling was not so prominent (**Fig. 4.2**). Swelling pattern did not vary between months (χ^2= 11.09; df= 11; p= 0.44); however swelling pattern varied between females (χ^2= 48.22; df= 5; p< 0.01).

A total of 8 inter-birth interval cases were recorded from 6 females. The mean inter-birth interval was 14.75±4.59$_{\text{SD}}$ months that ranged between 9 and 23 months, however, the variation between eight inter-birth intervals was not significant (χ^2= 10; df= 7; p= 0.19).

Months	**Pre-conception**						**Post-conception**					
Female ID	1	2	3	4	5	Conception	7	8	9	10	11	Birth
AU1	○	○	○	○	◔	◑	◑	◔	○	○	◔	◔
AU2	◑	◔	◑	○	◑	◑	◑	○	○	○	◔	◑
BY	◑	◕	○	○	◔	◑	◑	◔	◔	○	○	◔
PM	○	○	○	◔	◑	◑	◑	○	○	○	◔	◑
RE	◕	●	◕	●	◕	●	●	●	◑	◑	◕	◕
TE	●	◕	◕	●	◕	●	●	◕	◕	◕	◕	◕

Figure 4.2. Distribution of swelling intensity gradient in females, the non-filled circles represents no swelling (grade-0), quarter-filled circle- grade1, half-filled circle -grade 2 and three-quarter filled circle -grade 3 and completely filled circle represents highest intensity (grade-4) of swelling.

4.3.3. Reproductive behaviors in relation to the reproductive status of females:

Pre-conception period: The mating initiation and mating success by males, females and overall remain unchanged in the first four month of the pre-conception period, and sharply increased during the last month before conception (**Table 4.3, Fig. 4.3**) but did not differ between the months (**Table 4.4**). Throughout the pre-conception period, where mating initiation rate of male was higher than females, mating success showed the reverse pattern. The mating rate significantly increased after fourth month, but the ejaculation rate remained unchanged in all the months. However, the reproductive behaviors of females did not differ between the months (**Table 4.5**).

Post-conception period: In continuation to the pre-conception period, frequency of all reproductive behaviors remained high in the first month of the post conception period, and gradually decreased, however, many of the these behaviors were persist till fourth month of the post-conception period. Similar to the pre-conception period, mating initiation rate of male were higher than females, and female mating success was higher than males in the post-conception period. Where, mating initiation rate of both males and females gradually decreased and was absent from the fifth month of the gestation period. Further, the rate of mating success dropped sharply after the third month of gestation period and no mating occurred after fourth month of gestation period (**Fig. 4.3**). However, female mating initiation rate and male mating success rate varied significantly, variation of male mating initiation rate and female mating success were not significant (**Table 4.4**). Both mating rate and ejaculation rate were highest around conception period, and no mating with ejaculation was observed after three months prior to parturition, which showed a significant variation of mating and ejaculation rate during the post-conception period. However, post-conception reproductive behavioral patterns remained unchanged between females (**Table 4.5**).

Table 4.3. Distribution of reproductive behaviors in pre-conception, post-conception and post-parturition period.

Period	**Months**	**Male mating initiation rate (±SE)**	**Female mating initiation rate (±SE)**	**Male mating success per mating approach (±SE)**	**Female mating success per mating approach (±SE)**	**Mating success per mating approach (±SE)**	**Mating per hour (±SE)**	**Ejaculation per mating (±SE)**
Pre-conception	1	0.25 (±0.02)	0.14 (±0.02)	0.57 (±0.14)	0.85 (±0.10)	0.71 (±0.26)	0.16 (±0.04)	0.69 (±0.15)
	2	0.28 (±0.03)	0.11 (±0.03)	0.61 (±0.14)	0.81 (±0.04)	0.71 (±0.16)	0.18 (±0.04)	0.66 (±0.14)
	3	0.27 (±0.02)	0.12 (±0.03)	0.63 (±0.05)	0.90 (±0.23)	0.76 (±0.10)	0.15 (±0.03)	0.59 (±0.17)
	4	0.25 (±0.07)	0.12 (±0.02)	0.58 (±0.08)	0.85 (±0.17)	0.72 (±0.14)	0.15 (±0..04)	0.65 (±0.10)
	5	0.27 (±0.07)	0.15 (±0.07)	0.56 (±0.09)	0.90 (±0.17)	0.73 (±0.10)	0.16 (±0.06)	0.56 (±0.18)
	6	0.34 (±0.04)	0.16 (±0.06)	0.67 (±0.10)	0.96 (±0.18)	0.81 (±0.15)	0.25 (±0.03)	0.67 (±0.11)
Post-conception	7*	0.35 (±0.07)	0.15 (±0.02)	0.65 (±0.09)	0.92 (±0.11)	0.79 (±0.18)	0.25 (±0.04)	0.69 (±0.04)
	8	0.27 (±0.07)	0.15 (±0.03)	0.57 (±0.08)	0.84 (±0.18)	0.70 (±0.15)	0.17 (±0.02)	0.46 (±0.04)
	9	0.20 (±0.06)	0.12 (±0.02)	0.35 (±0.12)	0.78 (±0.12)	0.56 (±0.17)	0.11 (±0.03)	0.31 (±0.08)
	10	0.19 (±0.05)	0.10 (±0.02)	0.17 (±0.14)	0.33 (±0.19)	0.25 (±0.11)	0.04 (±0.02)	0.00 (±0.00)
	11	0.04 (±0.02)	0.00 (±0.00)	0.00 (±0.00)	0.00 (±0.00)	0.00 (±0.00)	0.00 (±0.00)	0.00 (±0.00)
	12**	0.01 (±0.00)	0.00 (±0.00)	0.00 (±0.00)	0.00 (±0.00)	0.00 (±0.00)	0.00 (±0.00)	0.00 (±0.00)
Post-parturition	13	0.08 (±0.04)	0.06 (±0.01)	0.18 (±0.02)	0.49 (±0.24)	0.34 (±0.10)	0.07 (±0.06)	0.30 (±0.21)
	14	0.18 (±0.06)	0.14 (±0.05)	0.41 (±0.13)	0.78 (±0.13)	0.60 (±0.19)	0.11 (±0.03)	0.44 (±0.19)
	15	0.25 (±0.12)	0.10 (±0.03)	0.53 (±0.15)	0.73 (±0.18)	0.63 (±0.08)	0.07 (±0.02)	0.60 (±0.12)
	16	0.23(±0.09)	0.11 (±0.03)	0.46 (±0.10)	0.84 (±0.17)	0.65 (±0.11)	0.09 (±0.02)	0.63 (±0.23)
	17	0.27 (±0.08)	0.13 (±0.03)	0.61 (±0.13)	0.89 (±0.20)	0.75 (±0.14)	0.16 (±0.05)	0.68 (±0.01)
	18	0.27(±0.07)	0.12 (±0.06)	0.54 (±0.05)	0.87 (±0.22)	0.71 (±0.11)	0.17 (±0.05)	0.59 (±0.14)

*Conception occurred in the middle of this month; **Birth occurred, in the end, this month

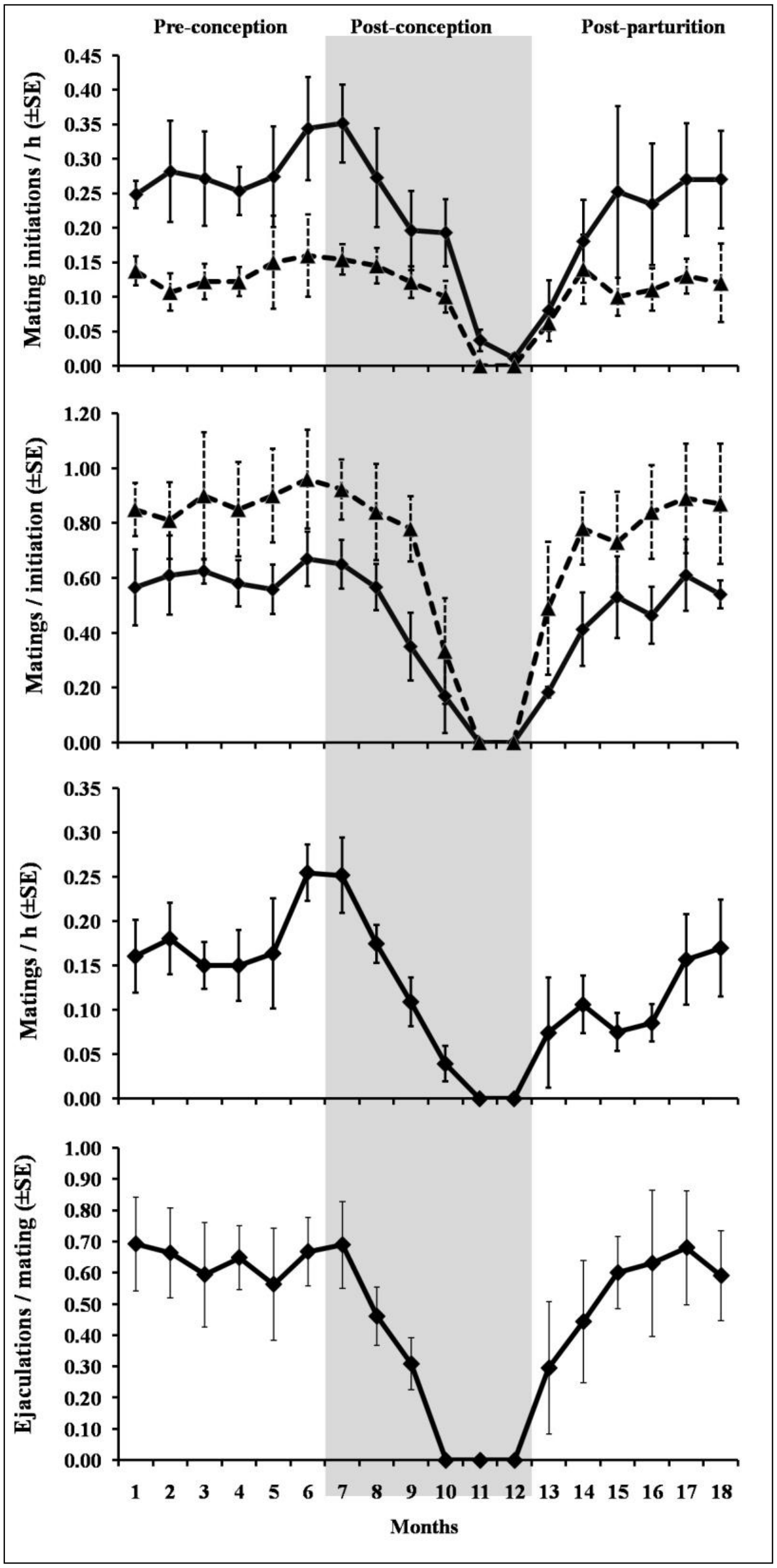

Fig. 4.3. Distribution of reproductive behaviors with reproductive status of females (Dotted line: female)

Table 4.4. Variation of reproductive behaviors between months in pre-conception, post-conception an post-parturition period, *<0.05p, **<0.005p, ***<0.001p

Variation between months (N=6)	Pre-conception			Post-conception			Post-parturition		
Behavior	χ^2	df	p	χ^2	df	p	χ^2	df	p
Male mating initiation rate	4.03	5	0.55	1.26	5	0.74	5.57	5	0.35
Female mating initiation rate	6.09	5	0.30	0.88	5	0.03*	2.36	5	0.80
Male mating success rate	6.56	5	0.26	1.73	5	0.04*	5.85	5	0.32
Feale mating success rate	8.38	5	0.14	4.00	5	0.55	3.81	5	0.58
Overall mating success rate	1.04	5	0.96	21.79	5	<0.01**	10.12	5	0.07
Mating rate	10.95	5	0.04*	28.17	5	<0.001***	6.26	5	0.28
Ejaculation rate	4.526	5	0.48	15.40	5	<0.01*	1.29	5	0.94

Table 4.5. Variation of reproductive behaviors between females in pre-conception, post-conception and post-parturition period:

Variation between females (N=6)	**Pre-conception**			**Post-conception**			**Post-parturition**		
Behavior	χ^2	df	p	χ^2	df	p	χ^2	df	p
Male mating initiation	7.43	5	0.19	7.40	5	0.19	4.37	5	0.36
Female mating initiation	6.71	5	0.24	9.15	5	0.10	6.11	5	0.19
Male mating success	7.75	5	0.17	9.45	5	0.09	2.95	5	0.57
Feale mating success	2.65	5	0.75	2.10	5	0.84	0.72	5	0.95
Overall mating success	6.67	5	0.25	8.86	5	0.12	2.73	5	0.60
Mating per rate	7.68	5	0.18	3.38	5	0.64	1.26	5	0.13
Ejaculation rate	7.61	5	0.18	4.56	5	0.47	2.79	5	0.59

Post-parturition period: Where, all reproductive behaviors were paused during the last two months of post-conception period, resumed again after parturition (**Fig. 4.3**). Mating initiation by both male and female was started from the first month after birth and become stable after the third month of post-parturition, while mating initiation by males remained higher afterwards. Similar pattern was observed for mating success, where mating success of both males and females increased sharply from the first month and stabilized after the second month from parturition, while mating success of females remained higher than males throughout the period. However, neither the mating initiation nor rate of mating success varied significantly in post-parturition period for both sexes (**Table 4.4**). Similarly, mating rate and ejaculation rate increased gradually from the first month of post-parturition and reached stability after the third and fifth month without showing any significant variation.

4.3.4. Relations between reproductive behaviors:

The mating success of both males and females were positively correlated with mating initiation by each sex during pre-conception, post-conception and post-parturition periods (**Table 4.6**). In the post-conception period, the mating rate was positively correlated with mating initiation as well as the mating success of both sexes. Similarly, the mating rate also correlated with overall mating success and ejaculatory rate during the post-conception period. Male mating success showed a positive correlation with female mating success only in the post-conception period.

Table 4.6. Correlation between reproductive behaviors in pre-conception, post-conception and post-parturition period, *<0.05p, **<0.005p, ***<0.001p.

Variation between females (N=6)	**Pre-conception**			**Post-conception**			**Post-parturition**		
Behavior	**r**	**N**	**p**	**r**	**N**	**p**	**r**	**N**	**p**
Mating rate / Ejaculation rate	0.39	6	0.44	0.99	6	0.00***	0.49	6	0.32
Mating rate / Mating success	0.76	6	0.08	0.96	6	0.002**	0.70	6	0.12
Male mating initiation rate / Female mating initiation	0.54	6	0.27	0.97	6	0.002*	0.67	6	0.14
Male mating success / Female mating success	0.57	6	0.24	0.89	6	0.01*	0.90	6	0.11
Male mating initiation / Male mating success	0.84	6	0.04*	0.96	6	0.002**	0.98	6	0.00*
Female mating initiation rate / Female mating success	0.78	6	0.04*	0.90	6	0.003**	0.87	6	0.01*
Mating rate / Male mating success	0.76	6	0.79	0.98	6	0.00***	0.62	6	0.19
Mating rate / Female mating success	0.60	6	0.21	0.93	6	0.01*	0.72	6	0.11
Mating rate / Female mating initiation rate	0.66	6	0.13	0.94	6	0.01*	0.61	6	0.20
Mating rate / Male mating initiation rate	0.58	6	0.22	0.88	6	0.02*	0.64	6	0.17

4.3.5. Mate competition:

The data during a non-migratory period when no male-migration happened in the TR group (1/11/13 - 30/5/14) showed that the mating rate significantly differed between males (χ^2= 309.83, df= 3, p< 0.001), and also negatively correlated with their social ranks (r= -0.98, p=

0.00, N= 4), which state that high ranking males mated more than low ranking males. However, ejaculation rate, thrust rate and duration of mating did not differ between males.

4.4. Discussion:

Nicobar long-tailed macaque showed polygynandrous mating throughout the year, where both sexes mated with multiple partners. However, participation in mating varied between males, but the pattern of reproductive behaviors remained similar. Intensity of sexual swelling varied between young and older females. The average inter-birth interval was 14.75 months and did not vary between females. Mating initiation rate and mating success showed same patterns for both sexes by reaching a peak in around conception month and then slowly decreased along with gestation periods. Highest mating was observed in the months around conception period, which continued up to about 4th month of the gestation period. Mating success was positively correlated with mating initiation by both sexes in pre and post-conception period, where the mating rate was positively correlated with mating success and ejaculation rate only in the post-conception period. High ranking males mated more than the low-ranking males.

Like many group living primates, macaques also show polygynandry mating system where mating success of male is skewed towards dominant rank as a result of mate monopolization (Kappeler and van Schaik 2002). This study also showed the consistency of such promiscuous mating system in *M. f. umbrosus* where individuals of both sexes mates with multiple partners of opposite sexes. Living in a linear hierarchical society, mate monopolization is the most evident strategy adopted by dominant male to increase their reproductive success (Soltis 2004). However, the monopolization of mate resources by a dominant male depends on the number of receptive females in the group (Kappeler and van Schaik 2004). In seasonal breeders, females show synchronized receptivity in a discrete period, the relative mate monopolization by a dominant male is lower than the non-seasonal breeders where females come into receptivity non-synchronously throughout the year (Paul 2004). As a result, mating success of a dominant male in non-seasonal macaques is higher than seasonal breeders (Paul 2004). Similarly, 81% of mating is by a dominant male FY shows the skewed distribution of mating among males. . Further the increase of mating success with higher ranking males also depicts the evidence of rank related allocation of mating success in *M. f. umbrosus*. Males had multiple-mount ejaculation which refers to a society where mate competition between male is high, multiple mount ejaculation acts as a component of mate guarding which increase the sperm competition by selecting sperm output per ejaculation and would benefit all males irrespective of their social rank (Bercovitch and Nürnberg 1996).

Like other subspecies (*M. f. fascicularis*: van Noordwijk 1985, Engelhardt et al. 2005), *M. f. umbrosus* females developed sexual swelling on their anogenital region, and it did not represent as the 'graded signal' of receptiveness. Moreover, it was less conspicuous for older (multi-parous) females than the younger females, which resulted in significant variation in swelling between females of similar reproductive stages. It suggests that such pattern of sexual swelling is more important for young females (nulliparous and primiparous) to exhibit their receptive phases than the old ones, further the prolonged sexual swelling with exceeding conceptive window would provide information about the probability of ovulation than the exact ovulation window (Engelhardt et al. 2005). On the other hand, it could be the adaptive strategy of females to provide incomplete information about their receptivity to males by concealing the particular period of ovulation (Nunn et al. 2001).

While females adapt various strategies to increase paternity confusion by making ovulation unpredictable to males, meanwhile, since the copulation requires high energy expenditure males also try to mate females more while the probability of ovulation is high (Bercovitch 1987). Therefore, distribution of mating and associative behaviors (mating initiation and ejaculatory mating) should depend on both the reproductive stages of females as well as the perception of males about the receptiveness of females. In *M. f. fascicularis,* where the sexual swelling did not synchronize with the ovulation period, certain behaviors like reaching back and solicitation by females become a clue for males to identify the probable ovulation period (Engelhardt et al. 2005). Similarly, the higher mating initiation by females in the month of conception than other pre, post-conception months, indicates that the males may have some cue which helps them to determine the receptive phase of the females, which is indicated by observed-peaks in mating initiation by males around conception period. Since, sperm production has high energy expenditure; males ejaculated more in and around conception period, resulted positive correlation between mating and ejaculation only in the post-conception period.

In non-seasonal breeders, females do not conceive in their first post-parturition estrus cycle, and conception depends on their health, weaning of last infant, food availability and other ecological and social factors (van Schaik and Brockman 2005). Therefore, conception often occurs after a series of non-fertile estrus cycles. No variation in reproductive behaviors within pre-conception period may be the resultant of prolonged receptive phase of females. Similar to other sub-species *M. f. fascicularis* (Engelhardt et al. 2007), M. *f. umbrosus* were involved in post-conception mating which continued longer than the other subspecies (80 days). The post-conception mating is an effective reproductive strategy of females to increase the paternity confusion in males by inviting them in mating while there is no chance of fertilization (Engelhardt et al. 2007). Moreover, mating initiation by males in post-conception period may be due to their inability to distinguish such non-fertile phase.

