Aggression and Conflict Resolution in Nicobar Long-Tailed Macaque *Macaca fascicularis umbrosus*

The thesis submitted to Bharathiar University
for the award of the Degree of

DOCTOR OF PHILOSOPHY IN ZOOLOGY

By

PARTHA SARATHI MISHRA

(Reg No: 2014R437)

Under the Supervision and Guidance of
Dr. H. N. Kumara

Co-Supervisor
Dr. Tha Thayumanavan

Sálim Ali Centre for Ornithology and Natural History

Coimbatore, India

October 2019

Certificate

CERTIFICATE

This is to certify that the thesis, entitled **"Aggression and Conflict Resolution in Nicobar Long-Tailed Macaque (*Macaca fascicularis umbrosus*)"** submitted to Bharathiar University, Coimbatore in partial fulfillment of the requirements for the award of the Degree of **DOCTOR OF PHILOSOPHY IN ZOOLOGY** is a record of original research work done by **PARTHA SARATHI MISHRA** during the period from November 2014 to October 2019 of his research in the Conservation Biology Division, Sálim Ali Centre for Ornithology and Natural History, Coimbatore under my supervision and guidance and the thesis has not formed the basis for the award of any Degree / Diploma /Associateship/ Fellowship or other similar title of any candidate of any University.

Date:

Place: Coimbatore

Head of the Department

डॉ. पी. आर. अरुन / Dr. P.R. Arun
वरिष्ठ प्रधान वैज्ञानिक / Senior Principal Scientist
सालिम अली पक्षिविज्ञान एवं प्रकृति विज्ञान केन्द्र
Sálim Ali Centre for Ornithology and Natural History
आनैकट्टी, कोयम्बत्तूर - 641 108
Anaikatty (Post), Coimbatore – 641 108

Signature of the Supervisor

[illegible]
प्रधान वैज्ञानिक / Principal Scientist
सालिम अली पक्षिविज्ञान एवं प्रकृति विज्ञान केन्द्र
Sálim Ali Centre for Ornithology and Natural History
आनैकट्टी, कोयम्बत्तूर - 641 108
Anaikatty (Post), Coimbatore - 641 108

Head of the Institution (Director)

डॉ. के शंकर / Dr. K Sankar
निदेशक / Director
सालिम अली पक्षिविज्ञान एवं प्रकृति विज्ञान केन्द्र
Sálim Ali Centre for Ornithology and Natural History
आनैकट्टी, कोयम्बत्तूर – 641 108
Anaikatty (Post), Coimbatore – 641 108

29/10/19

Signature of the Co-Supervisor

Dr. Tha. THAYUMANAVAN, M.Sc.,PGDNBT, Ph.D.,
Professor of Biotechnology,
KIT-Kalaignarkarunanidhi Inst. of Tech.,
Kannampalayam Post,
Coimbatore - 641 014. India.

Declaration

DECLARATION

I, **PARTHA SARATHI MISHRA**, hereby declare that the dissertation entitled, **"Aggression and Conflict Resolution in Nicobar Long-Tailed Macaque (*Macaca fascicularis umbrosus*)"** submitted to Bharathiar University, Coimbatore in partial fulfillment of the requirements for the award of Degree of **DOCTOR OF PHILOSOPHY IN ZOOLOGY** is a record of original and independent research work done by me during April 2014 to March 2019 under the supervision and guidance of **Dr. H. N. KUMARA**, Principal Scientist, Conservation Biology Division, Sálim Ali Centre for Ornithology and Natural History, Coimbatore, and it has not formed the basis for the award of any Degree/ Diploma/ Associateship/ Fellowship or other similar title to any candidate in any University.

Date: 29.10.2019
Place: COIMBATORE

Signature of the Candidate
(PARTHA SARATHI MISHRA)

Certificate of Genuineness of the Publications

CERTIFICATE OF GENUINENESS OF THE PUBLICATION

This is to certify that the Ph.D., candidate **Mr. PARTHA SARATHI MISHRA** working under my supervision has published his research articles in the SCIE journals named:

1. Pal, A., Kumara, H.N., **Mishra, P.S.**, Velankar, A.D. and Singh, M. (2018) Between-group encounters in Nicobar long-tailed macaque (*Macaca fascicularis umbrosus). Ethology, Ecology and Evolution* https://doi.org/10.1080/03949370.2018.1459866.
2. Pal, A., Kumara, H.N., Velankar, A.D., **Mishra, P.S**. and Singh, M. (2019) Changes in behaviour following a 'rank changeover by challenge' in the Nicobar long-tailed macaque (*Macaca fascicularis umbrosus*). *Current Science,* 117: 672-682.

The contents of the publication incorporate part of the results presented in his Synopsis/Thesis.