Generally, due to lactational amenorrhoea, there is a pause in estrus cycle during the first phase of reproductive cycle which makes the first few months of the post-parturition period infertile (Maninger et al. 2000). However, in these macaques, mating resumed just after parturition. In non-seasonal macaques, the risk of infanticide is high where lactation period is greater than gestation period and females carry their dependent infant (van Schaik 2000). Where, male can enforce females to resume their estrus cycle by killing dependent infants. Therefore, females often adapt counter-strategies like post-parturition proceptivity and mating which ultimately reduce the risk of infanticide. In the current study, the female ‘AU’ was observed to conceive three months after the parturition, and after the second birth both older (AN) and younger infants (AY) were suckling and weaned successfully (**Fig. 4.4**). This suggests that though lactational amenorrhoea is common in macaques, it can be disrupted by females to increase their reproductive success. van Schaik (2000) argued that overlapping gestation and lactation period can act as an infanticide inhibition strategy of females, where, the post-parturition cycling and short inter-birth interval may also motivate males to involve in post-parturition mating rather than killing the infant.

Moreover, in a biological market where mating acts as a commodity, males mate to impose their dominance over females (Soltis 2004), and females involved in mating to get tolerance, protection against infanticide and reduced the risk of coercion from group living males (Smuts and Smuts 1993). In this study observed mating initiation by both sexes throughout pre and post-conception periods, and positive relation with mating success may be the resultant of adopted strategies by both sexes to increase their inclusive fitness through reproductive as well as non-reproductive benefits.

Figure 4.4. AU carrying younger infant AY while the older infant AN suckling.

The *M. f. umbrosus* showed all species-specific reproductive traits by exhibiting similar matting patterns observed in other sub-species i.e. *M. f. umbrosus*. In *M. f. umbrosus*, both intra and inter-sex mate competition is very evident where both sexes adapted various reproductive strategies and counter-strategies to maximize reproductive success against each other. Although sexual swelling did not convey receptivity of females, males were able to identify the phase having a high probability of fertilization. The study provided a first-ever information on reproductive pattern and the strategies adapted by males and females to balance the trade-off of intra-inter-sexual mate competitions in *M. f. umbrosus*.

CHAPTER 5

Rank Changeover by Challenge

Consequences of a Male Reproductive Strategy on Society

"*The King is dead, long live the King!****"***

5.1. Introduction

In many group living species, dominance rank or status is a good predictor of mating success in both males and females (Clutton-Brock and Huchard 2013). This relation is strong among males in the species that mate polygynously (Alberts 2012). Although the influence of social rank on mating success varies, a top rank can help a male to monopolize mating resources (Kappeler and van Schaik 2002). A male can acquire the top dominance rank in three different ways: 1) a rank changeover by challenging and defeating the present dominant male by a resident or an out group male, 2) by forming a new group by ousting the resident males, or 3) through succession, after the death or the emigration of the previous dominant male (van Noordwijk and van Schaik 2004). In large groups of the Japanese macaque (*Macaca fuscata*), when the prime male (alpha) dies or becomes inactive, hierarchy shifts to the next dominant male without much aggression, whereas in smaller groups, it happens through aggressive challenge by the outer males (de Ruiter et al. 1994; van Schaik and Janson 2000). van Noordwijk and van Schaik (1985) reported from a long term study on the long-tailed macaque (*Macaca fascicularis*) that resident males generally succeeded in reaching the top rank (100% of replacements) while outer group males were less often successful (29% of replacements). Moreover, in crested macaque (*Macaca nigra*) of South Sulawesi, 56% of the rank changeover events happen through severe aggressive fight between top rank male and outer group male, where 44% rank changeover occur after opportunistic invade of outer group male while the resident male left the group or injured (Marty et al. 2017).

A sudden change in the social organization of a group has an immense impact on its members (Kumar et al. 2001; Singh et al. 2006). In the case of a rank changeover with an aggressive approach by a challenger male towards the dominant male of the group, the duration, and intensity of the agonistic interactions vary with the response of the prime male (Kumar et al. 2001; Singh et al. 2006). After being defeated, the former dominant male may leave the group immediately (Singh et al. 2006; Marty et al. 2017) or stay with the group as a subordinate individual (van Noordwijk and van Schaik 1988; de Ruiter et al. 1994; Hayakawa and Soltis 2011). The new alpha male may involve in agonistic interactions to establish dominance over the other group members (Saj and Sicotte 2005; Clarke et al. 2009). The new dominant male tries to increase reproductive access by initiating mating with adult females of the group (Hayakawa and Soltis 2011). If most females in the group are lactating or are in the non-cycling phase, they may not positively respond to the mating-initiation approaches by the male. In such a situation, the male may adopt strategies like a forced mating with a female (Smuts and Smuts 1993), and probable infanticide (Hrdy 1974; 1977; 1979) to attain reproductive success. In response, the females may also adopt various counter-strategies such as group defense to protect themselves from sexual coercion (Zinner and Deschner 2000), situation-dependent receptivity (de Ruiter et al. 1994), deceptive swelling (Hadidian and Bernstein 1979; Colmenares and Gomendio 1988; Takahata et al. 1996; Swedell 2000; Zinner and Deschner 2000), abrupt infant weaning (Teichroeb and Sicotte 2008; Zhao et al. 2011), and emigration from the group (Sterck et al. 2000) to secure the survival of their infants.

A rank changeover resulting from a challenge by outsider male is an infrequent but observed across macaques yet only in a few species (*M. fascicularis*: van Noordwijk and van Schaik 2001; *M. fuscata*: Sprague et al. 1998; Hayakawa and Soltis 2011; *M. nigra*: Marty et al. 2017; *M. radiata*: Singh et al. 2006; *M. silenus*: Kumar et al. 2001). Where most of the events were seen from the point of male migration and factors that determined the successful migration in acquiring the top rank in the group (Sprague et al. 1998; van Noordwijk and van Schaik 2001; Marty et al. 2017). However, the immediate effect of rank changeover on the behavioral ecology of the group is highly limited (**Table 5.1**).

In the Nicobar Islands, long-tailed macaques have a mean group size of 41.3 with about 13% of adult males and 30% of adult females (Velankar et al. 2016). The long-tailed macaque is a year-round breeder showing a birth peak between July and November (van Noordwijk and van Schaik 1999) and has an inter-birth interval of about 390 days (Hadidian and Bernstein 1979). It has a despotic social structure (Thierry 2004) where paternity concentration of the top dominant male is high (van Noordwijk and van Schaik 2001). Therefore, in long-tailed macaques, the social rank of a male has an impact on the mating success which makes rank changeover a successful reproductive strategy for the males. The long-tailed macaques fall under the high contest range (Thierry 2004), thus a rank changeover by challenge was expected to result in male initiated copulations, some of them with aggressive approaches (Smuts and Smuts 1993), and its associated consequences such as possible infanticide (van Schaik and Janson 2000), and a variety of counter strategies by the females (van Schaik 2000; Palombit 2015) such as group defense or pseudo sexual swelling. It has been observed in Nilgiri langurs (*Semnopithecus johnii*) that after a rank changeover by an outsider male challenge the group reduced and shifted its home range even to a resource poor area but resulting in less frequent intergroup encounters than before the shift (Kavana et al. 2014). Maybe following the rank changeover, the home range of the group might shift or reduce in size in order to avoid intergroup encounters during the period of social instability.

As the rank changeover by a challenge has been reported in the other subspecies of long-tailed macaques (*M. fascicularis fascicularis*: van Noordwijk and van Schaik 1988, 2001), the same event was anticipated in the study population. Such rank changeover was observed for the first time for the sub-species. The consequences of this rank changeover by a challenge on behavior and habitat use in the Nicobar long-tailed macaque is reported in this study, which will provide additional information to fill the lacuna in understanding the effect of rank changeover events in group living macaques.

5.2. Materials and Methods

5.2.1. Data collection: The study site was inhabited by five groups (LB, PI, TR, MG, MA) of Nicobar long-tailed macaques with an average group size of 35.60 animals/group, with a density of 1.10 groups/ km^2, or 39.16 macaques/ km^2 (**Figure 5.1**). Whereas all groups were monitored for demography and population dynamics, the TR group, for convenient logistic reasons, was the focal group for a long-term behavioral study. Just before the rank changeover by challenge by an out-group male, the study group comprised 18 individuals, including two adult males (HK, RY), eight adult females (AU, BY, LA, NI, PM, RE, SC, TE), one subadult male (MF), four juveniles (BA, KU, OE, UK) and three infants (AI, BN, PT). RY was the alpha male.

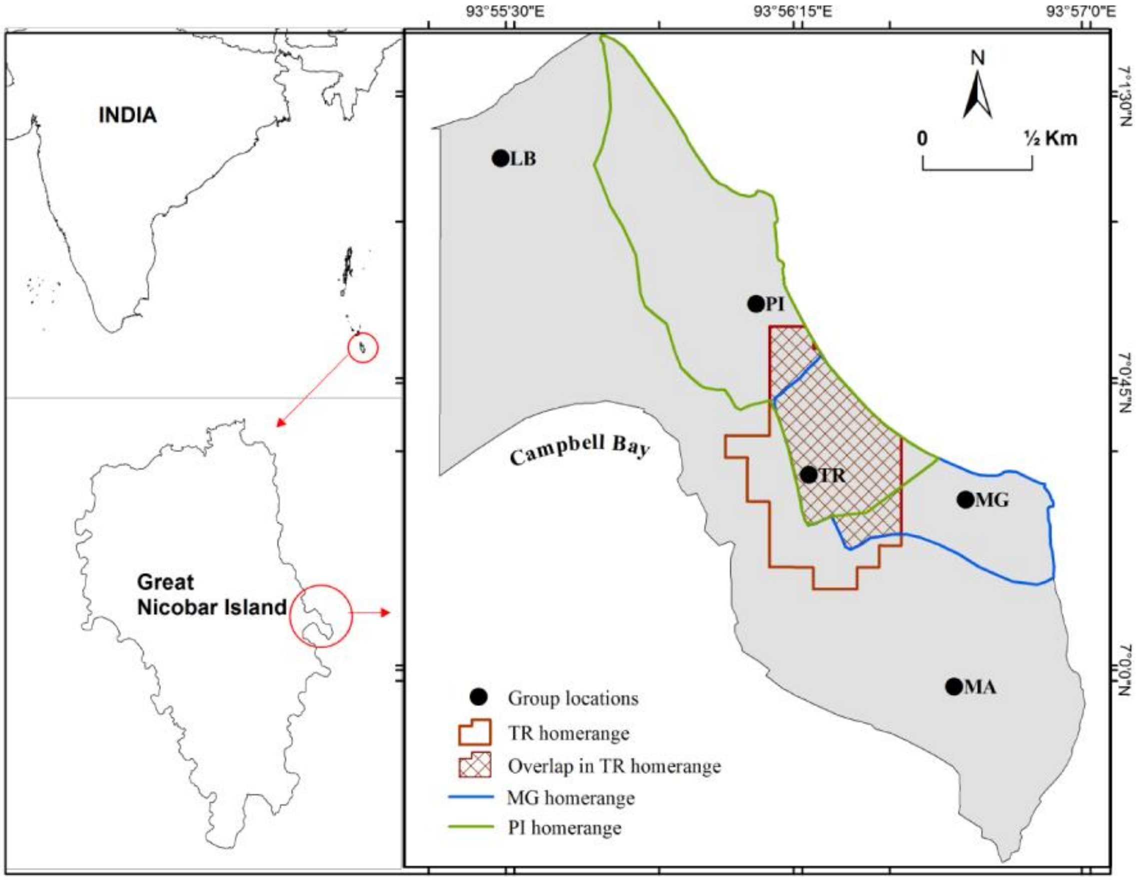

Figure 5.1. An overview of the study area showing locations of the macaque groups with their respective home ranges in Great Nicobar Island (the overlapping regions are crosshatched).

The first three months, was spent to habituate the monkeys to the presence of observers. Following this, a 2781 h study was carried out between August 2013 and December 2015. During this period, all individuals were identified using their facial markings and features and wound marks on the body. Based on the physical appearance of the monkeys, the age classes that were considered are adult: ≥ 4 years, sub-adult: 2.5-4 years, juvenile: 6 m-2.5 years, and infant: ≤ 6 m (Velankar et al. 2016). The group count and demography data were collected when all individuals were crossing a road or moving for roosting in a single line.

Three observers independently collected data on ecology and ranging, between-group encounters and reproductive behavior with different methodology and thus the effort for these behaviors studied varied. Observers followed the group for an entire day from 0600 to 1830 h. The group mostly ranged in a high visibility area and only occasionally moved into dense undergrowth or a restricted region like premises of Defense and Coast Guard, and the time spent there was not included in the total observation hours of that day. The geo-coordinates of the visually calculated center of the group were recorded using handheld geographic positioning system (Garmin GPSmap 76CSx) every 30 min during the follow of the group (Santhosh et al. 2015). The geo-coordinates of the sleeping site after termination and before initiation of daily movement of the group were recorded (Tsuji 2011). The presence/absence of individuals in the group and their identity was recorded every day.

Data on the between group encounters were collected as event sampling (Altmann 1974). Between-group encounters were considered as those occasions when two groups came close to each other in the visible range or in auditory contact that is about 50 m of proximity (Cooper et al. 2004). A between group encounter was classified as 'non-aggressive' if interactions were limited only to visual and vocal exchanges, and 'aggressive' when the groups involved in aggressive vocal and physical interactions that included chasing and fighting (Kumara et al. 2014). The frequency of overall as well as of each class of encounter was calculated by dividing the number of encounters by the number of observation hours per day.

All occurrences sampling method was used to collect data on copulations (Altmann 1974). The identity and activity of each individual involved in the pre-copulatory, copulatory and post-copulatory activity along with the mating approaches were recorded (Kowalewski and Garber 2010). A mating was considered to have occurred when there was a mounting with intromission and sequence of pelvic thrusts (Jones 1985). Ano-genital presentation and reaching back to a female, and genital inspection and aggressive approach for mating by a male, were considered as mating initiation approaches (Soltis et al. 1997). The data on presents, mounts, and copulations were collected through all occurrence sampling. The records on the rank changeover and migration events were obtained through *Ad libitum* sampling (Altmann 1974).

5.2.2. Data analysis: The rank changeover event took place on October 14, 2013 and the analysis was employed on data collected between July 2013 and January 2014. The period from July 2013 to October 14, 2013 was considered as the pre-rank changeover period, and from October 14, 2013 to the end of the study, January 2014, as the post-rank changeover period. All data were accordingly segregated and compared.

Between-group encounter: The between-group encounter data were collected for 864.75 h (111 days) with 388.75 h (60 days) and 476 h (51 days) in the pre and the post-rank changeover periods respectively. Each observation day was considered as one sample. The between group encounter rates of each day was calculated using the number of interactions (Overall, Non-aggressive and Aggressive) recorded against observation hours of that day and are presented as interactions per hour.

Ranging pattern: The Shape File of the study area was overlaid with one-hectare grid cells using fishnet tool in ArcGIS 10.2. The geo-coordinates collected during the group follow were plotted on these grid cells. The grid use was calculated as the proportion of the number of points in each grid cell by the total number of points recorded in each period. The proportion of the intensity of sleeping site use was calculated as the number of days each sleeping site was used by the total number of observation days in each period (Fig 2). The day range length (DRL) was calculated by joining the consecutive locations taken during the group follow using the Geospatial Modeling Environment (GME) extension (Santhosh et al. 2015) for ArcGIS 10.2. To estimate the DRL, only the follows for a minimum of eight hours of the observation period in a day were used, and the length was measured using a field calculator in ArcGIS 10.2. The home range of the study group was estimated by adding the area of all the grid cells visited by the study group for each period (Santhosh et al. 2015). Since, there was no control period for seasonal influence on ranging behavior, the data on home range use collected during the next year same period (14/10/2014 to 27/01/2015) was used as control and compared it against the post-rank changeover ranging data of the year 2013.

Reproductive behaviors: During the study period, the reproductive behavioral data were collected for 232.5 h (56 days) with 118.5 h (24 days) and 114 h (32 days) in the pre and the post-rank changeover periods respectively. Each day of the group follow was considered as one sample. The rates of different reproductive behaviors (mating, female initiation, male initiation and mating by individual females) were computed using the number of each behavior recorded against the number of observation hours of each day and projected as number per hour of observation. The proportion of aggressive mating approaches by a male was computed as the number of aggressive approaches for mating by males divided by the total number of mating initiations by males each day. The rates of successful mating (copulation) of male and female or mating success in each day were estimated as the number of matings in a day divided by the total initiations on that day by males and females respectively.

Statistical analysis: The rates of reproductive behaviors, the day-range length, and rates of encounters between the pre- and the post-rank changeover periods were compared using t test. To calculate the grid use intensity, the percentages of recorded location points (geo-coordinate) of each grid were classified into five levels (not used, ≤ 0.6, 0.7-6.6, 6.7-10, >10). The sleeping site use intensity was also categorized into five classes (not used, ≤ 2, 2.1-5, 5.1-10, >10) after calculating the percentage of sleeping records in each site. The percentages were calculated as the observed numbers in proportion to the total observations in the pre and the post-rank changeover within a gridded map to represent the home range and sleeping site use (**Figure 5.2**). To compare the pre and the post-rank changeover intensity of grid cells and sleeping sites use, Wilcoxon signed-ranks test was used for the computed percentage of grids and sleeping sites independently. The use and not-use data of the total grids and sleeping sites (both the pre and the post-rank changeover) were used in McNemar binomial test to compare the grid use and the sleeping site use (Price and Piedade, 2001; Fei et al. 2012). R v3.4.1 statistical language with IDE R Studio v1.0.143 (R Development Core Team 2008) was used for statistical analysis and Q-GIS 2.18 (QGIS Development Core Team 2009) for spatial analysis and study site mapping.

5.3. Results

5.3.1. Rank changeover event: An alpha male replacement was observed on October 14, 2013 with an outside male named FY successfully challenging the resident alpha male RY, leading to an alpha male change (henceforth called rank changeover) and subsequently to the death of the former alpha male (RY). After this rank changeover event till December 2015, two previously unknown individuals, viz. one adult male (now named GP) and one adult female (now named KB) immigrated, while ten individuals including the immigrated individuals, *viz.* two adult males (GP and HK), four sub-adult males (UK, OE, MF and BA), two adult females (KB and PM) and two male infants (PT and PY) disappeared from the group. PM also left the group with her one-month old infant (PY) on 10th December 2014. All individuals that emigrated from the group were not traceable in the vicinity.

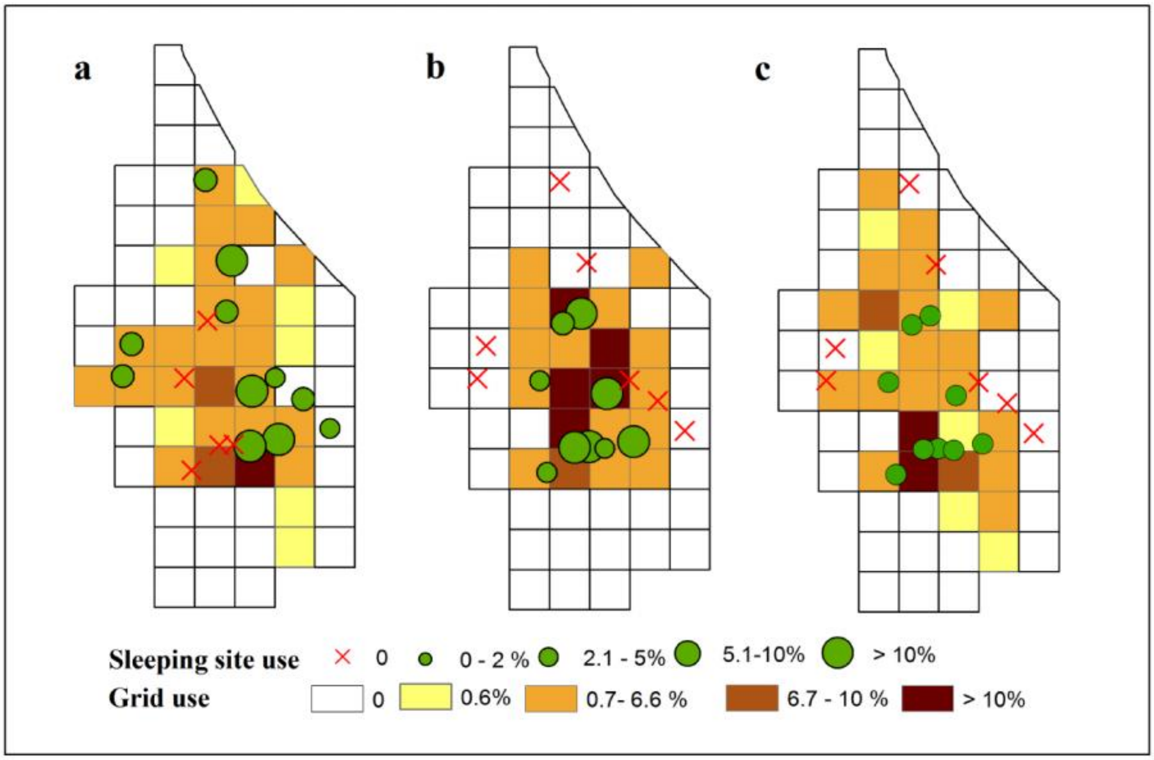

Figure 5.2. The intensity of use of grid cells and the sleeping sites by study group-TR (a. the pre-rank changeover pattern, b. the post-rank changeover pattern, c. control)

5.3.2. Habitat use pattern: The home range size (number of grids used) of the study group was 34 hectares for the seven month of rank changeover study period where 18 grids were used in both pre- and post-rank changeover periods, and the pre- and the post-rank changeover grid use was 32 and 21 hectares respectively, which differed significantly (2-tailed McNemar binomial test: $p < 0.01$). However, the intensity of grid use did not differ significantly between the pre- and the post-rank changeover (Wilcoxon signed-ranks test: $Z = 0.523$, $p = 0.601$). The number of grids used in post-rank changeover was significantly smaller than the number of grids used in the pre-rank changeover period and also in the same period in the next year (which was considered as a control for the seasonal influence on ranging pattern) (2-tailed McNemar binomial test: $p < 0.01$). The study group used 16 sleeping sites during the study period (Figure 4. 2) where four sleeping sites were used in both pre- and post-rank changeover periods. The number of sleeping sites during the pre- and the post rank changeover periods ($N = 11$ and $N = 9$ respectively) did not differ in a statistically significant way (2-tailed McNemar binomial test: $p = 0.780$). The intensity of use of the sleeping sites also did not differ between the pre- and the post-rank changeover (Wilcoxon signed-ranks test: $Z = 0.523$, $p =$

0.715). Further, the sleeping sites after the rank changeover were largely confined to the center of the home range. The day range length in the pre (999.18 m ± 225.52_{SD}) and the post (981.87 m ± 200.16_{SD}) rank changeover also did not differ (t= 0.195, df= 25, p= 0.874).

5.3.3. Between group interactions: The number of between group interactions in the pre- and the post-rank changeover was 11 and 9 respectively. The rate of between group interactions did not differ between the pre- and the post-rank changeover, which were 0.026 h^{-1} and 0.018 h^{-1} respectively (N= 20, t= 0.887, df= 109, p= 0.377). The aggressive between-group interactions (N= 10) in the post-rank changeover period (N= 3, 0.005 h^{-1}) were lesser than in the pre-rank changeover period (N= 7, 0.017 h^{-1}). However, both the non-aggressive and the aggressive between-group interactions did not differ between the pre- and the post rank changeover period (Non-aggressive: N= 10, pre= 4, post= 6, t= 0.40, df= 109, p= 0.680; aggressive: N= 10, pre= 7, post= 3, t= 1.56, df= 109, p= 0.120).

5.3.4. Reproductive behaviors: During the rank changeover period, three of the eight females were lactating, two were cycling (reddening of tail-root and ano-genital skin) and three were non-cycling. From the rank changeover day, a lactating female AU mated with FY after leaving her eight months old infant with the group while the other two lactating females BY and PM were carrying infants with ages of eight and nine months respectively. The other females avoided mating approaches by FY by participating in a group defense coalition with other females and males. Subsequently, aggression decreased and all females but PM started soliciting FY within two weeks after the rank changeover. On November 17, 2013, a severe fight occurred between FY and PM in a bush. PM came out with severe wounds on her left thigh, upper part of the abdomen, right arm pit and left palm. Her about one-month old male infant PT was not found thereafter. PM started mating with FY only after the disappearance of her infant. After the rank changeover, until December 2015, six of those eight females gave birth. The post-rank changeover first conception date of six females was calculated by back-calculating 165 days gestation period (van Noordwijk 1985) from parturition day, which ranged between 11 and 51 weeks with a mean of 30.6 ± 16.3_{SD} weeks from the day of the rank changeover (**Table 5.1**). This shows that no female became pregnant in a first sexual swelling phase following the post-rank changeover.

Table 5.1. Females' first - sexual swelling, conception and birth according to the rank changeover event in study group of Nicobar long-tailed macaque

Female ID	Reproductive status on acquisition period	Presence of swelling on acquisition period (Yes/No)	First appearance of sexual swelling after acquisition (weeks)	Conception date of post-acquisition first birth from acquisition period (weeks)
AU	Lactating	No	2	10
BY	Lactating	No	3	15
LA	Non-receptive	No	3	-
NI	Receptive	Yes	3	-
PM	Lactating	No	6	31
RE	Receptive	Yes	3	46
SC	Non-receptive	No	7	-
TE	Non-receptive	No	4	51

The number of matings observed in the pre- and the post-rank changeover was 55 and 117 respectively, and the number of matings per hour was significantly higher during the post-rank changeover than during the pre-rank changeover period ($t= 4.88$, $df= 54$, $p< 0.001$). In the pre-rank changeover period, RY (83.64%) was involved in the higher number of matings than in the post-rank changeover period. However, in the post-rank changeover period, FY (77.78%) mated most often and no mating was observed by RY. The rate of mating initiated by adult females between the pre ($0.30\ h^{-1}$) and the post ($0.33\ h^{-1}$) rank changeover did not differ ($t= 0.36$, $df= 54$, $p= 0.742$) (**Figure 5.3**). The rate of matings initiated by male differed significantly between the pre ($0.27\ h^{-1}$) and the post-rank changeover ($1.01\ h^{-1}$) ($t= -5.05$, $df= 54$, $p< 0.001$). The proportion of aggressive mating approaches by a male was significantly higher during the post-rank changeover than in the pre-rank changeover ($t= -4.26$, $df= 54$, $p< 0.001$). The rate of mating success of females and males in the pre- and the post rank changeover did not differ (female: $t= 1.27$, $df= 54$, $p= 0.211$; male: $t= 1.00$, $df= 54$, $p= 0.32$). Although the rate of mating with all the adult females increased during the post rank changeover period, the significant increase was seen with AU ($t= 2.462$, $df= 54$, $p= 0.017$), BY ($t= 3.484$, $df= 54$, $p= 0.001$), LA ($t= 2.00$, $df= 54$, $p= 0.05$) and NI ($t= 2.08$, $df= 54$, $p= 0.007$) (**Figure 5.4**).

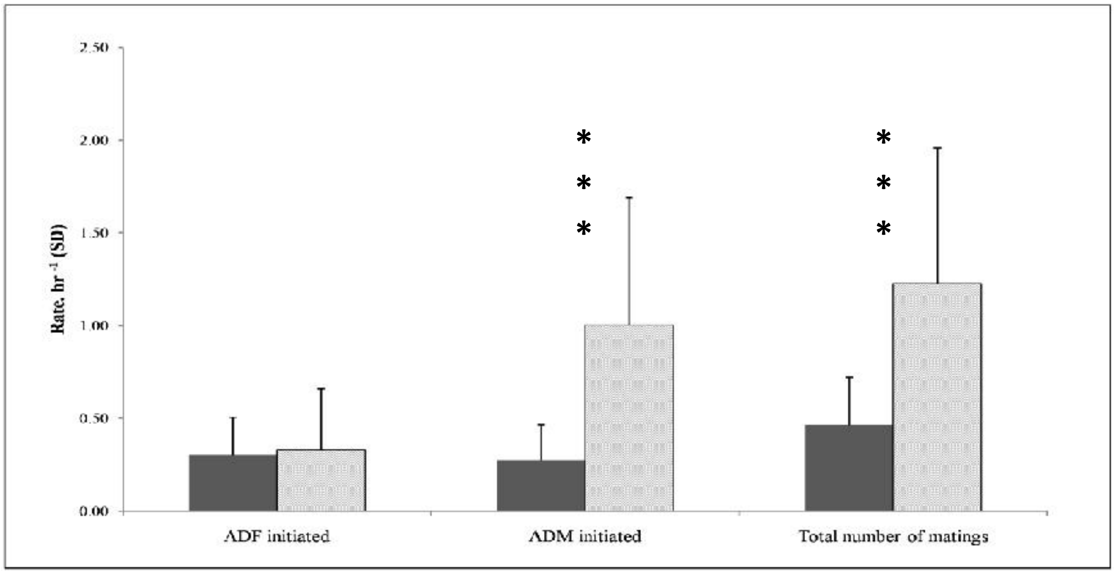

Figure 5.3 Frequency of mating initiation by adult female (ADF initiated), mating initiation by adult male (ADM initiated) and the total number of matings observed during the pre- and the post rank changeover in study group-TR (solid columns represent the pre rank changeover mating initiation rates and mating rates, crosshatched columns represent the post rank changeover mating initiation rates and mating rates, *<0.05p, **<0.005p, ***<0.001p).

5.4. Discussion

One rank changeover event by an outside male was recorded in a wild Nicobar long-tailed macaque group during a 30 months study on the Great Nicobar Island. The intensity of grid use and the day range length of the study group did not change after the rank changeover event, though the group used significantly lesser grids after rank changeover than in pre-rank changeover. The rate of between group interactions did not change after the rank changeover, although the rate of aggressive encounters was lower than in the pre-rank changeover event. The overall mating rate increased significantly with a higher rate of overall and aggressive mating approaches by the new male in the post rank changeover period than by the previous alpha male during the pre-rank changeover period. However, the rate of mating success was not different in the two periods. The mating rates of all adult females increased significantly after the rank changeover except for one female (PM). These findings add to the growing knowledge on rank changeovers and the resulting changes in behavior.

A shift and a decrease in grid use and sleeping sites were observed after the rank changeover. The ranging data of the post-rank changeover differed from the next year control data, which nullifies seasonality as a causal factor of change in the post rank changeover ranging pattern.

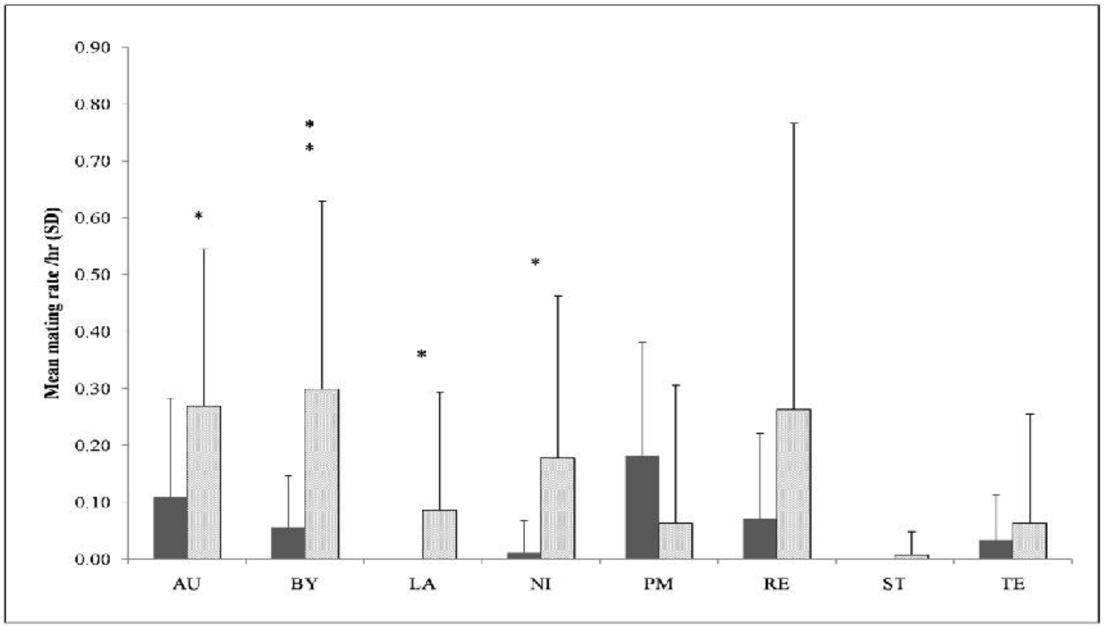

Figure 5.4. The rate of matings with individual females during the pre- and the post rank changeover in study group-TR (solid columns represent the pre-rank changeover mating rates, crosshatched columns represent the post rank changeover mating rates, *<0.05p, **<0.005p).

Although the group used significantly smaller area in the post-rank changeover period than in the pre-rank changeover period, the day range length did not vary, which indicates that the group moved, constantly changing positions in a smaller area than before the rank changeover. This could have resulted in a change in the ranging pattern as a strategy to avoid interaction with neighboring groups, as seen in *Papio cynocephalus* (Markham et al. 2012) and *Semnopithecus johnii* (Kavana et al. 2014).

The group cohesion and coordination becomes weaker due to the post-rank changeover aggressive and restrictive social interactions between the immigrant male and the other individuals (Hayakawa and Soltis 2011). The new male was recorded to stay in the periphery of the group in the cases of *Macaca fuscata* (Horiuchi 2005) and *Alouatta pigra* (van Belle et al. 2010), which may be a strategy to avoid coalitionary aggression of the group or of the resident males. The defeated male became peripheral and stayed away from the new male by forming a subgroup with natal males and sometimes with lactating and pregnant females (e.g. *M. fascicularis fascicularis*: van Schaik and van Noordwijk 1985; *M. fuscata*: Hayakawa 2007). Therefore, during the post rank changeover, a weak social coordination may increase the risk of intergroup encounters. During the present study, opting to use a smaller home range size and shift in the location of sleeping sites in the post-rank changeover by the group may be a strategy adopted to avoid interaction with other groups in this disturbed social state. The decreased aggressive interactions in the post-rank changeover period supported encounter avoidance, though this inference should be viewed with a little caution due to a small sample size in the present study.

The changes of group membership by adult males after rank changeover directly affect the toppled male. Frequent competition between the new prime male and the deposed male would take place, and such competition eventually is biased towards the new prime male for his physical or fighting ability. After being defeated, the toppled male may stay in the group as a submissive individual or emigrate immediately (van Noordwijk and van Schaik 2001). Emigration of males due to the rank changeover is common in *Cebus capucinus*, and a rank changeover is considered as the most responsible factor to induce dispersal of the native males in the species (Jack et al. 2012). The ousted male remains as a submissive or a peripheral male with the same group in some of the macaque species *e.g. M. fascicularis fascicularis* (van Noordwijk and van Schaik 1988), *M. silenus* (Kumar et al. 2001), *M. radiata* (Singh et al. 2006). The ousted male RY in the present study remained in the group as a submissive male to FY. Due to the severe injuries and disabilities after the fight, the movement of RY was restricted to the ground, thus being a submissive male in the current group may have been a more beneficial strategy on his part than to emigrate.

An increased mating rate and the aggressive mating approaches by a new male can be attributed to the imposition of an acquired dominance over the group. Previous studies reported that male initiated copulations increased significantly after a rank changeover (Hayakawa 2007; Roux et al. 2013). Meanwhile, females show a situation-dependent receptiveness and they mate at a high rate with the immigrated male (Hrdy 1979; van Schaik et al. 1999; Zinner and Deschner 2000). The increased mating rate has been considered as a female counter strategy to minimize aggression and aggressive mating approaches from the new male in the post rank changeover period (Smuts and Smuts 1993; Muller and Wrangham 2009). A similar pattern of high mating frequency was observed for all adult females except PM in the study group. Female long-tailed macaques show conspicuous sexual swelling between the month of January and May followed by the copulation peak between January and June (van Noordwijk 1985). It may be noted that the rank changeover event in the present study occurred in the month of October that is the middle of the birth season when the mating frequency is expected to be the lowest. At that time, three females were in lactating phase. The high mating frequency, therefore, was a consequence of mating initiation by the new male. If the unweaned offspring get accidentally or strategically killed, the new male may increase mating initiation as a strategy to mate the female whose infant got killed and jeopardize the reproductive output of the current male.

After an agonistic interaction with the new alpha male FY, the female PM was severely injured and her infant PT went missing. Although the reason for the infant disappearance could not be ascertained, it most likely resulted from infanticide. As studies indicate, infanticide by a new male is another widespread behavior occurring during rank changeover which is found in both wild and captive long-tailed macaque populations (Timmermans et al. 1981; de Ruiter et al. 1994). Infanticide by a new male is a widespread strategy in primate societies to access lactating females by disrupting their lactational amenorrhea (*Semnopithecus entellus*: Sugiyama 1965; Hrdy 1974; *Theropithecus gelada*: Beehner and Bergman 2008). Many studies have shown that after infanticide, mothers become receptive and have shorter inter-birth interval than the average (Beehner and Bergman 2008). However, the female long-tailed macaques adopt strategies like prolonged receptiveness, post-conception copulation, and promiscuous mating, which decrease the chance of infanticide by increasing paternity confusion (van Schaik 2000). Furthermore, in the case of non-seasonal breeders, where the immigrated male is unrelated to the infants and where the females get receptive after the infant loss, infanticide may increase the reproductive benefit to the immigrated male (de Ruiter et al. 1994).

At the time of the rank changeover in the study group, only two of the eight females were cycling. Just after the rank changeover, only one lactating female AU was involved in soliciting FY after leaving her infant AI. This sudden decrease in maternal care after the resumption of sexual activity of a mother is common in many macaque societies (e.g. *M. mulatta*: Berman et al. 1993; *M. fuscata*: Schino et al. 2001). Except AU, all other females adopted a group defense strategy by forming a coalition with the other females and males to avoid aggressive mating approach from the immigrated male. In some of the primate species, females were observed to form a defensive alliance with the toppled male or with other group males which may have helped them to avoid aggressive mating approaches by the new male

(Rudran 1973). Within two weeks after the rank changeover, except PM, all females were soliciting FY, developed ano-genital swelling of different intensity and started mating with FY which consequently increased the post rank changeover mating rate. The failure of the female PM to ensure the survival of her infant by resisting FY may indicate that resisting was neither a low cost nor an effective strategy. The sexual swelling is a graded indicator of females' receptivity (Nunn 1999 but see Zinner and Deschner 2000), however, no female conceived in the first post-rank changeover cycle which may indicate that those swelling were deceptive. The two lactating females *viz.* AU and BY adopted this deceptive swelling strategy and were able to secure the survival of their infants without breaking the post-partum amenorrhea or getting pregnant. Therefore, it could be suggested that like *M. fascicularis fascicularis* (Engelhardt et al. 2005), the Nicobar long-tailed macaque females also successfully use a situation-dependent swelling as a counterstrategy against agonistic approach by the immigrated male. After exhibiting pseudo-cycling, the females also mated with the two other males of the group. These swellings are deceptive and not associated with ovarian cycles since the mating did not result in fertilization. Primate females widely use this promiscuous polyandrous mating as a reproductive strategy to protect themselves and their offspring through paternity confusion (*M. fascicularis*: de Ruiter et al. 1994; *Alouatta seniculus*: Agoramoorthy and Rudran 1995). Thus, the females in the study group were observed to adopt different strategies with respect to their reproductive status to minimize the cost incurred due to the rank changeover. Emigration and immigration of several individuals following the rank changeover event in the present study indicated social instability, which has also been reported in other macaques (e.g. *M. radiata*: Singh et al. 2006).

This study reveals how a single event of rank changeover by challenge has repercussions which cascade from the individual level to the cumulative group level changes in behaviors. In other words, the sexual strategy of a new alpha male is countered by different strategies employed by the individuals of different age-sex and reproductive stages, which ultimately manifest as altered reproductive behaviors and home range use patterns. In this way, co-evolving sexual strategies and counter strategies contribute toward emergent complexities in primate societies.