Countersigned

Research Supervisor (with seal)

प्रधान वैज्ञानिक / Principal Scientist
सालिम अली पक्षिविज्ञान एवं प्रकृति विज्ञान केन्द्र
Salim Ali Centre for Ornithology and Natural History
आनैकट्टी, कोयम्बटूर - 641 108
Anaikatty (Post), Coimbatore - 641 108

Head of the Institution (Director)

डॉ. के शंकर / Dr. K Sankar
निदेशक / Director
सालिम अली पक्षिविज्ञान एवं प्रकृति विज्ञान केन्द्र
Salim Ali Centre for Ornithology and Natural History
आनैकट्टी, कोयम्बत्तूर – 641 108
Anaikatty (Post), Coimbatore – 641 108

29/10/19

Research Co-supervisor (with seal)

Dr. Tha. THAYUMANAVAN, M.Sc.,PGDNBT, Ph.D.,
Professor of Biotechnology,
KIT-Kalaignarkarunanidhi Inst. of Tech.,
Kannampalayam Post,
Coimbatore - 641 014. India.

Certification of Plagiarism Check

பாரதியார் பல்கலைக்கழகம்
BHARATHIAR UNIVERSITY
COIMBATORE - 641 046, TAMILNADU, INDIA.

State University | Re-accredited with "A" Grade by NAAC | Ranked 14th among Indian Universities by MHRD-NIRF

CERTIFICATE OF PLAGIARISM CHECK

1	Name of the Research Scholar	PARTHA SARATHI MISHRA
2	Course of study	M.Phil., / Ph.D.,
3	Title of the Thesis / Dissertation	AGGRESSION AND CONFLICT RESOLUTION IN NICOBAR LONG-TAILED MACAQUE (*Macaca fascicularis umbrosus*)
4	Name of the Supervisor	Dr. Honnavalli N. Kumara
5	Department / Institution/ Research Centre	Sálim Ali Centre for Ornithology and Natural History Coimbatore
6	% of Similarity of content Identified	01 %
7	Acceptable Maximum Limit	30 %
8	Software Used	URKUND
9	Date of verification	24 /10/ 2019

Report on plagiarism check, items with % of similarity is attached

Signature of the Supervisor
(Seal)

डॉ एच एन कुमारा / Dr. Kumara
प्रधान वैज्ञानिक / Principal 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 of the Researcher

R&D Director (BU) / Head of the Department
(Seal)

डॉ. पी. आर. अरुन / Dr. P. R. Arun
वरिष्ठ प्रधान वैज्ञानिक / Senior Principal Scientist
सालिम अली पक्षिविज्ञान एवं प्रकृति विज्ञान केन्द्र
Sálim Ali Centre for Ornithology and Natural History
आनैकट्टी, कोयम्बतूर - 641 108
Anaikatty (Post), Coimbatore - 641 108

24/10

University Librarian (BU)

University Librarian
Arignar Anna Central Library
Bharathiar University
Coimbatore - 641 046.

Research Coordinator (BU)

URKUND

Urkund Analysis Result

Analysed Document:	Partha Sarathi Mishra.docx (D57576213)
Submitted:	10/24/2019 11:25:00 AM
Submitted By:	rspani1967@gmail.com
Significance:	1 %

Sources included in the report:

https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4868865/

Instances where selected sources appear:

1

24/10

Contents

Contents

Acknowledgements

Acknowledgments

Rome was not built in a day and definitely not by one person. Ph.D. is nothing less than building Rome and like anything glorious, it would be wrong to take the sole claim to the throne without acknowledging each and every warrior who helped me build this brick to brick, line by line.

The path was set right by my Guru ***Dr. H. N. Kumara****, who gave me the opportunity to work on my dream i.e., working on primates. He not only gave methe academic freedom to pursue my own ideas but also gave me the strength to fight the hardships of fieldwork by giving his own examples from his own experience. Every failure was discouraging but he encouraged me to findan opportunity in every wrong step. I understand that he might have expected more and I could not always deliver. Hence, I will be forever grateful for his patience. I will keep working on everything I learned from him as a person and as a mentor. Ph.D. is always about the guide and I feel fortunate to work under his tutelage and make a researcher out of myself. I look up to him to be the guide and mentor I want to be.*

I am sincerely grateful to my co-supervisor ***Dr. Tha Thayumanavan,*** *who has always assisted me when I faced administrative hurdles in conducting the research and technical issues. Without him, there would not have been any thesis to write.*

I have been extremely fortunate to have been guided by ***Prof. Mewa Singh*** *and* ***Dr. Matthew A. Cooper,*** *who were a major force in enhancing my skills in both critical thinking and study design.*