CHAPTER 6

Between-group Encounter

When Not to Fight

“Look He will win who knows when to fight and when not to fight.”

‡ Sun Tzu ‡

6.1. Introduction

The between-group encounters are a regular phenomenon in group living primates (Cheney 1987). The nature of between-group encounters, however, is influenced by socio-ecological factors, and varies widely within and between species (Cooper et al. 2004). During a between-group encounter, animals may mingle peacefully (*Papio cynocephalus*: Kitchen et al. 2004), show mutual avoidance (*Macaca silenus*: Kumara et al. 2014), or approach aggressively, which, in some cases, may become lethal (*Pan troglodytes*: Wilson et al. 2001). Often a between-group encounter occurs as a result of a contest for resources like food, mate, and shelter, and such encounters may lead to intense aggression (Cheney 1987; Cooper et al. 2004; Crofoot et al. 2008). Analyses of various socioecological models have identified two major functional factors that explain the complexity of between-group encounters; resource defense (Wrangham 1980) and male defense of mates (Trivers 1972). Males may exhibit direct mate defense (i.e. female-defense polygyny; van Schaik et al. 1992; Fashing 2001) or defend mates indirectly by defending resources (Rubenstein 1986).

The genetic success of a male appears to be primarily influenced by the number of females he impregnates (Trivers 1972). The number of female partners available to a male at any onetime depends on the number of receptive females available and this may be strongly influenced by season in seasonally breeding species. These factors are therefore expected to influence the frequency and intensity of male intergroup aggressive encounters (Borries 2000; Fashing 2001; Kitchen and Beehner 2007). For example, the frequency of between-group encounters, and the intensity of aggression displayed, was higher in both *Macaca fuscata* (Saito et al. 1998), and *Macaca radiata* during the mating season (Cooper et al. 2004). These studies support the male mate defense hypothesis. The number of receptive females varies temporally in non-seasonal breeders and, in *Papio cynocephalus*, males participated in prolonged and intense aggression in between-group encounters when more resident females were in estrus (Kitchen et al. 2004). Female receptivity, therefore, is one of the more important factors influencing the frequency and intensity of aggression in between-group encounters.

On the other hand, genetic fitness of females depends more on food resources than on the number of breeding partners available (Wrangham 1980). Thus, females may use males as ‘hired guns’ (Rubenstein 1986; Fashing 2001) and also actively participate in between-group encounters (*Clorocebus aethiops*: Cheney et al. 1981; *Colubus guereza*: Fashing 2001; *Macaca fuscata*: Saito et al. 1998; *Macaca radiata*: Cooper et al. 2004; *Macaca silenus*: Kumar and Kurup 1985; *Macaca sylvanus*: Mehlman and Parkhill 1988; *Seminopithecus entellus*: Borries 1993) in defense of food resources. Females may participate more often and more vigorously if the food is clumped and abundant. *M. radiata* females in a temple group with locally clumped food resources, more aggressively participated in between-group encounters than did females in a group ina forest habitat (Cooper et al. 2004). Similarly, females of *Colobus polykomos* participated more frequently in between-group encounters to defend high caloric *Pentaclethra macrophylla* seeds during the fruiting season when they were abundant than in the non-fruiting season when they were scarce (Korstjens et al. 2005).

The availability of food resources varies temporally and spatially in heterogeneous environments. The temporal variation in food resources is the result of plant phenology which is ultimately dependent on seasonal characteristics like temperature and rainfall (van Schaik and Pfannes 2005). Therefore, Okamoto and Matsumura (2002) predicted that the frequency of encounters would decrease in rainy months when the food resources would be abundant and widely distributed. The between-group encounters in *Cercocebus galeritus* groups were less frequent and more peaceful in the months with uniformly distributed food resources than in the months with patchily distributed resources (Kinnaird 1992). In a habitat where the distribution of food resources is clumped, between-group encounters would happen more frequently and aggressively in those patches where abundance or quality of food is higher than in the rest of the home range (Wrangham 1980; van Schaik 1989). Thus, the spatial distribution of food resources also acts as an influential factor in between-group encounters. *Pan troglodytes* frequently encountered neighboring groups at the resource rich edge areas of their home range (Wilson et al. 2012). In contrast, *Colobus guereza* defended the food resource rich core area, where the frequency of between-group encounter was higher than in the rest of the home range (Harris 2006). When food was heterogeneously distributed in their home range, *Cercopithecus ascanius* and *Lophocebus albigena* defended monopolizable feeding sites with aggressive between-group encounters (Brown 2013).

The availability of mate and food resources is further influenced by some socioecological factors like group density and space availability. Frequency of between-group encounters in *M. fuscata* was higher in a population with high density than in one with low population density (Sugiura et al. 2000). Density can be dependent on space availability when a population is forced into a smaller area by human reductions in their habitat. This appears to account for the rate of between-group encounters in a study of *M. silenus* (Kumara et al. 2014). Apart from mate and food resources, the chance of a between-group encounter might increase while sharing 'non- or slowly depleting resources' (Harris 2007) which cannot be monopolized. For example, in the dry season, *Cebus capucinus* spent more time near a running water source, which was shared by neighboring groups leading to frequent between-group encounters (Perry 1996).

Models indicate that a group should participate in a between-group encounter when the benefit or chance of a win is more than the cost or chance of losing the encounter (Crofoot et al. 2008; Roth and Cords 2016). However, the ability to win the encounter partly depends on the number of participants on each side, which often corresponds to group size (Cheney 1987; Isbell 1991; Wilson et al. 2001; Radford and du Plessis 2004; Roth and Cords 2016). Empirical data on between-group encounters show that the larger (*Alouatta pigra*: Kitchen 2006; *Pan troglodytes*: Mitani and Watts 2005; *Papio cynocephalus*: Kitchen et al. 2004) and dominant groups (*Alouatta pigra*: Kitchen 2004; *M. radiata*: Cooper et al. 2004) were more likely to participate in between-group encounters than small and subordinate groups (*M. fuscata*: Sugiura et al. 2000; *Pan troglodytes*: Watts and Mitani 2001; Wilson et al. 2001). Large groups often dominate small groups (*Alouatta pigra*: Kitchen 2004; *Cebus capucinus*: Crofoot et al. 2008; *M. fuscata*: Sugiura et al. 2000; *Pan troglodytes*: Wilson et al. 2001). Therefore, it can be expected that a large group will experience relatively low rates of between-group encounters due to an active avoidance by relatively smaller neighboring groups (Okamoto and Matsumura 2002). Since males more often participate and show intensive aggression in between-group encounters than females (Cheney 1987; Fashing 2001; Cooper 2004), the relative number of males participating in a between-group encounter often predicts the outcome of the encounter (Cheney 1987; Wilson et al. 2001; Markham et al. 2012). Along with numerical superiority, the location-based payoff may also confer advantages in between-group contests, where the odds of winning decrease with the increased distance of the location of an encounter from the center of the home range as reported in *Cebus capucinus* by Crofoot et al. 2008. In *Cercopithecus mitis*, the odds of winning an encounter were also increased when the contest occurred in the intensely used core area and the center of the home range of the group (Roth and Cords 2016). Hence, various socioecological factors act independently on frequency, intensity and even the outcome of a between-group encounter. It can be expected that groups will adopt various strategies to balance the trade-off between cost and benefit of a between-group encounter with respect to these factors.

A long-term study was carried out on the ecology and behavior of a subspecies of long-tailed macaques, the Nicobar long-tailed macaque (*Macaca fascicularis umbrosus*) which is endemic to the Nicobar series of islands of India and found on only three isolated islands viz. Great Nicobar, Little Nicobar, and Katchal (Umapathy et al. 2003). The habitats in these islands are being constantly modified due to natural and anthropogenic activities as well as occasional catastrophes such as the massive tsunami of 2004 (Velankar et al. 2016). During this long-term observation, several instances of between-group encounters were recorded in these macaques. In the study area, one group of long-tailed macaques was the focal group and there were several other groups with home ranges overlapping with the focal study group. In the context of the review of literature above, it was questioned if (a) the observed rate of between-group encounters was the same as the expected one calculated from the ideal gas model, (b) there was influence of the location of food resources within the home range on between-group encounters, (c) socio-ecological factors like group size, number of adult males in the group, number of cycling females in the group, and rainfall could predict between-group encounters, and (d) there were proximate factors like relative number of participants in a between–group encounters which predicted the outcome of a between-group encounter.

6.2. Materials and Methods

6.2.1. Data collection: Between-group encounters in three wild Nicobar long-tailed macaque groups (TR, PI, and MG), with overlapping home ranges, were studied between July 2013 and March 2015 (245 observation days) (**Figure 6.1**). During the study period, the mean group size of TR, PI, and MG was 16.67 ± 1.70_{SD}, 37.50 ± 4.05_{SD}, and 79.00 ± 5.35_{SD} respectively (**Table 6.1**). The study area was inhabited by five groups of long-tailed macaques.

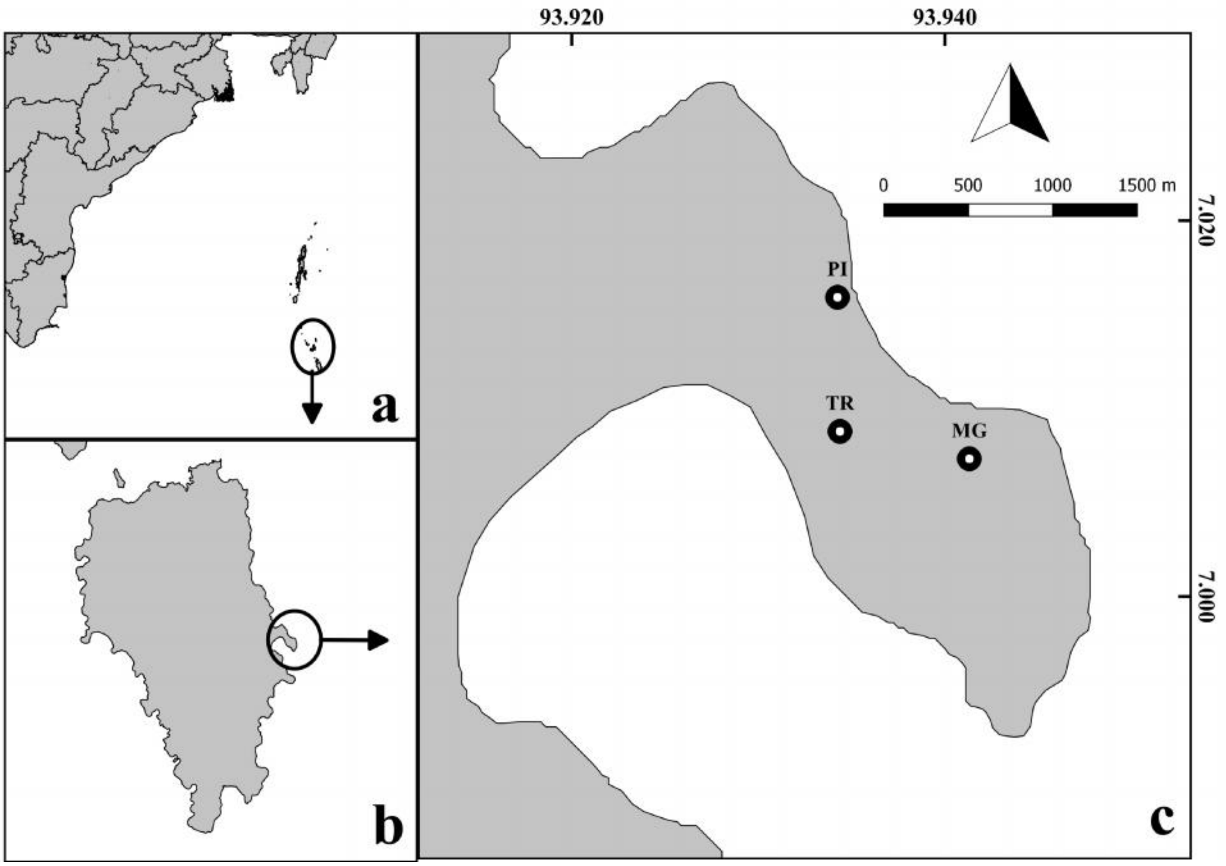

Figure 6.1. Location of the study site: (a) Great Nicobar Island in Andaman Nicobar archipelago, (b) Campbell bay in Great Nicobar Island and (c) Study area in Campbell bay.

Table 6.1. Demography of three neighbouring group TR, MG and PI

Group	Adult male (Mean ± SD)	Adult female (Mean ± SD)	Sub-adult (Mean ± SD)	Juvenile (Mean ± SD)	Infant (Mean ± SD)	Group size (Mean ± SD)
TR	2.67 ± 1.25	6.67 ± 0.94	2.33 ± 0.47	2.00 ± 1.00	3.00 ± 0.82	16.67 ± 1.70
PI	13.00 ± 1.85	25.67 ± 2.05	11.33 ± 0.94	17.00 ± 2.45	12.00 ± 2.16	79.00 ± 5.35
MG	7.00 ± 1.00	11.50 ± 1.50	5.00 ± 0.57	10.5 ± 5.00	6.00 ± 2.00	37.50 ± 4.05

During the study period, three observers (A. Pal, P.S. Mishra, and A.D. Velankar) followed the study groups to collect data on ecology and behavior. Data on demography and ranging were collected from all three groups, whereas the data on feeding, ecology, and social and reproductive behavior were collected only from the focal group i.e. TR group. TR group was followed for at least 10 days in a month, and the PI and MG groups were followed for 4 days a month. The geo-coordinates and sleeping site data of PI and MG groups were also collected opportunistically while observing other groups at the study site.

All individuals of TR group were identified using their facial morphology. Based on the physical appearance, the age classes considered are: adult: ≥ 4 years, sub-adult: 2.5 to 4 years, juvenile: 6 months to 2.5 years and infant: ≤ 6 months (Velankar et al. 2016). The TR group was followed for 2034 hr (230 days) during the study period, while the MG and PI groups were followed for 36 and 44 days respectively. On each observation day, the study groups were followed from dawn (06:00 hr) to dusk (18:00 hr) or until the group entered inaccessible dense undergrowth. While following TR group, every 30 min, a scan was carried on all individuals within a period of 5 min. Scan sampling recorded six major activities: feeding (ingestion of food), foraging (searching and extracting food), moving (moment on trees and ground), resting (sleeping and sitting), socializing (groom, play, aggressive and affiliative interactions) and social association (proximity between individuals). For TR group, mating data (individuals involved in copulation and related behavior) were collected by all-occurrence sampling opportunistically (Altmann 1974).

Group size and the demography of all three groups were recorded in the 3rd week of every month. The counts were made when individuals were crossing roads or moving to the roosting site, usually in a single file. The geo-coordinates of the group center of the study groups were recorded every 30 min during a follow of the group. The geo-coordinates of MG and PI groups were recorded opportunistically while following TR group as well as during the days when these groups were followed. The data on group spread were collected during 30 min interval scan sampling, where the distance between two exterior individuals of a group in both axis was recorded (Altmann 1974).

The data on between-group encounters were collected by all-occurrences sampling method (Altmann 1974). A between-group encounter was considered as an occasion when two groups came within visible range or close enough to be in auditory contact (approximately 150 m) (Cooper et al. 2004). During a between-group encounter, the front runners and those individuals of interacting groups who made vocal, gestural or physical responses towards the opponent group, were considered as the participants in the encounter. Between-group encounters were categorized as either ‘aggressive’ or ‘non-aggressive’ encounters. In a non-aggressive encounter, the interactions were limited to visual and vocal contacts while interacting groups were foraging and resting, or after detecting the presence of another group, one group moved away. In an aggressive encounter, the interacting groups participated in aggressive vocal and physical encounters including chase and fight. During a between-group encounter, the interacting groups were continuously followed by two observers, where one observer was recorded behavioral data on the identity of individuals initiating approaches and their behavior during the approach and initiation of behavioral approaches and response of the other group members to the approaching individual. This observer also recorded the number of individuals of both groups participating in the encounter, inter-group aggression and matings. The other observer collected data on the focal group during a between group encounter, including presence and absence of intra-group male to female aggression, and intra-group mating, using ad libitum sampling with structured data sheets (Altmann 1974). The locations of between-group encounters and sleeping sites were recorded using a handheld geographic positioning system (Garmin GPSmap 76CSx).

The geo-referenced layer of the study site was overlaid with one-hectare grids in Q-GIS and numbered. The grid layer was uploaded to GPS to recognize the sampling location on the ground. The list of food trees of macaque was prepared from scan sampling. In each grid, three random 20 m radius circular plots were laid, and in each sampling plot, the food trees with > 10 cm GBH were counted. The percent shrub cover was visually estimated in each sampling plot. The Google-Earth image for the study area was downloaded and the built-up area, vegetation cover, and water were digitized. Over the digitized land cover, the same 1 ha grid layer was overlaid, and the percent of each major land cover was enumerated for each grid.

Monthly rainfall (mm) data for the study period in the Great Nicobar Islands were collected from the Indian Meteorological Department, Andaman, Nicobar and Lakshadweep group of Islands, Ministry of Earth Science, Government of India.

6.2.2. Data analysis

A monthly frequency of encounters in a day (per 12 hr) of each between-group encounter category was calculated (encounter/day). The Ideal Gas Model was used to calculate expected frequencies of between-group encounters per day (Waser 1976; Kumara et al. 2014). The expected frequency of between-group encounter (f) was calculated with the basic Ideal Gas Model formula:

$$f = 4\rho v/\pi(2d+s)$$

Where, ρ is group density/km^2; v the daily path length or group movement km/day; d is the distance between two groups considered as a between-group encounter, and s is the group spread in km.

The 5.5 km^2 study site was inhabited by five groups (LB, PI, TR, MG, and MA) of Nicobar long-tailed macaques with a density (ρ) of 1.10 groups/km^2. Sequential daily ranging data points (observation period > 8hr) were connected with minimum distance paths and the total distance across all the data points was considered as path length for that day (Santhosh et al. 2015). To calculate the expected rate of between-group encounters, the calculated data on group density ($\rho = 1.10/\text{km}^2$), mean daily path length ($v = 0.99$ km), the distance considered for a between-group encounter ($d = 0.15$ km) and the mean group spread ($s = 0.08$ km) were used in the Ideal Gas Model.

The geo-coordinates collected during the group follow of each group were plotted over the grid cells. Since, full day observation data were less for MG and PI groups, the geo-coordinates of opportunistic sightings were used to estimate the home ranges of MG and PI groups but these data were not used in any other statistical analysis. TR group did not encounter LB and MA groups. A grid with at least one point was considered for the home range estimation for each group. The home range size of the TR group was 34 ha (34 grid cells), of which 33 (97%) grid cells overlapped with the home ranges of the neighboring groups i.e. 26 (77%) and 30 (88%) grid cells with the home ranges of PI and MG groups respectively (**Figure 6.2**). A total of 13 sleeping sites were recorded for the TR group, of which 10 (77%) were also used by PI and MG groups. The number of geo-coordinates in each grid represented the intensity of grid use by the group. To depict the intensity of grid use, the percentage of total location points recorded in each grid cell were classified into four classes (0.01-0.50%, 0.51-1.00%, 1.01-5.00% and > 5.00%). The geo-coordinates of between-group encounters and location of sleeping sites were plotted over the grid cells. A few sleeping sites fell on the margin of grid cells, where the surrounding areas of those sleeping sites also included part of the neighboring grid cell. Therefore, to minimize the grid-wise calculation bias, a buffer of 100 m radius was created around each sleeping site, and the grids that included buffer region of ≥ 50% were considered as grids having sleeping sites.