I am thankful to the ***Department of Science and Technology, Government of India*** *for the financial assistance provided to my research supervisor, Dr. H. N. Kumara (Grant No.SR/SO/AS-49/2011), and SERB J. C. Bose Fellowship to Prof. Mewa Singh (Grant No. SB/S2/JCB-056/2015), for carrying out the research work. My work would not have been so seamless without the permission (Permit No. CWLW/WL/134/566) and constant* *encouragement from the* ***Andaman and Nicobar Forest Department****. I want to sincerely thank the* ***Principal Chief Conservator of Forests, Port Blair, Andaman and Nicobar Islands*** *for granting permission for the study and to the* ***Assistant Commissioner, Andaman and Nicobar Administration*** *for providing the necessary permits to access the tribal areas of Nicobar.*

I would like to express my sincerest gratitude to ***Dr. Azeez P.A****, former Director and* ***Dr. K. Sankar****, current Director, Sálim Ali Centre for Ornithology and Natural History, for constant encouragement and support during the study tenure. I express my sincere gratitude to Dr. P. Balasubramaniam for easing the process of Ph.D and related formalities. I sincerely thank* ***Dr. P.A. Arun*** *for university related processes. I would like to thank* ***Dr. Shomita Mukherjee*** *for her support during the research work. I thank the faculty of SACON for being there to assist whenever I faced a problem, may be be academic or non-academic.I thank all the Hostel wardens, administration, finance and hospitality management for making the stay enjoyable.*

The legacy of Rome will not be without its architects. The special people whom I would really like to thank in a few words as they won't ever be enough are ***Arijit*** *and* ***Avadhoot****, with whom not only did I enjoyed research time but also the time after it. I owe my thesis to them. I would like to sincerely thank* ***Dhee, Snehaa, Marishia, Nikita, and Sheethal****, who helped me put every brick that was required under adverse conditions.*

Research work conducted in Great Nicobar Island was the most defining and fulfilling experience and it would not have been possible without the constant interaction with ***Nicobar Forest Division****. Interactions with* ***Divisional Forest Officers*** *kept me motivated for my work and kept me informed about the conservation issues on the island. I express my gratitude to* ***Mr. Agni Mitra, Mr. Jabestin A., Mr. Jiss K. Varkey,*** *and* ***Mr. Thomas Varghese*** *for the same.*

As Machiavelli puts it, establishing a new colony is never possible without the acceptance of locals. I would like to thank ***Mr. A. Simachalam****, who provided the best food one can possibly get being away from home and cared like a family. I would especially like to thank him to cater to my whims, cravings and for all the desserts. I would like to thank* ***Shailen da*** *for his ever helpful nature;* ***Mr. Thinagaran****,* ***neighborhood grocery shop, Suruchi restaurant,*** *and* ***teashop-owner annachi*** *who made it possible for me to sustain myself even when I was having financial troubles. Despite anything, their warmth never faded. I would especially like to thank all the house-owners and* ***Krishnaji*** *who helped me with stay during the research work. In a remote place, it is easy to get isolated. But I was fortunate to have friends like* ***Ajay, Gaurav, Pringle, Asim da, Casper and Gerund****.*

Friendship has a special meaning in primatology and only the strongest bondstested through tough times lead to friendship. I am grateful to ***Aakriti, Swapnali, Pallavi, Suraj, Munjhe, Jins, Anup Raj, and Aishwarya*** *who have been my pillars of strength. I would like to thank my contemporaries who were making their own Rome,* ***Divyapriya C., Shanthala ma'am*** *and* ***Anoop*** *for discussion, admin help and complaining about Ph.D. I would like to thank special people,* ***Aditi, Amruta, Alexandra, Ovee, Revathe, Sumithra, Rathnavel, Mahi*** *and* ***Parveen*** *who despite everything stood by my side, constantly pushed me towards positivity and never allowed me to get overwhelmed by my ever-fluctuating emotional level and stay focused.*

The acknowledgment has already crossed too many pages, yet I still haven't mentioned the most important people who made it possible for me to reach this stage where I am able to write this as a message. ***Baba, Maa, and AnnieThing the Sister, you guys made me. There are not enough words to pay tribute to the sacrifices you made so that I could reach where I am today. I can perhaps write pages about each of you but I would rather dedicate my thesis to you. ROME IS YOURS.***

List of Tables

List of Tables

List of Figures

List of Figures

Chapter 1:

Introduction

Chapter 1

Introduction

Living in groups has certain benefits like defense from predators, mate defense, finding suitable patches of food. However, it is not without its challenges (van Schaik 1983). Staying in close proximity to other individuals leads to competition for space, food, and mates. Simultaneous needs and consumption of the same resources lead to competition among the members of a group. Such challenges are underpinnings of conflict and cooperation in animal societies including primates (Aureli and de Waal 2000). Cooperation, although seen as a positive effect, has hidden costs as each member has to maintain certain coordination to achieve maximum benefits from group-living (Dugatkin 1997). However, the interests of every individual will not be the same as each member has the propensity to maximize their fitness so that their genes are transmitted to the next generation. The maximum fitness is thus achieved through accessing valuable resources. Besides, not every animal in a group will have equal strength to maximize all the resources and hence there is a dissimilarity among the individuals based on age, sex, rank and reproductive condition. This dissimilarity leads to the difference in motivations among the members of a group to compete for the resources (Aureli and de Waal 2000). In other words, patterns of aggression and affiliation vary between individuals of a group.

Aggression has been a widely studied topic in primatology with two major school-of-thoughts explaining its role in society:

a) Aggression is an antisocial tendency: This model suggests that aggression is detrimental to the relationships and closely-bonded individuals seldom take part in aggressive encounters (Kummer 1978). It is hence considered as antisocial behavior (Krebs and Miller 1985).

b) Relational Model: It says that aggression and post-aggression affiliation are common among individuals who have a strong bond among themselves. Post-conflict contact establishes a "calming effect" among aggressive competitors and not only restores but also increases friendly interactions among individuals thus making the relationships stronger. In fact, aggression is considered to be one of several ways to settle conflict (de Waal 1996, Fig 1.1).

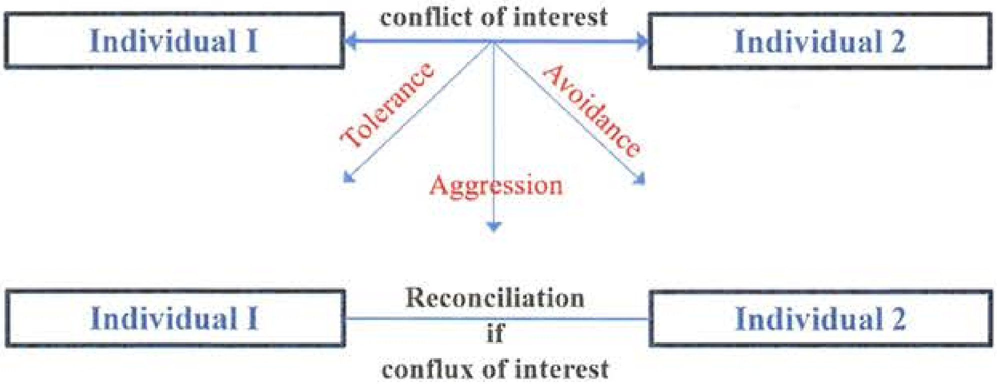


Figure 1.1 Relational Model (de Waal 1996) suggesting that aggression is a model to resolve conflicts

The relational model suggests that propensity to initiate aggression increases with an increase in competition, resource availability and the reparability of a relationship. It decreases with an increase in the risk of physical injury and value of relationship (Aureli and de Waal 2000). Hence, individuals are aware of the relationships they have with other individuals through an experience such as affiliation exchanged over time according to which the aggression towards those individuals is comparatively lower (Aureli and de Waal 2000).

According to the relational model, one way to understand aggression among the individuals is to understand the competitive regime of the group which influences individual fitness. Trivers (1972) suggests that males and females differ significantly for the resources they compete for. He postulated that males compete for mates, which is a non-sharable resource and hence it would lead to contest competition and thus aggressive encounters among them. However, the patterns of aggression are variable among species as seen in the case of macaques where it varies among the lineages depending on the synchronicity of female fertile phases and reliability of sexual swellings (Carnes et al. 2011, Nunn 1999, Ostner and Schulke 2014). High synchronicity of fertile phases in females would mean that at a particular time/season most of the females are sexually receptive to the males in the group and thus monopolization of females for mating is difficult. This leads to conflict between males for gaining access to females leading to high aggression and low affiliation rates among the males. If females have deceptive sexual swellings, that would also lead to high competition among males to access the female showing receptivity through swelling (Engelhardt et al. 2005). Under such regimes, males do not form differentiated bonds and usually have a high rate of aggression (Ostner and Schulke 2014). Contrasting results are found for the species that breed throughout the year and have more reliable signals as seen in *Macaca fascicularis* (Engelhardt et al. 2005).