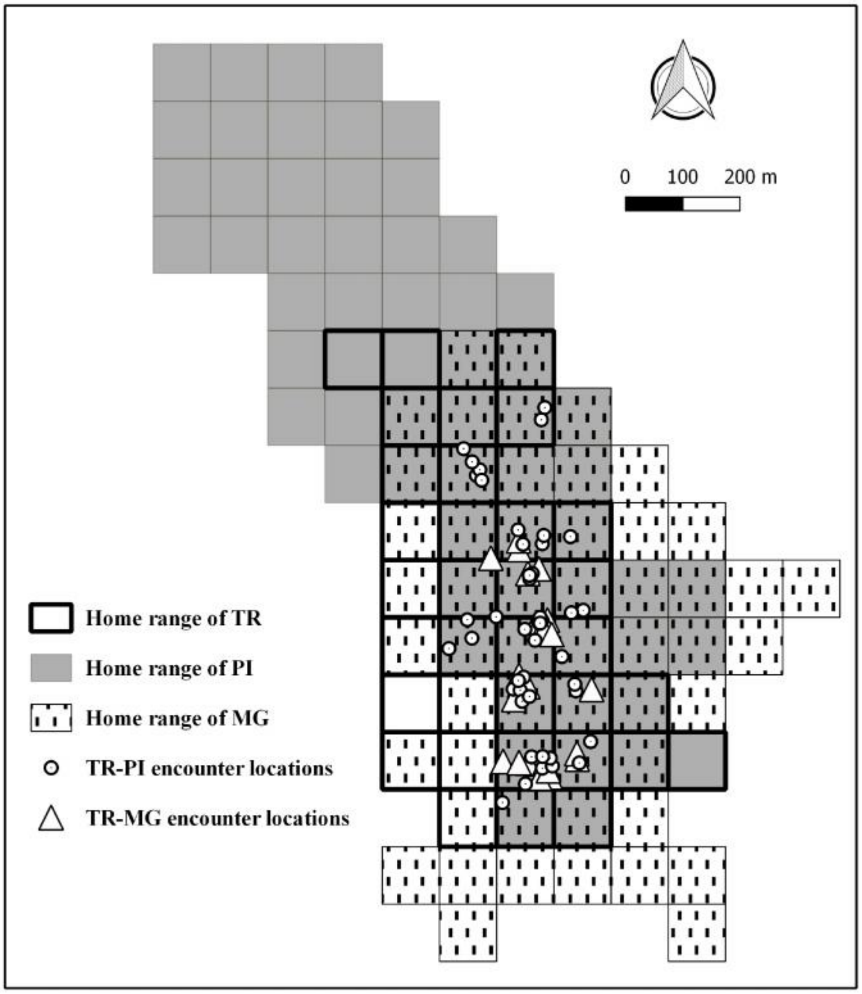

Figure 6.2. Distribution of between group encounters between TR and two neighboring groups PI and MG in their overlapped home range.

A total of 12 priori GLM models were constructed (Poisson distribution, link = log) to examine the effect of spatial variables on the distribution and intensity of between-group encounters throughout the home range of the TR group. Home range grids (N = 34) were considered as nominal variables and the number of between-group encounters in each grid was considered as the response variable. After removing auto-correlated variables, four spatial variables (grid wise) including percent vegetation cover (vc), percent shrub cover (sc), density of feeding trees per ha (ftd), and presence of sleeping sites (sleep) were used as explanatory variables. All constructed models ware ranked based on AIC$_c$ (Akaike's Information Criterion corrected for small sample size bias) value to select the parsimonious model with the lowest AIC$_c$ and the highest model weight (Anderson and Burnham 1998). The GLM model selection table was constructed with package “AICcmodavg” of R statistical language (Mazerolle 2017).

A chi-squared test was applied to check the variation of outcomes of between-group encounters in all three interacting groups. Participants of TR and opponent groups in between-group encounters were compared with independent sample *t*-test.

Pearson product-moment correlation test was employed to determine the relationship of the number of adult males and cycling females with the rate of between-group encounters. Similarly, the relationship was also determined between amount of monthly rainfall and the rate of between-group encounters.

G-test of independence was used to compare the percentages of intra-group male to female aggression and intra-group mating in TR between aggressive and non-aggressive encounters. Similarly, G-test was also employed to examine the variation of between-group encounter withdrawal by TR between aggressive and non-aggressive between-group encounters.

R v3.4.1 statistical language with IDE R Studio v1.0.143 (R Development Core Team 2008) was used for statistical analysis and Q-GIS 2.18 (QGIS Development Core Team 2009) for spatial analysis and study site mapping.

6.3. Results

A total of 72 between-group encounters of the study group, TR, with neighbouring groups PI and MG were recorded providing a mean encounter rate of $0.45 \pm 0.23_{SD}$ encounters/day which was relatively lower than the expected rate of 0.53 encounters/day that was calculated using the Ideal Gas Model equation.

Of the 72 between-group encounters, 33 (46%) were aggressive and 39 (54%) were non-aggressive encounters; the difference was non-significant (G-test: G= 0.50, df= 1, p= 0.99) (**Table 6.2**). The rate of aggressive and non-aggressive encounters was $0.24 \pm 0.15_{SD}$ and $0.22 \pm 0.22_{SD}$ encounters/day respectively. The number of between-group encounters between TR with PI and MG groups were 46 (aggressive: 22, non-aggressive: 24) and 26 (aggressive: 11, non-aggressive: 15) respectively.

Table 6.2. Distribution of behavioral approaches in overall, aggressive and non-aggressive between-group encounters.

Parameter	**Overall**	**Aggressive**	**Non-aggressive**
Number of between group encounters	72	33 (46%)	39 (54%)
Between group encounter/day (mean ± SD)	0.45 ± 0.23	0.24 ± 0.15	0.22 ± 0.22
TR males participated	72 (100%)	33 (100%)	39 (100%)
TR females participated	14 (19%)	8 (24%)	6 (15%)
Intra-group male to female aggression in TR	41 (57%)	17 (52%)	24 (62%)
Intra group mating in TR	45 (63%)	23 (70%)	22 (56%)
No. of between group encounter: TR-PI	46	22 (48%)	24 (52%)
No. of between group encounter: TR-MG	26	11 (42%)	15 (58%)

All the between-group encounters were recorded in 16 (47%) grid cells, however, the number of encounters in each grid cell varied from one to 15 (**Figure 6.3**). The number of between-group encounters was highest in the intensively used grids. In order to identify the factors in spatial location that determined the intensity of a between-group encounter, the habitat parameters were related with the intensity of the between-group encounter in each grid cell. The most parsimonious model with the lowest AIC_c value (159.57) and the highest model weight (w_i = 0.63) was ‘vc + sleep’ model (GLM: r^2= 0.27, N= 34, p< 0.001) (**Table 6.3**). In this model, ‘vc’ and ‘sleep’ were surrogates for vegetation cover and sleeping sites respectively, which indicated that the presence of sleeping sites (β= 2.49 ± 0.51_{SE}, Wald’s Z= 4.83) and high vegetation cover (β= 0.01 ± 0.01_{SE}, Wald’s Z= 2.88) influenced the number of between-group encounters in the grid cells.

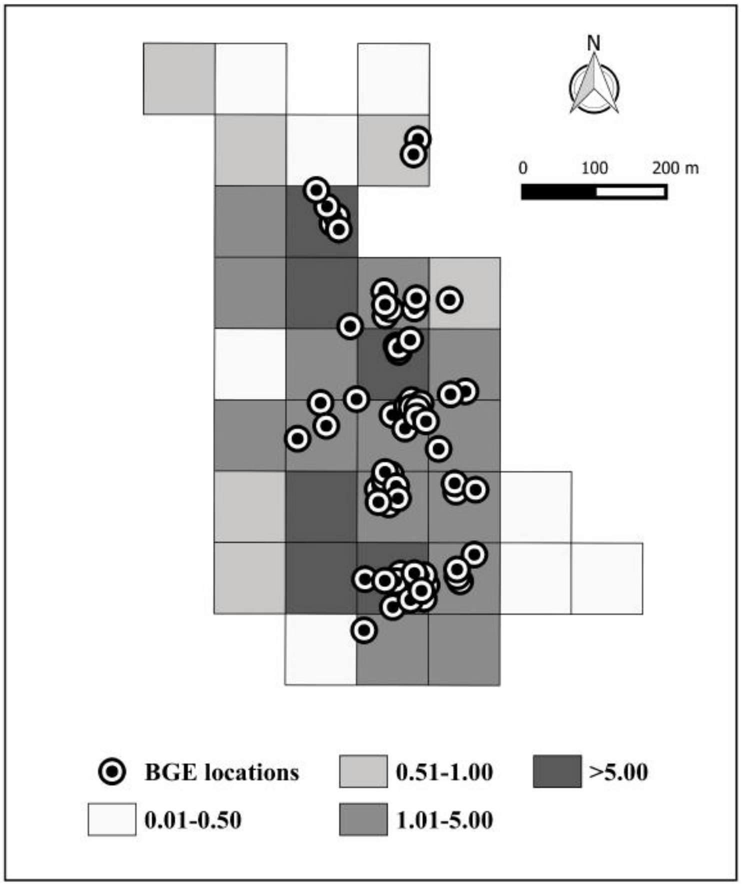

Figure 6.3. Percentage use of grids by TR group and the distribution of between-group encounter locations in their home range.

Table 6.3. Model selection table: summary of models for explanatory variables influencing the distribution and abundance of between-group encounters

Model	**K**	**AIC_c**	**$\Delta\ \text{AIC}_c$**	**w_i**	**r^2**
vc + sleep	3	159.57	0.00	0.63	0.27
sc + vc + ftd + sleep	5	161.97	2.40	0.19	0.28
sc + sleep	3	162.79	3.22	0.13	0.25
sleep	2	165.18	5.61	0.4	0.23
ftd + sleep	3	167.49	7.93	0.01	0.23
ftd + vc	3	202.43	42.87	0.00	0.07
sc + vc + ftd	4	203.01	43.44	0.00	0.07
vc	2	205.96	46.39	0.00	0.04
sc + vc	3	207.93	48.37	0.00	0.04
sc	2	211.33	51.76	0.00	0.01
sc + ftd	3	212.44	52.88	0.00	0.02
ftd	2	213.26	53.70	0.00	< 0.001

vc: percent of vegetation cover; sleep: presence of sleeping site; sc: percent of shrub cover; ftd: feeding tree density; K: number of parameter estimated by the model; AIC_c: AIC corrected for small sample size biased; $\Delta\ \text{AIC}_c$: difference of AIC_c value from the lowest AIC_c model; w_i: model weight and r^2: McFadden coefficient of determination.

The rate of overall and aggressive between-group encounters decreased with increase in rainfall (Pearson correlation test- overall: r= -0.44, N= 21, p< 0.05, aggressive: r= -0.58, N = 21, p< 0.01) (**Figure 6.4**). The overall frequency of five outcomes of between-group encounters varied greatly (Chi-squared test: χ^2= 19.81, df= 4, p< 0.001) (**Table 6.4**). The frequency of initial avoidance by TR group immediately after recognizing the presence of other group N= 25 (34.72%) was higher than successfully defending the site N= 18 (25.00%), getting chased away by the opponent group N= 15 (20.83%), being avoided by the opponent group N= 12 (16.67%) and mutual tolerance N= 2 (2.78%). However, whereas the overall frequencies differed significantly, this was due to encounters with group PI. The frequency of outcomes in between-group encounters with MG did not differ (Chi-squared test: χ^2= 4.77, df= 4, p= 0.31). Differences with PI did differ significantly (Chi-squared test: χ^2= 18.78, df= 4, p< 0.001). Although, the TR group defended 23.91% of the times against the PI group, initial avoidance (41.30%) was higher than all other outcomes.

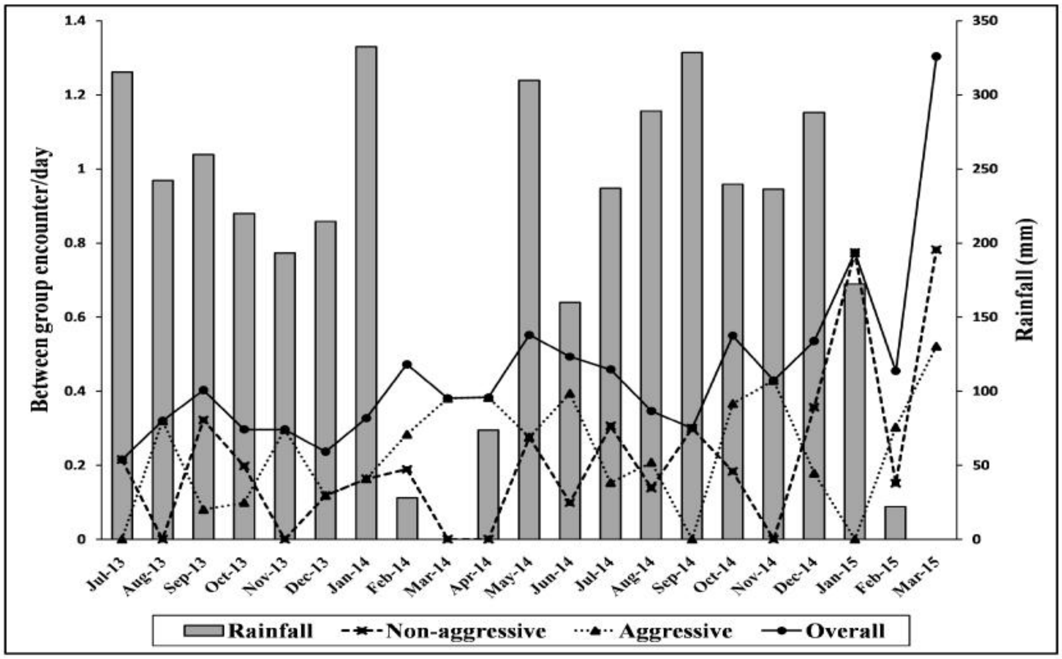

Figure 6.4. Monthly variation in the frequency of different categories between-group encounters (aggressive, non-aggressive and overall) and rainfall.

Table 6.4. Distribution of outcome of between-group encounters

Outcomes	Overall (%) N = 72	MG (%) N = 26	PI (%) N = 46
TR initially avoided encounters	25 (34.72)	6 (23.07)	19 (41.30)
Groups tolerated each other	2 (2.78)	1 (3.85)	1 (2.17)
TR successfully defended the opponent groups	18 (25.00)	7 (26.92)	11 (23.91)
TR got chased away by the opponent group	15 (20.83)	7 (26.92)	8 (17.39)
Opponent group avoided encounters	12 (16.67)	5 (19.23)	7 (15.22)

Since, all members of each group did not participate in all between-group encounters, the mean number of participants for a group was less than the size of the study groups (**Table 6.5**). The mean number of participants in TR and the opponent groups did not differ significantly in encounters where TR successfully defended against the opponent groups (Independent sample *t*-test: $t= -0.40$, $df= 34$, $p= 0.69$). On the other hand, TR group got chased more often by opponent groups when the mean number of participants of the TR group was significantly lower than in the opponent groups (Independent sample *t*-test: $t= -2.10$, $df= 28$, $p< 0.05$).

Table 6.5. Mean number of individuals that participated in different types of between-group encounter

Outcomes of encounters	Overall encounters		MG-TR encounters		PI-TR encounters	
	Opponent group (± SD)	**TR (± SD)**	**MG (± SD)**	**TR (± SD)**	**PI (± SD)**	**TR (± SD)**
TR successfully defended the opponent group	14.28 (± 24.91)	11.83 (±7.06)	8.14 (±13.02)	10.86 (± 7.71)	18.18 (± 30.17)	12.46 (± 6.92)
TR got chased away by opponent group	20.67 (± 22.27)	8.00 (±7.07)	27.29 (±16.63)	10.86 (± 6.23)	14.89 (± 25.93)	5.50 (± 7.17)

The males of TR group participated in all between-group encounters, where the females participated only in eight (24%) aggressive between-group encounters. The rate of aggressive encounters was positively correlated with the number of adult males in the TR group (Pearson correlation test: $p= 0.46$, $N= 21$, $p< 0.05$), and the overall encounter rate increased with an increase in the number of cycling females in the group (Pearson correlation test: $r= 0.48$, $N= 21$, $p< 0.05$).

The intra-group male to female aggression was recorded in 41 (57%) between-group encounters, however, the number of aggressive and non-aggressive encounters was nearly equal [aggressive 17 (52%) and non-aggressive 24 (62%) encounters] (G-test: G= 0.88, df= 1, p= 0.35). The intra-group mating frequency during aggressive encounters [23 (70%)] and non-aggressive encounters [22 (56%)], did not differ significantly (G-test: G= 1.56, df= 1, p= 0.21). Only one inter-group mating between a female of the TR group and a male of the PI group were recorded during an aggressive encounter.

6.4. Discussion

The study group was involved in 0.45 between-group encounters/day, which was less than the expected rate of 0.53 encounters/day based on the Ideal Gas Model. There was a 97% overlap of home ranges and the areas where between-group encounters occurred were areas with sleeping sites for both groups and with dense vegetation cover. TR group more often avoided encounters with the other two groups than either avoided TR. TR defeated an opponent group when the relative number of participants did not differ between TR and the interacting groups but it was chased away by the opponent group when the number of participants was smaller in it than in the opponent group. A total of 46% of the encounters were aggressive, and females participated less often than did males. The frequency of aggressive and overall encounters increased with the number of adult males and cycling females in the TR group. There were fewer between-group encounters when it was raining.

Although the observed rate of between-group encounter in the Nicobar long-tailed macaque (0.45) was lower than the expected rate, it was on a par with the average of $0.47 \pm 0.37_{SD}$ encounters in many macaque species as calculated from the review by Cooper (2004). Participation in a between-group encounter is often costly due to the chances of injuries (Cheney 1987) and short term effects like restricted movement in the feeding ground (Markham et al. 2012). Therefore, the decision to participate in an encounter depends on the fighting ability or resource holding potential of a group (Crofoot et al. 2008; Roth and Cords 2016), which is often assessed by the relative number of opponents (Hammerstein 1981; Arnott and Elwood 2008), familiarity, and the threat from the individuals of the opponent group (Wich and Sterck 2007; Herbinger et al. 2009). The TR group, being smaller than the neighboring groups, had fewer chances of winning, which may have resulted in the lower than expected rate of between-group encounters (e.g. as reported in *Alouatta pigra*: Kitchen 2004;

Cebus capucinus: Crofoot et al. 2008; *M. fuscata*: Sugiura et al. 2000; *Pan troglodytes*: Mitani and Watts 2005).

Groups participate in a between-group encounter to defend valuable and limited resources from competing groups (Cheney 1987; Fashing 2001; Harris 2007; Kitchen and Beehner 2007). The competition becomes severe when the home range of the neighboring groups overlaps extensively (Kumara et al. 2014). If a large number of sleeping sites are also shared by the neighboring groups in their overlapping ranges, sleeping sites become a limited resource to defend (Anderson 1984). In *M. radiata*, sleeping sites are generally near food sources (Rahaman and Parthasarathy 1969), and in the case of water scarcity, *M. mulatta* sleeps close to water sources (Lindburg 1971), as a result, such sites become even more important to the group. In *Colobus vellerosus*, the focal groups slept close to feeding areas and aggressively approached intruding groups spotted on the edge of the core area (Teichroeb et al. 2012). Thus, the high frequency of between-group encounters around the sleeping sites observed in the present study may be the result of the study group defending those sleeping sites.

The available space and the habitat in the Nicobar group of Islands, including the Great Nicobar, shrank due to at tsunami in 2004 (Velankar et al. 2016). During the years following the tsunami, population of the Nicobar long-tailed macaque experienced a high growth rate with a present high density in the Islands (Velankar et al. 2016). The increased density compelled the macaque groups to expand their ranges into commercial plantations and human habitations, and increased the area of overlap in home ranges. TR group, situated in the juxtaposition of a coastal littoral forest and human habitation, acquired food largely by raiding orchards, plantations, and human habitations, but it also used adjoining forest habitat for foraging. The forest patch may be the most desirable habitat for all the groups in the study, and vegetation cover is an important determining factor influencing the rate of between-group encounters in. High group density has been found to result in high intergroup encounter rates (Kumara et al. 2014; Singh et al. 2006).

The numerical strength of a group often decides the outcome of an encounter, since larger groups have greater fighting ability (Crofoot et al. 2008; Roth and Cords 2016). In the present study, the small TR group remained vulnerable while facing relatively larger opponent groups and avoided them. However, irrespective of group size, the number of participants in an encounter also influences the outcome (Cheney 1987; Kitchen and Beehner 2007; Markham et al. 2012). Thus, in asymmetric contests where there were fewer participants from the TR group, the TR group got chased away. In a relatively symmetrical contest when the participants of the TR and an opponent group did not differ, the TR group was able to defend the place against the opponent group.

Though resources are valuable for both sexes, aggressive participation in between-group encounter varies between the sexes; females participate less often than do males (Cheney 1987; Fashing 2001; Cooper 2004; Kitchen and Beehner 2007). This has been observed in other macaque species as well (*M. maurus*: Okamoto and Matsumura 2002; *M. fuscata*: Saito et al. 1998; Sugiura et al. 2000; *M. radiata*: Cooper et al. 2004; *M. silenus*: Kumar and Kurup 1985). Similarly, females of the Nicobar long-tailed macaque participated less often in aggressive encounters than did males.

An aggressive encounter occurs when a group counterchallenges the approach of a neighboring group and the vigor of the defense increases with the number of adult males in the group (Cheney 1987; Wilson et al. 2001; Markham et al. 2012). Therefore, a group is more likely to enter an aggressive encounter when the number of adult males in the group is relatively large (e.g. *P. troglodytes*: Wilson et al. 2001, 2012; *P. cynocephalus*: Markham et al. 2012). This was observed in the TR group where the rate of aggressive encounters correlated with the number of adult males in the group. Further, the number of cycling females in the group attracted outer-group males to participate in between-group encounters (*M. radiata*: Singh et al. 2006; *Semnopithecus entellus*: Borries 2000; *Cercopithecus* sp.: Cords 2000), and the group males to defend their mate resource (for review see Fashing 2001; Kitchen and Beehner 2007). In the present study, the number of cycling females also correlated positively with the number of between-group encounters. Similarly, *P. cynocephalus* also participated in an encounter more when the number of estrus females was higher in the group than when the number was low (Kitchen et al. 2004). Apart from defending against outer group males with aggression, the Nicobar long-tailed macaque males also showed aggression towards within-group females and also mated with them during the between-group encounters. Such intra-group aggression and mating during between-group encounter were also observed in *M. radiata* (Cooper et al. 2004) and *M. silenus* (Kumar and Kurup 1985).

According to the food resource defense model (Wrangham 1980), the group should participate in encounters to defend food resources less intensely when food abundance is higher (van Schaik 1989; Isbell 1991; Brown 2013). Rainfall influences the abundance of food in a habitat in the tropical evergreen forests (van Schaik and Pfannes 2005), and rainfall, therefore, can be taken as a proxy for food resource abundance. A significantly lesser number of between-group encounters occurred during the rainy season than in the dry season in the Nicobar long-tailed macaques, indicating the effect of resource abundance on such encounters.

Nicobar long-tailed macaques showed notable similarity in between-group encounters with other macaques, where the environmental characteristics of home range influenced spatial distribution of encounters. In these macaques, participation in a between-group contest and the outcome of the encounter were dependent on the comparative numerical strength of the participants in an encounter, rather than group size. Groups participated in between-group contests to defend mate resources, and the intensity of aggression in an encounter depended on the number of adult males in a group. In conclusion, the Nicobar long-tailed macaque groups participated in between group contests to defend monopolizable resources only after assessing the trade-off of the encounter by considering the relative resource holding potential of the group and the value of the contested resource.

Synthesis

"Science has explained nothing;
the more we know the more fantastic the world becomes
and the profounder the surrounding darkness."

‡ Aldous Huxley ‡

The long-tailed macaque (*Macaca fascicularis*) is the widely distributed macaque of South-East Asia, where distributions of seven out of ten sub-species are restricted in small isolated islands. The macaque shows highly ecological plasticity which helped them to survive in such wild range of habitats. Nicobar long-tailed macaque (*Macaca fascicularis umbrosus*) is one of the isolated sub-species distributed in three small isolated Nicobar Islands. The natural catastrophes like tsunami, cyclones, El Niño, and anthropogenic pressures like habitat fragmentation and habitat loss are always pushing this vulnerable macaque towards the threshold of their vulnerability. Despite these negative impacts, the sub-species is a proliferate breeder that has not only managed to survive in the stressful environments but has also achieved similar reproductive success recorded in other sub-species from relatively less-disturbed environments. This suggests a high degree of similarity in the demographic traits and social organization between the sub-species, and further reflects the high adaptability of *M. f. umbrosus* to manage the traits by coping with the stressful and catastrophic conditions. Contrasting to other sub-species, the distinct behavioral traits like the variation in age-sex ratio and non-seasonal breeding pattern in these macaques are the adaptive strategies to achieve the conservative life history traits which ultimately maximize the reproductive output. The distinct characteristics observed in the social organization and life history traits in *M. f. umbrosus* were adopted as a result of trade-offs between environmental constraints and selective advantages of various characters. Where, in this highly competitive environment, the members of the group are more intended to affiliate amongst each other by their immediate needs, rather than the hierarchical linearity of the society. Competition for mate resources was very evident in *M. f. umbrosus*, where individuals of both the sexes were involved in intra and inter-sexual competition to increase their reproductive success. The competition between males corresponded with their social ranks wherein the top rank male monopolized maximum mate resources. The uneven parental investments also lead to inter-sexual competition, where both the sexes adapted various sexual strategies and alternative counter-strategies to maximize individual reproductive success. Where, males aimed to maximize mating success through mating initiation in both aggressive and non-aggressive approaches, female adapted proceptive behaviors and post-conception mating as sexual strategies to increase paternity confusion. Moreover, males showed intense aggressive behavior to increase individual reproductive success, for example, when an alpha male involved in a lethal fight to defend his social status and died after a rank changeover by a challenge from an outer group male. The new dominant male then imposed his dominance through agonistic interactions with new group-mates and probably even killed infant to maximize his reproductive success. Just after the rank-changeover event, group females showed deceptive swelling and solicited the new male to reduce the risk of infanticide as well as coercion. Even one of the philopatric female and young males left their natal group to minimize the effect of coercion in post-rank changeover period. The repercussions after an immigration event, altered behaviors from the individual level to a group level, which explains that these macaques adopt situation based sexual strategies and counter-strategies to optimize their reproductive success. This suggests that the social hierarchy has a direct impact on the heterogeneous distribution of mate and food resources between individuals with different social status, which ultimately shapes the social organization in *M. f. umbrosus*. Consequently, to balance the disadvantages of living in such hierarchical group, individuals make a trade-off by adopting different behavioral strategies through policing specific inter-individual relationships.

The *M. f. umbrosus* also participated in between group contest to defend monopolizable resources only after assessing the trade-offs of the encounter by considering the relative resource holding potential of the group. Where, both frequency and aggressiveness of encounters was influenced by the number of females cycling and the number of males present in the study group. The between-group encounters were influenced by the number of females and the distribution of food, rather than geography. Therefore, it can be concluded that these macaques were engaged in encounters to defend food resources and mates rather than defending their territory.

This study provided first-ever information about demography, social organization, reproductive behaviors, birth seasonality, and intra and inter-group competition in Nicobar long-tailed macaques. It also revealed that in due course of interactions with its environment, a species could become flexible with life history traits and adopt different strategies to increase survivability as well as inclusive fitness.

The continued anthropogenic pressure in these islands is increasing the challenge for survival of this vulnerable macaque. This species continues to be vulnerable in a catastrophic time-scale, therefore, continuous long-term monitoring of the macaques and their habitat along with taking steps to ensure the sustainable survival of these macaques is a need. The current findings of the study enhanced our knowledge on this subspecies as well as which helps in preparing the *in-situ* and *ex-situ* conservation and management plans for these vulnerable Nicobar long-tailed macaques.

REFERENCES

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

Agoramoorthy, G., and Rudran, R. (1995). Infanticide by Adult and Subadult Males in Free-ranging Red Howler Monkeys, *Alouatta seniculus*, in Venezuela. *Ethology*, *99*(1-2), 75-88.

Alberts, S. C. (2012). Magnitude and sources of variation in male reproductive performance. In: Mitani, C. J., Call, J., Kappeler, Palombit, R. A., and Silk, J. B., (Eds) *The evolution of primate societies*, The University of Chicago, London, United Kingdom, pp. 412-431.

Altman, D. G., Machin, D., Bryant, T. N., and Gardner, M. J. (2000). Statistics with Confidence: Confidence intervals and statistical guidelines 2nd edition. *London: British Medical Journal Books*, United Kingdom.

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour, 49*(3), 227-266.

Anderson, J. R. (1984). Ethology and ecology of sleep in monkeys and apes. *Advances in the Study of Behavior*. 14, 165-229.

Andrews, H. V. (2001). Threatened herpetofauna of the Andaman and Nicobar Islands. *An over view of the threatened herpetofauna of South Asia. IUCN Sri Lanka and Asia Regional Biodiversity Programme, Colombo, Sri Lanka*, 39-47.

Andrews, H. V., Krishnan, S., and Biswas, P. (2001). The status and distribution of marine turtles around the Andaman and Nicobar Archipelago. *GOI-UNDP Sea Turtle Project*, pp. 29-55.

Andrews, H. V., Krishnan, S., and Biswas, P. (2006). Distribution and status of marine turtles in the Andaman and Nicobar Islands. *Marine turtles of India. Universities Press, Hyderabad, India*, pp. 33-57.

Anonymous, Indian Wildlife Protection Act. Govt. of India; 1972.

Arnott, G., and Elwood, R. W. (2008). Information gathering and decision making about resource value in animal contests. *Animal Behaviour*, *76*(3), 529-542.

Aujard, F., Heistermann, M., Thierry, B., and Hodges, J. K. (1998). Functional significance of behavioral, morphological, and endocrine correlates across the ovarian cycle in semifree ranging female Tonkean macaques. *American Journal of Primatology*, *46*(4), 285-309.

Balasubramaniam, K. N., Dittmar, K., Berman, C. M., Butovskaya, M., Cooper, M. A., Majolo, B. et al. (2012). Hierarchical steepness and phylogenetic models: phylogenetic signals in Macaca. *Animal Behaviour*, *83*(5), 1207-1218.

Beehner, J. C., and Bergman, T. J. (2008). Infant mortality following male takeovers in wild geladas. *American Journal of Primatology, 70*(12), 1152-1159.

Beisner, B. A., Jackson, M. E., Cameron, A., and McCowan, B. (2011). Effects of natal male alliances on aggression and power dynamics in rhesus macaques. *American Journal of Primatology, 73*(8), 790-801.

Bercovitch, F. B. (1991). Social stratification, social strategies, and reproductive success in primates. *Ethology and Sociobiology*, *12*(4), 315-333.

Bercovitch, F. B. (1997). Reproductive strategies of rhesus macaques. *Primates, 38*(3), 247-263.

Bercovitch, F. B., and Harvey, N. C. (2004). Reproductive life history. In: Thierry, B., Singh, M., and Kaumanns, W. (Eds.) *Macaque societies: A model for the study of social organization*, Cambridge University Press, Cambridge, United Kingdom, pp. 61-83.

Bercovitch, F. B., and Nürnberg, P. (1996). Socioendocrine and morphological correlates of paternity in rhesus macaques (Macaca mulatta). *Journal of Reproduction and Fertility*, *107*(1), 59-68.

Berman, C. M., Rasmussen, K. L. R., and Suomi, S. J. (1993). Reproductive consequences of maternal care patterns during estrus among free-ranging rhesus monkeys. *Behavioral Ecology and Sociobiology*, *32*(6), 391-399.

Borries, C. (1993). Ecology of female social relationships: Hanuman langurs (*Presbytis entellus*) and the van Schaik model. *Folia Primatologica*, *61*(1), 21-30.

Borries, C. (2000). Male dispersal and mating season influxes in Hanuman langurs living in multi-male groups. In: Kappeler P. M., (Ed.) *Primate males: Causes and consequences of variation in group composition*, Cambridge University Press, Cambridge, United Kingdom, pp. 146-158.

Brockman, D. K., and van Schaik, C. P. (2005). Seasonality and reproductive function. In: Brockman, D. K., and Van Schaik, C. P. (Eds.) *Seasonality in primates: studies of living and extinct human and non-human primates*. Cambridge University Press. Cambridge, United Kingdom, pp. 269-306.

Brown, M. (2013). Food and range defence in group-living primates. *Animal Behaviour*, *85*(4), 807-816.

Butovskaya, M., Kozintsev, A., and Welker, C. (1995). Grooming and social rank by birth: the case of *Macaca fascicularis*. *Folia Primatologica*, *65*(1), 30-33.

Campbell, I. (2007). Chi-squared and Fisher–Irwin tests of two-by-two tables with small sample recommendations. *Statistics in medicine, 26*(19), 3661-3675.

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

Carne, C., Wiper, S., and Semple, S. (2011). Reciprocation and interchange of grooming, agonistic support, feeding tolerance, and aggression in semi-free-ranging Barbary macaques. *American Journal of Primatology*, *73*(11), 1127-1133.

Chapais, B. (2004). How kinship generates dominance structures: a comparative perspective. In: Thierry, B., Singh, M., and Kaumanns, W. (Eds.) *Macaque societies: A model for the study of social organization*, Cambridge University Press, Cambridge, United Kingdom, pp. 186-208.

Chapman, C. A., and Rothman, J. M. (2009). Within-species differences in primate social structure: evolution of plasticity and phylogenetic constraints. *Primates*, *50*(1), 12.

Cheney, D. L. (1987). Interactions and relationships between groups. In: Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., and Struhsaker, T. T. (Eds.) *Primate societies*. University of Chicago Press, Chicago, 267-281.

Cheney, D. L., Lee, P. C., and Seyfarth, R. M. (1981). Behavioral correlates of non-random mortality among free-ranging female vervet monkeys. *Behavioral Ecology and Sociobiology*, *9*(2), 153-161.

Chitale, V. S., Behera, M. D., and Roy, P. S. (2015). Global biodiversity hotspots in India: significant yet under studied. *Current Science, 108*(2), 149-50.

Clarke, A. S., Harvey, N. C., and Lindburg, D. G. (1993). Extended postpregnancy estrous cycles in fernale lion-tailed macaques. *American Journal of Primatology*, *31*(4), 275-285.

Clarke, P. M. R., Henzi, S. P., and Barrett, L. (2009). Sexual conflict in chacma baboons, *Papio hamadryas* ursinus: absent males select for proactive females. *Animal Behaviour*, *77*(5), 1217-1225.

Clutton-Brock, T. H. (1974). Primate social organisation and ecology. *Nature*, *250*(5467), 539.

Clutton-Brock, T. H. (1989). Review lecture: mammalian mating systems. *Proc. R. Soc. Lond. B*, *236*(1285), 339-372.

Clutton-Brock, T. H., and Huchard, E. (2013). Social competition and selection in males and females. *Phil. Trans. R. Soc. B*, *368*(1631), 20130074.

Colmenares, F., and Gomendio, M. (1988). Changes in female reproductive condition following male take-overs in a colony of hamadryas and hybrid baboons. *Folia Primatologica*, *50*(3-4), 157-174.

Cooper, M. A. (2004). Inter-group relationships (Box 9). In: Thierry, B., Singh, M., and Kaumanns, W. (Eds.) *Macaque societies: A model for the study of social organization*. Cambridge University Press, Cambridge, United Kingdom, pp. 204-208.

Cooper, M. A., and Bernstein, I. S. (2000). Social grooming in Assamese macaques (*Macaca assamensis*). *American Journal of Primatology*, *50*(1), 77-85.

Cooper, M. A., Aureli, F., and Singh, M. (2004). Between-group encounters among bonnet macaques (*Macaca radiata*). *Behavioral Ecology and Sociobiology*, *56*(3), 217-227.

Cords, M. (2000). The number of males in guenon groups In: Kappeler P. M., (Ed.) *Primate males: Causes and consequences of variation in group composition*. Cambridge University Press, Cambridge, United Kingdom, pp. 84-96.

Cords, M., and Chowdhury, S. (2010). Life history of *Cercopithecus mitis stuhlmanni* in the Kakamega Forest, Kenya. *International Journal of Primatology*, *31*(3), 433-455.

Crofoot, M. C., Gilby, I. C., Wikelski, M. C., and Kays, R. W. (2008). Interaction location outweighs the competitive advantage of numerical superiority in *Cebus capucinus* intergroup contests. *Proceedings of the National Academy of Sciences*, *105*(2), 577-581.

Dang, D. C. (1977). Absence of seasonal variation in the length of the menstrual cycle and the fertility of the crab-eating macaque (*Macaca fascicularis*) raised under natural daylight ratio. *Annales de Biologie Animale Biochimie Biophysique*, *17*(1), 1-7.

Dang, D. C., and Meusy-Dessolle, N. (1981). Annual plasma testosterone cycle and ejaculatory ability in the laboratory-housed crab-eating macaque (*Macaca fascicularis*). *Reproduction Nutrition Développement*, *21*(1), 59-68.

de Ruiter, J. R., Van Hooff, J. A., and Scheffrahn, W. (1994). Social and genetic aspects of paternity in wild long-tailed macaques (*Macaca fascicularis*). *Behaviour*, *129*(3), 203-224.

de Vries, H., Stevens, J. M., and Vervaecke, H. (2006). Measuring and testing the steepness of dominance hierarchies. *Animal Behaviour*, *71*(3), 585-592.

de Waal, F., and Luttrell, L. M. (1989). Toward a comparative socioecology of the genus Macaca: different dominance styles in rhesus and stumptail monkeys. *American Journal of Primatology*, *19*(2), 83-109.

Delson, E. (1980). Fossil macaques, phyletic relationships and a scenario of deployment. In Lindburg, D. G. (Ed.) *The macaques: Studies in ecology, behavior and evolution*. University of Michigan, Michigan, USA, pp. 10-30.

Dittus, W. (2004). Demography: a window to social evolution. In: Thierry, B., Singh, M., and Kaumanns, W. (Eds.) *Macaque societies: A model for the study of social organization*. Cambridge University Press, Cambridge, United Kingdom, pp. 87-116.

Dittus, W. (2004). Demography: a window to social evolution. *Cambridge Studies in Bbiological and Evolutionary Anthropology*, 87-111.

Dittus, W. P. (1975). Population dynamics of the toque monkey, *Macaca sinica*. *Socioecology and psychology of primates*, *42*, 125-151.

Eberle, M., and Kappeler, P. M. (2002). Mouse lemurs in space and time: a test of the socioecological model. *Behavioral Ecology and Sociobiology*, *51*(2), 131-139.

Engel, G., and Jones-Engel, L. (2011). The role of *Macaca fascicularis* in infectious agent transmission. *Cambridge studies in biological and evolutionary anthropology*, *1*(60), 183-203.

Engelhardt, A., Heistermann, M., Hodges, J. K., Nürnberg, P., and Niemitz, C. (2006). Determinants of male reproductive success in wild long-tailed macaques (*Macaca fascicularis*)—male monopolisation, female mate choice or post-copulatory mechanisms?. *Behavioral Ecology and Sociobiology*, *59*(6), 740-752.

Engelhardt, A., Hodges, J. K., and Heistermann, M. (2007). Post-conception mating in wild long-tailed macaques (*Macaca fascicularis*): characterization, endocrine correlates and functional significance. *Hormones and Behavior*, *51*(1), 3-10.

Engelhardt, A., Hodges, J. K., Niemitz, C., and Heistermann, M. (2005). Female sexual behavior, but not sex skin swelling, reliably indicates the timing of the fertile phase in wild long-tailed macaques (*Macaca fascicularis*). *Hormones and behavior*, *47*(2), 195-204.

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

Fashing, P. J. (2001). Male and female strategies during intergroup encounters in guerezas (*Colobus guereza*): evidence for resource defense mediated through males and a comparison with other primates. *Behavioral Ecology and Sociobiology*, *50*(3), 219-230.

Fei, H. L., Scott, M. B., Zhang, W., M. A, C. Y., Xiang, Z. F., and Fan, P. F. (2012). Sleeping tree selection of cao vit gibbon (*Nomascus nasutus*) living in degraded karst forest in Bangliang, Jingxi, China. *American Journal of Primatology*, *74*(11), 998-1005.

Fietz, J., Zischler, H., Schwiegk, C., Tomiuk, J., Dausmann, K. H., and Ganzhorn, J. U. (2000). High rates of extra-pair young in the pair-living fat-tailed dwarf lemur, *Cheirogaleus medius*. *Behavioral Ecology and Sociobiology*, *49*(1), 8-17.