In females, the pattern of conflict is based on the availability of food and thus, ecology-dependent (Trivers 1972). The dominant model which explains the conflict in females is the Socioecological model which suggests that females fight for clumped and less abundant food (Clutton-Brock and Janson 2012, Isbell and Young 2002, Sterck et al. 1997, van Schaik 1989, Wrangham 1980). Hence, the affiliation is expected more than aggression among females where food is distributed evenly.

de Waal and van Roosmalen (1979) showed for the first time that two adult female chimpanzees were involved in friendly interactions after an aggressive encounter. It was henceforth known as reconciliation. The valuable relationship hypothesis predicts that individuals form strong bonds with some individuals and will show higher reconciliatory tendencies (Aureli et al. 2002). The form and function of reconciliation have been described to reduce aggression between former partners (Petit et al. 1997) and reduce social tension

(Watts 2006). As it is known that animals differentiate among themselves based on costs and benefits they gain from each other and thus, the measure of conflict resolution varies among dyads. In fact, it also differs between populations and species as well. This measure of conflict resolution which is also known as the conciliatory tendency is expected to lower formore despotic species like Rhesus macaque (*M. mulatta*), Japanese macaque (*M. fuscata*) and long-tailed macaque (*M. fascicularis*) (Thierry 2007, Thierry et al. 2008).

Rationale

M. f. umbrosus is an island-dwelling subspecies of long-tailed macaque found on three isolated islands of Nicobar group of islands in Andaman and Nicobar Archipelago (Umapathy et al. 2003). These three populations on the islands viz., Katchal, Great Nicobar Island and Little Nicobar Island have been separated since last 0.65 mya (Fooden 1995). A recent study on a population of long-tailed macaques at Great Nicobar Island has shown that there is low synchronicity in the fertile phases with a mild peak in female receptiveness among the females i.e only a certain number of females were receptive in a particular season (Pal 2018). Further, females did not exhibit honest fertility signals (Pal 2018). Thus, I predict that males will show moderate affiliation among themselves which is characteristic of the species and lineage (Ostner and Schulke 2014). In addition, affiliation may not be reciprocated and equitable among the males. Hence, these affiliative interactions will not be differentiated i.e., some individuals will not be more favored for affiliation, and the rate of aggression in the males as well as the linearity should be intermediate to species of other lineages. The conciliatory tendency should then be high which is the characteristic of the species and the lineage.

The vegetation on Great Nicobar Island is primarily evergreen forest and coastal littoral forests along the coastline (Hajra et al. 1999). Large extent of forests have been converted to agricultural land and human settlement after the introduction of settlers on the islands since

1969 (Pabla 2018). The vegetation and habitat was significantly changed after the devastating tsunami of 2004 which caused further decline in the population of macaques (Sivakumar 2010). Many groups of long-tailed macaques have home ranges overlapping with human settlements especially after the tsunami (Sivakumar 2010, Velankar et al. 2016).

The human settlements have orchards of fruits dominated by coconut and gardens/fields with vegetables. Hence, the availability of high quality food is expected to be clumped for these macaques inhabiting human habitations. Hence, I hypothesised that the

(a) Females in *M. f. umbrosus* will have high aggression rate with linear dominance hierarchy and high steepness.

(b) Affiliation rate would be low and will be directed more towards the high ranking females

(c) Rank-directed grooming is expected to gain proximity towards the high ranking females for accessing food.

I evaluated the results of female behavior upon change in male migration after an event of male migration and rank changover. To evaluate these predictions, I conducted a study on a group of Nicobar long-tailed macaque Temple Run (TR, henceforth), at Great Nicobar Island.

Objectives:

1. To study the effects of food availability and distribution, and social factors on within-group aggression in Nicobar long-tailed macaque

    a) Resource factors:

    - How spatial abundance of food in the home range influence the aggression in a group?
    - Whether provisioning leads to agonistic interactions in a group? If yes, then how?

    b) Social factors:

    - How dominance hierarchies in both sexes influence within-group aggression?
    - How male migrations affect the hierarchies and aggression in the group?
    - How receptivity of females and the presence of infants affect the aggression within the group?

2. To investigate the conflict resolution in the Nicobar long-tailed macaques.

    a) Whether conciliatory tendency is present in the individuals?
    b) What are the various modes of conciliation in a group?
    c) How conciliation influence the dominance hierarchies and dyadic aggression in a group?

Study Area

This is the first-ever study that was planned to understand the social behavior of Nicobar long-tailed macaques (*M. f. umbrosus*). After the survey of Nicobar long-tailed macaques in the three islands (Velankar et al. 2016), I selected a group of Nicobar long-tailed macaques at Campbell Bay, a south-eastern settlement at Great Nicobar Island (93° 55' 8.417"- 93° 56'51.95" E and 7° 1' 39.34"- 6° 59' 31.47" N) to carry out the study (Fig 1.2).

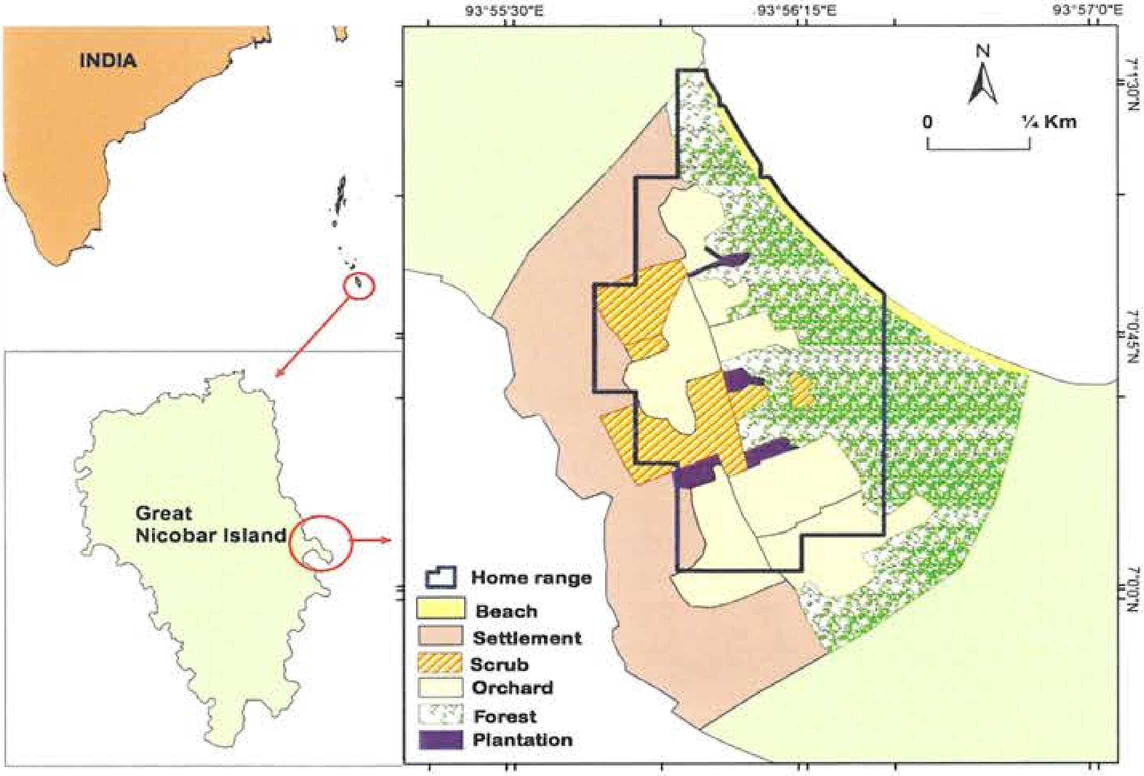


Figure 1.2 Map of Campbell Bay region of Great Nicobar withthe home range of study group (TR) demarcated by dark blue lines.

The important points that were considered for choosing the site and study were

(a) Ease of access to the island.

(b) Logistical ease to carry out the study.

(c) Presence of the group in the human-dominated landscape to study the presence of provisioning and its effect.

(d) Ease of following the group in the human-modified landscape as it was difficult to follow the group through the dense canopy and understorey flora elsewhere.

(e) Ease of habituation of the group as the group was familiar with humans in the home range.

Lying in the south of tropic of cancer, the island receives 4200 mm of annual rainfall, and the temperature varies between 22-32°C (Indian Meteorological Department, Andaman and Nicobar Islands). The vegetation of the selected site consisted of primary hilly tropical evergreen forest, low-land littoral forest, vegetable orchards, and coconut and areca nut plantations (Hajra et al. 1999).

Study Group

I habituated the chosen group of *M. f. umbrosus* as the focal group for the study. The group was named TR after differentiating its identity from the neighboring groups. Initially, I followed the selected group between October 2013 to March 2014 to habituate and identify the individuals. The näive range of the group is depicted in Fig.1.2. The group was chosen due to the ease of following and observing it for longer durations as other groups spent a considerable time in restricted military areas and/or in very dense evergreen forests. The individuals were identified based on the facial patterns and body markings. The age of individuals were determined by their body size, canine size for males and nipple size for females. The size of the study group changed during the study period between 15-19 as I recorded 5 deaths/disappearances (3 adult males and 2 adult females) and 8 births (7 males and 1 female). The mean group size during the study period was 16.67 ± 1.70_{SD} (Pal *et al.* 2018) (Table 1.1). Data were collected for all the 5 males (FY, KU, BE, HK, AI) and 6 females (NI, TE, AU, BY, RE, ST) residing in the study group throughout the study period. Kinship was not known among the group members.