Flack, J. C., and De Waal, F. B. (2004). Dominance style, social power, and conflict management: a conceptual framework. In: Thierry, B., Singh, M., and Kaumanns, W. (Eds.) *Macaque societies: A model for the study of social organization*. Cambridge University Press, Cambridge, United Kingdom, pp. 157-185.

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

Fooden, J. (2006). Comparative review of fascicularis-group species of macaques (Primates: Macaca). *Fieldiana Zoology*, 1-43.

Fooden, J. A. C. K. (1976). Provisional classification and key to living species of macaques (Primates: *Macaca*). *Folia primatologica*, *25*(2-3), 225-236.

Fooden, J., and Aimi, M. (2005). Systematic review of Japanese macaques, *Macaca fuscata*. *Fieldiana Zoology*, 1-198.

Fooden, Jack, and Mitsuru Aimi. "Systematic review of Japanese macaques, Macaca fuscata." *Fieldiana Zoology*(2005): 1-198.

Gammell, M. P., de Vries, H., Jennings, D. J., Carlin, C. M., and Hayden, T. J. (2003). David's score: a more appropriate dominance ranking method than Clutton-Brock et al.'s index.

Girard-Buttoz, C., Heistermann, M., Rahmi, E., Agil, M., Fauzan, P. A., and Engelhardt, A. (2014). Costs of and investment in mate-guarding in wild long-tailed macaques (*Macaca fascicularis*): influences of female characteristics and male–female social bonds. *International journal of primatology*, *35*(3-4), 701-724.

Groves, C. (2001). Primate taxonomy. Smithsonian, Washington, USA.

Gumert, M. D. (2007). Grooming and infant handling interchange in *Macaca fascicularis*: the relationship between infant supply and grooming payment. *International Journal of Primatology*, *28*(5), 1059-1074.

Gumert, M. D. (2010). Dominance and reciprocity in the grooming relationships of female long-tailed macaques (*Macaca fascicularis*) in Indonesia. In *Indonesian Primates*(pp. 309-341). Springer, New York, NY.

Gumert, M. D. (2011). The common monkey of Southeast Asia: Longtailed macaque populations, ethnophoresy, and their occurrence in human environments. In: Gumert, M. D., Fuentes, A., and Jones-Engel, L. (Eds.) *Monkeys on the edge: ecology and management of long-tailed macaques and their interface with humans.* Cambridge University Press, Cambridge, United Kingdom, pp. 3-44.

Gumert, M. D., Fuentes, A., and Jones-Engel, L. (Eds.) (2011). *Monkeys on the edge: ecology and management of long-tailed macaques and their interface with humans*. Cambridge University Press, Cambridge, United Kingdom.

Gumert, M. D., and Ho, M. H. R. (2008). The trade balance of grooming and its coordination of reciprocation and tolerance in Indonesian long-tailed macaques (*Macaca fascicularis*). *Primates*, *49*(3), 176.

Gygax, L. (1995). Hiding behaviour of Longtailed macaques (*Macaca fascicularis*). I. Theoretical background and data on mating. *Ethology*, *101*(1), 10-24.

Hadidian, J., and Bernstein, I. S. (1979). Female reproductive cycles and birth data from an Old World monkey colony. *Primates*, *20*(3), 429-442.

Hajra, P. K., Rao, P. S. N. and Sinha, B. K. (1999). Flora of Great Nicobar islands. Botanical Survey of India, Calcutta.

Hammerstein, P. (1981). The role of asymmetries in animal contests. *Animal Behaviour*, *29*(1), 193-205.

Harris, T. R. (2006). Between-group contest competition for food in a highly folivorous population of black and white colobus monkeys (*Colobus guereza*). *Behavioral Ecology and Sociobiology*, *61*(2), 317-329.

Harris, T. R. (2007). Testing mate, resource and infant defence functions of intergroup aggression in non-human primates: issues and methodology. *Behaviour*, *144*(12), 1521-1535.

Hayakawa, S. (2007). Female defensibility in a small troops of Japanese macaques vis-à-vis nontroop males and copulation on the periphery of the troop. *International Journal of Primatology*, *28*(1), 73-96.

Hayakawa, S., and Soltis, J. (2011). Troop takeover and reproductive success of wild male Japanese macaques on Yakushima Island (*Macaca fuscata yakui*). *International Journal of Zoology*, *2011*.

Henzi, S. P., and Barrett, L. (2002). Infants as a commodity in a baboon market. *Animal Behaviour*, *63*(5), 915-921.

Herbinger, I., Papworth, S., Boesch, C., and Zuberbühler, K. (2009). Vocal, gestural and locomotor responses of wild chimpanzees to familiar and unfamiliar intruders: a playback study. *Animal Behaviour*, *78*(6), 1389-1396.

Hestermann, M., Ziegler, T., Van Schaik, C. P., Launhardt, K., Winkler, P., and Hodges, J. K. (2001). Loss of oestrus, concealed ovulation and paternity confusion in free-ranging Hanuman langurs. *Proceedings of the Royal Society of London B: Biological Sciences*, *268*(1484), 2445-2451.

Horiuchi, S. (2005). Affiliative relations among male Japanese macaques (*Macaca fuscata yakui*) within and outside a troop on Yakushima Island. *Primates*, *46*(3), 191-197.

Hrdy, S. B. (1974). Male-male competition and infanticide among the langurs (*Presbytis entellus*) of Abu, Rajasthan. *Folia primatologica*, *22*(1), 19-58.

Hrdy, S. B. (1977). Infanticide as a primate reproductive strategy. *American Scientist*, *65*(1), 40-49.

Hrdy, S. B. (1979). Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology 1*, 13-40.

Hrdy, S. B. (1986). Empathy, polyandry, and the myth of the coy female. In: R. Bleier (ed.), *Feminist Approaches to Science*. Pergamon Press, New York, USA, pp. 119–146.

Hsu, M. J., Agoramoorthy, G., and Lin, J. F. (2001). Birth seasonality and interbirth intervals in free-ranging Formosan macaques, Macaca cyclopis, at Mt. Longevity, Taiwan. *Primates*, *42*(1), 15-25.

Hsu, M. J., Lin, J. F., and Agoramoorthy, G. (2006). Effects of group size on birth rate, infant mortality and social interactions in Formosan macaques at Mt Longevity, Taiwan. *Ethology Ecology and Evolution*, *18*(1), 3-17.

Inoue, M., Takenaka, A., Tanaka, S., Kominami, R., and Takenaka, O. (1990). Paternity discrimination in a Japanese macaque group by DNA fingerprinting. *Primates*, *31*(4), 563-570.

Isbell, L. A. (1991). Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behavioral ecology*, *2*(2), 143-155.

IUCN 2011. *The IUCN Red List of Threatened Species. Version 2011-2*. <http://www.iucnredlist.org>. Downloaded on 05 December 2011.

IUCN 2017. *The IUCN Red List of Threatened Species. Version 2017-3*. <http://www.iucnredlist.org>. Downloaded on 05 December 2017.

Jack, K. M., Sheller, C., and Fedigan, L. M. (2012). Social factors influencing natal dispersal in male white-faced capuchins (*Cebus capucinus*). *American journal of primatology*, *74*(4), 359-365.

Janson, C. H., and van Schaik, C. P. (2000) The behavioral ecology of infanticides by males. In: van Schaik, C. P., and Janson, C. H. (Eds.). (2000). *Infanticide by males and its implications*. Cambridge University Press, Cambridge, United Kindom, pp. 469-494.

Jiang, J., Yu, J., Li, J., Li, P., Fan, Z., Niu, L., et al. (2016). Mitochondrial genome and nuclear markers provide new insight into the evolutionary history of macaques. *PloS one*, *11*(5), e0154665.

Jones, C. B. (1985). Reproductive patterns in mantled howler monkeys: estrus, mate choice and copulation. *Primates*, *26*(2), 130-142.

Jones-Engel, L., Engel, G., Gumert, M. D., and Fuentes, A. (2011). Developing sustainable human–macaque communities. In: Gumert, M. D., Fuentes, A., and Jones-Engel, L. (Eds.) *Monkeys on the edge: ecology and management of long-tailed macaques and their interface with humans*. Cambridge University Press, Cambridge, United Kingdom, pp. 295-327.

Kamilar, J. M., and Cooper, N. (2013). Phylogenetic signal in primate behaviour, ecology and life history. *Phil. Trans. R. Soc. B*, *368*(1618), 20120341.

Kappeler, P. M. (Ed.) (2000). *Primate males: causes and consequences of variation in group composition*. Cambridge University Press. Cambridge, United Kingdom.

Kappeler, P. M., and van Schaik, C. P. (2002). Evolution of primate social systems. *International journal of primatology*, *23*(4), 707-740.

Kappeler, P. M., and van Schaik, C. P. (2004). Sexual selection in primates: review and selective preview. In. Kappeler, P. M., and van Schaik, C. P. (Eds.) *Sexual selection in primates: News and comparative perspective*. Chembridge University Press, USA, pp. 3-23.

Kapsalis, E., and Berman, C. M. (1996). Models of affiliative relationships among free-ranging rhesus monkeys (*Macaca mulatta*). *Behaviour*, *133*(15), 1235-1263.

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

Kavanagh, M., and Laursen, E. (1984). Breeding seasonality among long-tailed macaques, *Macaca fascicularis*, in peninsular Malaysia. *International journal of primatology*, *5*(1), 17-29.

Keverne, E. B., Martensz, N. D., and Tuite, B. (1989). Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. *Psychoneuroendocrinology*, *14*(1-2), 155-161.

Kier, G., Kreft, H., Lee, T. M., Jetz, W., Ibisch, P. L., Nowicki, C., *et, al.* (2009). A global assessment of endemism and species richness across island and mainland regions. *Proceedings of the National Academy of Sciences*, *106*(23), 9322-9327.

Kinnaird, M. F. (1992). Variable resource defense by the Tana River crested mangabey. *Behavioral Ecology and Sociobiology*, *31*(2), 115-122.

Kitchen, D. M. (2004). Alpha male black howler monkey responses to loud calls: effect of numeric odds, male companion behaviour and reproductive investment. *Animal Behaviour*, *67*(1), 125-139.

Kitchen, D. M. (2006). Experimental test of female black howler monkey (*Alouatta pigra*) responses to loud calls from potentially infanticidal males: effects of numeric odds, vulnerable offspring, and companion behavior. *American journal of physical anthropology*, *131*(1), 73-83.

Kitchen, D. M., and Beehner, J. C. (2007). Factors affecting individual participation in group-level aggression among non-human primates. *Behaviour*, *144*(12), 1551-1581.

Kitchen, D. M., Cheney, D. L., and Seyfarth, R. M. (2004). Factors mediating inter-group encounters in savannah baboons (*Papio cynocephalus ursinus*). *Behaviour*, *141*(2), 197-218.

Korstjens, A. H., Nijssen, E. C., and Noë, R. (2005). Intergroup relationships in western black-and-white colobus, *Colobus polykomos polykomos*. *International Journal of Primatology*, *26*(6), 1267-1289.

Kowalewski, M. M., and Garber, P. A. (2010). Mating promiscuity and reproductive tactics in female black and gold howler monkeys (*Alouatta caraya*) inhabiting an island on the Parana River, Argentina. *American Journal of Primatology*, *72*(8), 734-748.

Krishna, B. A., Singh, M., and Singh, M. (2006). Population dynamics of a group of lion-tailed macaques (*Macaca silenus*) inhabiting a rainforest fragment in the Western Ghats, India. *Folia Primatologica*, *77*(5), 377-386.

Kuester, J., Paul, A., and Arnemann, J. (1994). Kinship, familiarity and mating avoidance in Barbary macaques, Macaca sylvanus. *Animal Behaviour*, *48*(5), 1183-1194.

Kumar, A. and Kurup, G. U. (1985). Inter-troop interactions in the lion-tailed macaque *Macaca silenus*. In: Heltne, P. G. (Eds.) *The lion-tailed macaque: status and conservation*. Wiley-Liss Publications, New York, pp. 91–107.

Kumar, A. (1987). The ecology and population dynamics of the lion-tailed macaque *(Macaca silenus)* in South India. Doctoral dissertation, University of Cambridge.

Kumar, A. (1995). Birth rate and survival in relation to group size in the lion-tailed macaque, *Macaca silenus*. *Primates*, *36*(1), 1-9.

Kumar, A., M., Singh, M., Kumara, H. N., Sharma, A. K., and Bertsch, C. (2001). Male migration in lion-tailed macaques. *Primate Report*, *59*, 5-17.

Kumara, H. N., Singh, M., Sharma, A. K., Santhosh, K., and Pal, A. (2014). Impact of forest fragment size on between-group encounters in lion-tailed macaques. *Primates*, *55*(4), 543-548.

Kurup, G. U. (1988). The grooming pattern in Bonnet macaque, Macaca radiata (E. Geoffroy). *Annals of the New York Academy of Sciences*, *525*(1), 414-416.

Le Roux, A., Snyder-Mackler, N., Roberts, E. K., Beehner, J. C., and Bergman, T. J. (2013). Evidence for tactical concealment in a wild primate. *Nature communications*, *4*, 1462.

Leca, J. B., Gunst, N., and Huffman, M. A. (2010). Indirect social influence in the maintenance of the stone-handling tradition in Japanese macaques, *Macaca fuscata*. *Animal Behaviour*, *79*(1), 117-126.

Lee, P, C. (2008). XXII th congress of the International Primatological Society (IPS): Abstracts, August 3-8, Edinburg, UK.

Lehmann, J., Korstjens, A. H., and Dunbar, R. I. M. (2007). Group size, grooming and social cohesion in primates. *Animal Behaviour*, *74*(6), 1617-1629.

Li, C., Zhao, C., and Fan, P. F. (2015). White-cheeked macaque (*Macaca leucogenys*): A new macaque species from Medog, southeastern Tibet. *American Journal of Primatology*, *77*(7), 753-766.

Li, X. F., Dong, H. L., Huang, X. Y., Qiu, Y. F., Wang, H. J., Deng, Y. Q., et al. (2016). Characterization of a 2016 clinical isolate of Zika virus in non-human primates. *EBioMedicine*, *12*, 170-177.

Lindburg, D. G. (1971). The rhesus monkey in North India: an ecological and behavioral study. *Primate behavior: developments in field and laboratory research*, *2*, 1-106.

Macdonald, S., Schülke, O., and Ostner, J. (2013). The absence of grooming for rank-related benefits in female Assamese macaques (*Macaca assamensis*). *International Journal of Primatology*, *34*(3), 571-584.

Maninger, N., Sackett, G. P., and Ruppenthal, G. C. (2000). Weaning, body weight, and postpartum amenorrhea duration in pigtailed macaques (*Macaca nemestrina*). *American Journal of Primatology*, *52*(2), 81-91.

Manson, J. H. (1992). Measuring female mate choice in Cayo Santiago rhesus macaques. *Animal Behaviour*, *44*, 405-416.

Manson, J. H. (1996). Male dominance and mount series duration in Cayo Santiago rhesus macaques. *Animal Behaviour*, *51*(6), 1219-1231.

Manson, J. H., and Perry, S. E. (1993). Inbreeding avoidance in rhesus macaques: whose choice?. *American Journal of Physical Anthropology*, *90*(3), 335-344.

Markham, A. C., Alberts, S. C., and Altmann, J. (2012). Intergroup conflict: ecological predictors of winning and consequences of defeat in a wild primate population. *Animal behaviour*, *84*(2), 399-403.

Marty, P. R., Hodges, K., Agil, M., and Engelhardt, A. (2015). Alpha male replacements and delayed dispersal in crested macaques (*Macaca nigra*). *American journal of primatology*, 79: e22448.

Matsubara, M. (2003). Costs of mate guarding and opportunistic mating among wild male Japanese macaques. *International Journal of Primatology*, *24*(5), 1057-1075.

Matsumura, S. (1993). Female reproductive cycles and the sexual behavior of moor macaques (*Macaca maurus*) in their natural habitat, South Sulawesi, Indonesia. *Primates*, *34*(1), 99-103.

Mazerolle, J. M. (2017). AICcmodavg: Model selection and multi model inference based on (Q)AIC(c). R package version 2.1-1. https://cran.r-project.org/package=AICcmodavgg

McComb, K., Packer, C., and Pusey, A. (1994). Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. *Animal Behaviour*, *47*(2), 379-387.

Mehlman, P. T. and Parkhill, R. S. (1988). Intergroup interaction in wild Barbary macaques (*Macaca sylvanus*), Ghomaranrif mountains, Morocco. *American Journal of Primatology*, *15*, 31-44.

Melnick, D. J. (1987). The genetic consequences of primate social organization: a review of macaques, baboons and vervet monkeys. *Genetica*, *73*(1-2), 117-135.

Menard, N. (2004). Do ecological factors explain variation in social organizations? In: Thierry, B., Singh, M., and Kaumanns, W. (Eds.) *Macaque societies: A model for the study of social organization*, Cambridge University Press, Cambridge, United Kingdom, pp. 237-266.

Michael, R. P., and Zumpe, D. (1993). Medroxyprogesterone acetate decreases the sexual activity of male cynomolgus monkeys (*Macaca fascicularis*): An action on the brain?. *Physiology and behavior*, *53*(4), 783-788.

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

Mitani, J. C., and Watts, D. P. (2005). Correlates of territorial boundary patrol behaviour in wild chimpanzees. *Animal Behaviour*, *70*(5), 1079-1086.

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

Molur, S., Brandon-Jones, D., Dittus, W., Eudey, A., Kumar, A., Singh, M., et al. (2003). The status of South Asian primates: conservation assessment and management plan (CAMP) workshop report.

Muller, M. N., and Wrangham, R. W. (Eds.). (2009). *Sexual coercion in primates and humans*. Harvard University Press.

Nehru, P. (2012). Natural recovery of tsunami impacted littoral and mangrove forests in Nicobar Islands, India. Ph. D. Thesis, Bharathiar University.

Nellemann, C., Miles, L., Kaltenborn, B. P., Virtue, M., and Ahlenius, H. (2007). The last stand of the orangutan. *State of Emergency: Illegal Logging, Fire, and Palm Oil in Indonesia's National Parks. Arendal, Norway: United Nations Environment Programme-GRID*.

Niemeyer, C. L., and Chamove, A. S. (1983). Motivation of harassment of matings in stumptailed macaques. *Behaviour*, *87*(3), 298-322.

Nieuwenhuijsen, K., de Neef, K. J., and Slob, A. K. (1986). Sexual behaviour during ovarian cycles, pregnancy and lactation in group-living stumptail macaques (*Macaca arctoides*). *Human Reproduction*, *1*(3), 159-169.

Nieuwenhuijsen, K., Slob, A. K., and Ten, J. J. V. D. W. (1988). Gender-related behaviors in group-living stumptail macaques. *Psychobiology*, *16*(4), 357-371.

Nikitopoulos, E., Heistermann, M., de Vries, H., van Hooff, J. A., and Sterck, E. H. (2005). A pair choice test to identify female mating pattern relative to ovulation in long-tailed macaques, Macaca fascicularis. *Animal Behaviour*, *70*(6), 1283-1296.

Noë, R., and Hammerstein, P. (1994). Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioral ecology and sociobiology*, *35*(1), 1-11.

Nunn, C. L. (1999). The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. *Animal behaviour*, *58*(2), 229-246.

Nunn, C. L., Schaik, C. P. V., and Zinner, D. (2001). Do exaggerated sexual swellings function in female mating competition in primates? A comparative test of the reliable indicator hypothesis. *Behavioral Ecology*, *12*(5), 646-654.

Oi, T. (1996). Sexual behaviour and mating system of the wild pig-tailed macaque in West Sumatra. *Evolution and ecology of macaque societies*.

Okamoto, K., and Matsumura, S. (2002). Intergroup encounters in wild moor macaques (*Macaca maurus*). *Primates*, *43*(2), 119-125.

Palombit, R. A. (2015). Infanticide as sexual conflict: coevolution of male strategies and female counterstrategies. *Cold Spring Harbor perspectives in biology*, *7*(6), a017640.

Paul, A. (2004). Dominance and paternity (Box 6). In: Thierry, B., Singh, M., and Kaumanns, W. (Eds.) *Macaque societies: A model for the study of social organization,* Cambridge University Press, Cambridge, United Kingdom, pp. 131-134.