Table 1.1 Variation in group size and age-sex class during the study period for the group TR (ADM = Adult Male, ADF = Adult Female, IMM = Immature)

Group ID	Year	GroupSize	ADM	ADF	IMM
TR	2013	16	3	6	7
	2014	19	4	8	7
	2015	15	1	6	8
Mean (SD)		16.67 (±1.70)	2.67 (±1.25)	6.67 (±0.94)	7.33 (±0.47)

Habitat in the naïve range of the study group.
(Top: Vegetation structure, Bottom: Human-dominated landscape)

Methodology

The study was conducted between October 2013 and October 2017 for a total of 2100 h of observation. The group was followed from 05:00 to 17:00 h and the data were collected by maintaining a distance of 2-5 m from the group. Because the group spent considerable time in thick vegetation with cane and pandanus, they could not be kept in eye contact continuously for a long period of time.

Focal animal sampling : To record individual activities, I used 5 min focal animal sampling (Altmann 1974). An individual was chosen in a pseudo-random order and was followed for 5 minutes. The activities were divided as frequency-based (self-directed behaviors: scratching, yawning; affiliative behaviors: muzzle contact, genital touch, silent bared-teeth display, sitting in contact, inspection, embrace, active and passive touch, lip-smacking; agonistic and submissive behaviors: slap, bite, lunge, chase, charge, flee, canine flash, brow-raise, open-mouth threat, tail-raise) (Table 1.2), and duration-based (explore, feed, object/food manipulation, movement, infant carrying, resting/sleeping, vigilance, social and non-social play, grooming) (Aureli 1992). For each dyadic interaction from a focal sample, I recorded the identities of actor and receiver. I collected focal samples of each individual from 05:00 to 17:00 h by dividing it in blocks of 2 hrs. When the focal individual could not be followed or it moved out of sight, an attempt was made to track it for the next 5 minutes and the duration of disappearance was recorded. If the individual was not found, I resumed sampling for the next randomly selected individual and the incomplete sample was not considered for analysis. In addition, an individual was sampled only once in a two-hour sampling block to maintain uniformity. Although I made a subsequent attempt to increase sampling for the less-sampled individuals, cumulatively there was a considerable variation among the focal samples between the individuals. A total of 253.62 h of focal data was collected for the study group

(Females: 190.77 h, Mean ± SE = 36.19 ± 13.12 h; Males: 62.85 h, Mean ± SE = 12.57 ± 7.61 h).

Table 1.2 Description of the behaviors for the focal animal sampling

Affiliation	**Description**
Muzzle contact	Touching the muzzle of another individual by its own muzzle. Displayed by both sexes.
Genital Touch	Touching or holding the penis of another male by an individual. Behavior exclusive to males.
Silent bared-teeth display	Retracting lips upwards to expose teeth to the other individual as a sign of affiliation. Displayed by both sexes.
Sitting in contact	Individuals sitting in close proximity with parts of their bodies touching. Although this behavior is mostly seen among the females, males have been observed to sit in close proximity as well.
Inspection	Touching and sniffing the genitals of another individual for mating. This behavior usually involves a male touching and sniffing the sexual swellings of a female.
Embrace	Embracing is defined as wrapping the forelimbs around another individual while facing it. Displayed by both sexes.
Active Touch and Passive Touch	Active touch involves an individual to intentionally touch another individual using any part of the body whereas, passive touch involves accidental touch by one individual to the other using any part of the body.
Lip smacking	Lip smacking involves pursing of lips with the lower jaw moving up and down in rhythm producing a soft sound audible only at short distances (Micheletta et al 2013).

Aggression	**Description**
Slap	Contact another individual in aggression with rapid and forceful touch with hand. Displayed in both sexes.
Lunge	Sudden thrust to attack another individual with arm outstretched. Displayed by both sexes.
Chase	Following another individual to attack, typically with running after and driving the other individual. Exhibited by both sexes.
Charge	Pursuing towards another individual to attack not followed by the victim running away. Displayed by both sexes.
Flee	Running away and avoiding being attacked by a chasing individual. Displayed by both sexes.
Canine Flash	Sudden exposure of canines to threaten other individual in visual range, can

	lead to chase or charge. Displayed by both sexes.
Open-mouth threat	Mouth is tensely open and lips cover the teeth from exposure (Symons 1974).
Brow-raise	Both eyebrows are raised upwards along with open-mouth threat to threaten another individual. Displayed irrespective of sex.
Tail-raise	Observed usually in the dominant males who raise and arch their tails amd move towards the subordinate males or females to threaten them.

Scan Sampling (Altmann 1974): Sample was taken every half an hour for 5 minutes to record the behavior of the group (Table 1.3). Additionally, the interindividual distances between all the individuals were measured to ascertain the group-spread area.