Paul, A., Kuester, J., and Arnemann, J. (1996). The sociobiology of male–infant interactions in Barbary macaques, *Macaca sylvanus*. *Animal Behaviour*, *51*(1), 155-170.

Perry, S. (1996). Intergroup encounters in wild white-faced capuchins (*Cebus capucinus*). *International Journal of Primatology*, *17*(3), 309-330.

Poirier, F. E., and Smith, E. O. (1974). The Crab-Eating Macaques (*Macaca fascicularis*) of Angaur Island, Palau, Micronesia (Part 1 of 2). *Folia Primatologica*, *22*(4), 258-282.

Porwal, M. C., Padalia, H., and 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.

Price, E. C., and Piedade, H. M. (2001). Ranging behavior and intraspecific relationships of masked titi monkeys (*Callicebus personatus personatus*). *American Journal of Primatology*, *53*(2), 87-92.

QGIS Development Team, 2009. QGIS Geographic Information System. Open Source Geospatial Foundation. URL http://qgis.osgeo.org

Radford, A. N., and du Plessis, M. A. (2004). Territorial vocal rallying in the green woodhoopoe: factors affecting contest length and outcome. *Animal Behaviour*, *68*(4), 803-810.

Rahaman, H., and Parthasarathy, M. D. (1969). Studies on the social behaviour of bonnet monkeys. *Primates*, *10*(2), 149-162.

Rahaman, H., and Parthasarathy, M. D. (1969). Studies on the social behaviour of bonnet monkeys. *Primates*, *10*(2), 149-162.

Ramachandran, S., Anitha, S., Balamurugan, V., Dharanirajan, K., Vendhan, K. E., Divien, M. I. P., et al. (2005). Ecological impact of tsunami on Nicobar islands (Camorta, Katchal, Nancowry and Trinkat). *Current Science*, *89*(1), 195-200.

R Development Core Team.2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Reddy, C. S., Satish, K. V., Pasha, S. V., Jha, C. S., and Dadhwal, V. K. (2016). Assessment and monitoring of deforestation and land-use changes (1976–2014) in Andaman and Nicobar Islands, India using remote sensing and GIS. *Current Sci*ence, *111*, 1492-1499.

Reichard, U. (1995). Extra-pair copulations in a monogamous gibbon (*Hylobates lar*). *Ethology*, *100*(2), 99-112.

Reichard, U. H., and Boesch, C. (Eds.). (2003). *Monogamy: mating strategies and partnerships in birds, humans and other mammals*. Cambridge University Press, New York, USA.

Rendall, D., and Taylor, L. L. (1991). Female sexual behavior in the absence of male-male competition in captive Japanese macaques (*Macaca fuscata*). *Zoo Biology*, *10*(4), 319-328.

Richter, C., Mevis, L., Malaivijitnond, S., Schülke, O., and Ostner, J. (2009). Social relationships in free-ranging male *Macaca arctoides*. *International journal of primatology*, *30*(4), 625-642.

Roth, A. M., and Cords, M. (2016). Effects of group size and contest location on the outcome and intensity of intergroup contests in wild blue monkeys. *Animal behaviour*, *113*, 49-58.

Rowe, N., and Myers, M. (2016). *All the World's primates*. Pogonias Press, Charlestown, Boston, USA.

Rubenstein, D. (1986). Ecology and Sociality in Horses and Zebras. In: Rubenstein, D. I., and Wrangham, R. W., (Eds.) *Ecological Determinants of Social Evolution.* Princeton University Press, Princeton, New Jersey, USA, pp. 282-302.

Rudran, R. (1973). Adult male replacement in one-male troops of purple-faced langurs (*Presbytis senex senex*) and its effect on population structure. *Folia primatologica*, *19*(2-3), 166-192.

Ryan, S. J., Starks, P. T., Milton, K., and Getz, W. M. (2008). Intersexual conflict and group size in *Alouatta palliata*: a 23-year evaluation. *International Journal of Primatology*, *29*(2), 405-420.

Saito, C., Sato, S., Suzuki, S., Sugiura, H., Agetsuma, N., Takahata, Y., et al. (1998). Aggressive intergroup encounters in two populations of Japanese macaques (*Macaca fuscata*). *Primates*, *39*(3), 303-312.

Saj, T. L., and Sicotte, P. (2005). Male takeover in *Colobus vellerosus* at boabeng-fiema monkey sanctuary, central Ghana. *Primates*, *46*(3), 211-214.

Sankaran, R. (1998). An annotated list of the endemic avifauna of the Nicobar islands. *Forktail*, 17-22.

Sankaran, R (2005). Impact of the earth quack and the tsunami on the Nicobar Islands. In: Kaul, R., and Menon, V. (Eds.) *The ground beneath the waves: Post-tsunami impact assessment of wildlife and their habitats in India.* Vol. 2. The Islands. Wildlife Trust of India. New Delhi, pp. 10-77.

Sankaran, R. (1995). The Nicobar Megapode and other endemic avifauna of the Nicobar Islands (Status and Conservation). Technical Report: 2, SACON, India.

Santhosh, K., Kumara, H. N., Velankar, A. D., and 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.

Schaik, C. P. V., and Noordwijk, M. A. V. (1985). Interannual variability in fruit abundance and the reproductive seasonality in Sumatran long-tailed macaques (*Macaca fascicularis*). *Journal of Zoology*, *206*(4), 533-549.

Schino, G., and Aureli, F. (2008). Grooming reciprocation among female primates: a meta-analysis. *Biology Letters*, *4*(1), 9-11.

Schino, G., Majolo, B., Ventura, R., and Troisi, A. (2001). Resumption of sexual activity affects mother-infant interactions in Japanese macaques. *Behaviour*, *138*(2), 261-275.

Schino, G., Scucchi, S., Maestripieri, D., and Turillazzi, P. G. (1988). Allogrooming as a tension-reduction mechanism: a behavioral approach. *American Journal of Primatology*, *16*(1), 43-50.

Schmid, V. S., and de Vries, H. (2013). Finding a dominance order most consistent with a linear hierarchy: an improved algorithm for the IandSI method. *Animal behaviour*, *86*(5), 1097-1105.

Seyfarth, R. M. (1977). A model of social grooming among adult female monkeys. *Journal of theoretical Biology*, *65*(4), 671-698.

Sha, J. C. M., Gumert, M. D., Lee, B. P. H., Fuentes, A., Rajathurai, S., Chan, S., and Jones-Engel, L. (2009). Status of the long-tailed macaque *Macaca fascicularis* in Singapore and implications for management. *Biodiversity and Conservation*, *18*(11), 2909-2926.

Singh, M., Kumara, H. N., Kavana, T. S., Erinjery, J. J., and Kumar, S. (2016). Demography and reproductive output in langurs of the Western Ghats, India. *Primates*, *57*(4), 501-508.

Singh, M., Kumara, H. N., Kumar, M. A., Singh, M., and Cooper, M. (2006). Male influx, infanticide, and female transfer in *Macaca radiata radiata*. *International Journal of Primatology*, *27*(2), 515.

Singh, M., Singh, M., Sharma, A. K., and Krishna, B. A. (2003). Methodological considerations in measurement of dominance in primates. *Current Science*, *84*(5), 709-713.

Sivakumar, K. (2010). Impact of the tsunami (December, 2004) on the long tailed macaque of Nicobar Islands, India. *Hystrix-the Italian Journal of Mammalogy*, *21*(1). doi:10.4404/hystrix-21.1-4484

Small, M. F. (1990). Promiscuity in Barbary macaques (*Macaca sylvanus*). *American Journal of Primatology*, *20*(4), 267-282.

Smith, S. (1986). Infant cross-fostering in rhesus monkeys (*Macaca mulatta*): A procedure for the long-term management of captive populations. *American journal of primatology*, *11*(3), 229-237.

Smuts, B. B., and Smuts, R. W. (1993). Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Advances in the Study of Behavior*, *22*(22), 1-63.

Smuts, B. B., and Smuts, R. W. (1993). Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Advances in the Study of Behavior*, *22*(22), 1-63.

Soltis, J. (1999). Measuring male-female relationships during the mating season in wild Japanese macaques (*Macaca fuscata yakui*). *Primates*, *40*(3), 453-467.

Soltis, J. (2004). Mating systems. In: Thierry, B., Singh, M., and Kaumanns, W. (Eds.) *Macaque societies: A model for the study of social organization*, Cambridge University Press, Cambridge, United Kingdom, pp. 135-154.

Soltis, J., Mitsunaga, F., Shimizu, K., Yanagihara, Y., and Nozaki, M. (1999). Female mating strategy in an enclosed group of Japanese macaques. *American Journal of Primatology*, *47*(4), 263-278.

Soltis, J., Mitsunaga, F., Shimizu, K., Yanagihara, Y., and Nozaki, M. (1997). Sexual selection in Japanese macaques I: female mate choice or male sexual coercion?. *Animal Behaviour*, *54*(3), 725-736.

Soltis, J., Thomsen, R., and Takenaka, O. (2001). The interaction of male and female reproductive strategies and paternity in wild Japanese macaques, *Macaca fuscata*. *Animal Behaviour*, *62*(3), 485-494.

Sprague, D. S., Suzuki, S., Takahashi, H., and Sato, S. (1998). Male life history in natural populations of Japanese macaques: migration, dominance rank, and troop participation of males in two habitats. *Primates*, *39*(3), 351-363.

Sterck, E. H. (2000). Female dispersal and infanticide avoidance in primates. *Infanticide by males and its implications*, 293-321.

Sueur, C., Jacobs, A., Amblard, F., Petit, O., and King, A. J. (2011). How can social network analysis improve the study of primate behavior? *American Journal of Primatology*, *73*(8), 703-719.

Sueur, C., Petit, O., De Marco, A., Jacobs, A. T., Watanabe, K., and Thierry, B. (2011). A comparative network analysis of social style in macaques. *Animal Behaviour*, *82*(4), 845-852.

Sugiura, H., Saito, C., Sato, S., Agetsuma, N., Takahashi, H., Tanaka, T., ... and Takahata, Y. (2000). Variation in intergroup encounters in two populations of Japanese macaques. *International Journal of Primatology*, *21*(3), 519-535.

Sugiura, H., Saito, C., Sato, S., Agetsuma, N., Takahashi, H., Tanaka, T., et al. (2000). Variation in intergroup encounters in two populations of Japanese macaques. *International Journal of Primatology*, *21*(3), 519-535.

Sugiyama, Y. (1965). On the social change of Hanuman langurs (*Presbytis entellus*) in their natural condition. *Primates*, *6*(3-4), 381-418.

Swedell, L. (2000). Two takeovers in wild hamadryas baboons. *Folia Primatologica*, *71*(3), 169-172.

Takahata, Y., Ihobe, H. and Idani, G. (1996). Comparing copulations of chimpanzees and bonobos: do females exhibit proceptivity or receptivity? In: McGrew, W. C., Marchant, L. F., and Nishida, T. (Eds.) *Great apes societies.* Cambridge University Press, Cambridge, United Kingdom, pp. 146-158.

Takahata, Y., Suzuki, S., Okayasu, N., Sugiura, H., Takahashi, H., Yamagiwa, J., et al. (1998). Does troop size of wild Japanese macaques influence birth rate and infant mortality in the absence of predators? *Primates*, *39*(2), 245-251.

Teichroeb, J. A., and Sicotte, P. (2008). Infanticide in ursine colobus monkeys (*Colobus vellerosus*) in Ghana: new cases and a test of the existing hypotheses. *Behaviour*, *145*(6), 727-755.

Teichroeb, J. A., Holmes, T. D., and Sicotte, P. (2012). Use of sleeping trees by ursine colobus monkeys (*Colobus vellerosus*) demonstrates the importance of nearby food. *Primates*, *53*(3), 287-296.

Thierry, B. (2004). Social epigenesis. In: Thierry, B., Singh, M., and Kaumanns, W. (Eds.) *Macaque societies: A model for the study of social organization,* Cambridge University Press, Cambridge, United Kingdom, pp. 267-294.

Thierry, B. (2007). Unity in diversity: lessons from macaque societies. *Evolutionary Anthropology: Issues, News, and Reviews*, *16*(6), 224-238.

Thierry, B., Gauthier, C., and Peignot, P. (1990). Social grooming in Tonkean macaques (*Macaca tonkeana*). *International Journal of primatology*, *11*(4), 357-375.

Thierry, B., Iwaniuk, A. N., and Pellis, S. M. (2000). The influence of phylogeny on the social behaviour of macaques (Primates: Cercopithecidae, genus *Macaca*). *Ethology*, *106*(8), 713-728.

Thierry, B., Singh, M., Kaumanns, W. (2004). Why macaque societies? In: Thierry, B., Singh, M., and Kaumanns, W. (Eds.) *Macaque societies: A model for the study of social organization*, Cambridge University Press, Cambridge, United Kingdom, pp. 3-10.

Thomson, J. A., Hess, D. L., Dahl, K. D., Iliff-Sizemore, S. A., Stouffer, R. L., and Wolf, D. P. (1992). The Sulawesi crested black macaque (*Macaca nigra*) menstrual cycle: changes in perineal tumescence and serum estradiol, progesterone, follicle-stimulating hormone, and luteinizing hormone levels. *Biology of reproduction*, *46*(5), 879-884.

Timmermans, P. J. A., Schouten, W. G. P., and Krijnen, J. C. M. (1981). Reproduction of cynomolgus monkeys (*Macaca fascicularis*) in harems. *Laboratory animals*, *15*(2), 119-123.

Trivers, R. (1972). *Parental investment and sexual selection* (Vol. 136, p. 179). Cambridge, MA: Biological Laboratories, Harvard University.

Tsuji, Y. (2011). Sleeping-site preferences of wild Japanese macaques (Macaca fuscata): the importance of nonpredatory factors. *Journal of Mammalogy*, *92*(6), 1261-1269.

Tsukahara, T. (1990). Initiation and solicitation in male-female grooming in a wild Japanese macaque troop on Yakushima Island. *Primates*, *31*(2), 147-156.

Umapathy, G., Singh, M., and 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 Belle, S., Kulp, A. E., Thiessen-Bock, R., Garcia, M., and Estrada, A. (2010). Observed infanticides following a male immigration event in black howler monkeys, *Alouatta pigra*, at Palenque National Park, Mexico. *Primates*, *51*(4), 279-284.

van Noordwijk, M. A. (1985). Sexual Behaviour of Sumatran Long-tailed Macaques (Macaca fascicularis). *Ethology*, *70*(4), 277-296.

van Noordwijk, M. A., and Van Schaik, C. P. (1985). Male migration and rank acquisition in wild long-tailed macaques (*Macaca fascicularis*). *Animal Behaviour*, *33*(3), 849-861.

van Noordwijk, M. A., and Van Schaik, C. P. (1987). Competition among female long-tailed macaques, *Macaca fascicularis*. *Animal Behaviour*, *35*(2), 577-589.

van Noordwijk, M. A., and Van Schaik, C. P. (1988). Male Careers in Sumatran Long-Tailed Macaques (*Macaca Fascicularis*). *Behaviour*, *107*(1), 24-43.

van Noordwijk, M. A., and van Schaik, C. P. (1999). The effects of dominance rank and group size on female lifetime reproductive success in wild long-tailed macaques, *Macaca fascicularis*. *Primates*, *40*(1), 105-130.

van Noordwijk, M. A., and Van Schaik, C. P. (2001). Career moves: transfer and rank challenge decisions by male long-tailed macaques. *Behaviour*, *138*(3), 359-395.

van Noordwijk, M. A., and Van Schaik, C. P. (2004). 12 Sexual selection and the careers of primate males: paternity concentration, dominance-acquisition tactics and transfer decisions. *Sexual selection in primates*, 208.

van Schaik, C. P. (1983). Why are diurnal primates living in groups?. *Behaviour*, *87*(1), 120-144.

van Schaik, C. P. (1989). The ecology of social relationships amongst female primates. *Comparative socioecology*, 195-218.

van Schaik, C. P. (2000). Social counterstrategies against infanticide by males in primates and other mammals. In: Kappeler P. M., (Ed.) *Primate males: Causes and consequences of variation in group composition*, Cambridge University Press, Cambridge, United Kingdom, pp. 34-52.

van Schaik, C. P., and Brockman, D. K. (2005). Seasonally in primate ecology, reproduction, and life history: an overview. In: Brockman, D. K., and Van Schaik, C. P. (Eds.) *Seasonality in primates: studies of living and extinct human and non-human primates*. Cambridge University Press. Cambridge, United Kingdom, pp. 3-20.

van Schaik, C. P., and Janson, C. H. (Eds.). (2000). *Infanticide by males and its implications*. Cambridge University Press, Cambridge, United Kindom.

van Schaik, C. P., Assink, P. R., and Salafsky, N. (1992). Territorial behavior in Southeast Asian langurs: resource defense or mate defense?. *American Journal of Primatology*, *26*(4), 233-242.

van Schaik, C. P., Netto, W. J., Van Amerongen, A. J. J., and 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., Pfannes, K. R. (2005). 2 Tropical climates and phenology: a primate perspective In: Brockman, D. K., and Van Schaik, C. P. (Eds.) *Seasonality in primates: studies of living and extinct human and non-human primates*. Cambridge University Press. Cambridge, United Kingdom, pp. 23-54.

van Schaik, C. P., Terborgh, J. W., and Wright, S. J. (1993). The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of ecology and Systematics*, *24*(1), 353-377.

van Schaik, C. P., Van Noordwijk, M. A., de Boer, R. J., and 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.

Velankar, A. D., Kumara, H. N., Pal, A., Mishra, P. S., and 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.Waser, P. M. (1976). *Cercocebus albigena*: site attachment, avoidance, and intergroup spacing. *The American Naturalist*, *110*(976), 911-935.

Waser, P. M., Austad, S. N., and Keane, B. (1986). When should animals tolerate inbreeding?. *The American Naturalist*, *128*(4), 529-537.

Watts, D. P., and Mitani, J. C. (2001). Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour*, *138*(3), 299-327.

Wheatley, B. P. (1999). *Sacred monkeys of Bali*. Prospects Heights, IL, Waveland Press.

Wich, S. A., and Sterck, E. H. (2007). Familiarity and threat of opponents determine variation in Thomas langur (*Presbytis thomasi*) male behaviour during between-group encounters. *Behaviour*, *144*(12), 1583-1598.

Willoughby, P. R. (2005). Palaeoanthropology and the evolutionary place of humans in nature. *International journal of comparative psychology*, *18*(1).

Wilson, M. L., Hauser, M. D., and Wrangham, R. W. (2001). Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees?. *Animal Behaviour*, *61*(6), 1203-1216.

Wilson, M. L., Kahlenberg, S. M., Wells, M., and Wrangham, R. W. (2012). Ecological and social factors affect the occurrence and outcomes of intergroup encounters in chimpanzees. *Animal Behaviour*, *83*(1), 277-291.

Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour*, *75*(3), 262-300.

Xia, D., Li, J., Garber, P. A., Sun, L., Zhu, Y., and Sun, B. (2012). Grooming reciprocity in female Tibetan macaques Macaca thibetana. *American journal of Primatology*, *74*(6), 569-579.

Zhang, R., Wang, Y. Q., and Su, B. (2008). Molecular evolution of a primate-specific microRNA family. *Molecular biology and evolution*, *25*(7), 1493-1502.

Zhao, Q., Borries, C., and Pan, W. (2011). Male takeover, infanticide, and female countertactics in white-headed leaf monkeys (*Trachypithecus leucocephalus*). *Behavioral Ecology and Sociobiology*, *65*(8), 1535-1547.

Zinner, D., and Deschner, T. (2000). Sexual swellings in female hamadryas baboons after male take-overs:“deceptive” swellings as a possible female counter-strategy against infanticide. *American Journal of Primatology*, *52*(4), 157-168.

Zinner, D., Wertheimer, J., Liedigk, R., Groeneveld, L. F., and Roos, C. (2013). Baboon phylogeny as inferred from complete mitochondrial genomes. *American journal of physical anthropology*, *150*(1), 133-140.

Zumpe, D., and Michael, R. P. (1987). Relation between the dominance rank of female rhesus monkeys and their access to males. *American Journal of Primatology*, *13*(2), 155-169.