Table 1.3 Description of the behaviors for the scan sampling

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

Ad libitum Sampling (Altmann 1974): I used ad libitum sampling in addition to focal animal sampling to record the agonistic behaviors as well as submissive behaviors mentioned above which were used to construct the dominance hierarchy in the group. I also used ad libitum sampling to observe provisioning and the percentage of aggressive encounters as well as role of dominance in such conditions.

PC-MC Sampling (Aureli 1992): Post conflict (PC) data were collected immediately after an aggressive encounter for 5 minutes. Data on the identities of the participants of the interaction, type of interaction, context of the aggression, whether the aggression was renewed among the individuals, and presence of third party intervention were collected. Behavior of both victim and aggressor was recorded for 5 minutes which included inter-individual distances between the victim and aggressor and all the affiliative interactions between them. If there was renewed aggression among the participants, PC data was collected after the encounter was over for the next 5 minutes. If there were multiple participants in an encounter, the most intense or the interaction with longest duration was considered for PC data.

Matched control (MC) samples of 5 minutes were collected from the focal samples which matched these conditions with PC conditions: group behavior, sub-group composition, time of the day. A focal sample which was closest to the date of PC occurrence and which matched the conditions mentioned above was chosen as the MC sample.

Aggressive behaviors in Nicobar long-tailed macaque.
(Top: Chase, Bottom: Open-mouth threat)

Analysis

Dominance calculation: To measure the dominance hierarchy among the males and females of the group using the software DomiCalc developed by Schmid and de Vries (2013). I used normalized David Scores (nDS) to evaluate the dominance rank of each individual. David scores (David 1987, 1988) were appropriate for the study animals as it is a robust measure for repeated measures and for equal number of interactions when calculating hierarchy for individuals in a group.

Social Network Analysis: I used the following metrics to understand the exchange of dyadic interactions in the group among the different individuals:

a) Degree and/or Strength: Degree is the number of connections/edges each individual/node has (Newman 2003). In case of a weighted network, the sum of weights (grooming rate in this case) on the edges for each node is the strength of that node (Barthélemy et al. 2005), In this study, I tested whether high ranking individuals have highest node strength which in other words shows that the dominant individuals play major role in directing the grooming in the group.

b) Eigenvector centrality: Eigenvector centrality calculates individual with highest centrality affecting the overall social network; in this case, it shows the influence of an individual on the overall affiliation and also grooming (Hannemann and Riddle 2005). I employ this metric to ascertain whether dominant individuals are the most central individuals in the affiliation network.

Structure of the thesis

Chapter 1 introduces the study, with the theory of competition and aggression in focus. This is accompanied by the rationale of my study, area of study, study species and group description. **Chapter 2** is the review of literature describing dfferent school-of thoughts that evolved the study and understanding of aggression in non-human primates. It also describes the research which laid path in investigating aggression in Macaca species and on *Macaca fascicularis umbrosus.* This chapter clarifies the rationale behind the study. **Chapter 3** discusses the competition, affiliation, and aggression in females with respect to the distribution of food, provisioning and how dominance hierarchy plays a role in female sociality. It also explains whether male migrations have any effect on hierarchies and aggression in the group. **Chapter 4** explains the competition in males for receptive females in the group and how the dominance hierarchy plays a role among the males in the group. **Chapter 5** describes the conflict resolution and conciliatory tendency in the individuals and how these are affected by sociality and dominance hierarchy. **Chapter 6** summarizes the findings of the study and explains the existing patterns of aggression, affilation and conflict resolution in long-tailed macaques and lays down the roadmap for future research.

Chapter 2:

Review of Literature

Chapter 2

Review of Literature

Aggression

What is aggression? This question has always intrigued the evolutionary psychologists and anthropologists. The function of aggression has been a topic that has found major contradictions and debates. The discussion was based on human aggression which was believed to be innate and instinctive making it hard to control (Ardrey 1967, Lorenz 1967, Morris 1967). The thought was cemented that aggression was a detrimental behavior if not present will wipe out a species. However, the theories were debated and were shown that restraint on aggression or in other words, controlled aggression can be actually beneficial for group members (Goodall 1986, Wrangham and Peterson 1996). This concept of aggression being a disadvantageous behavior was refuted upon finding out that each individual needs to maximize their fitness based on the available resources and the group-living individuals would require a certain level of cohesiveness and cooperation to gain maximum advantage from the group (Dugatkin 1997, van Schaik 1983).

Conflict resolution

Research on aggressive behavior has shown that aggression is not essentially a negative or otherwise known as anti-social interaction. It is the management of conflict that determines the value of aggression in the group. In a group, not all the individuals interact with each other equally, also known as homophily (Lazarsfeld and Merton 1954). This suggests that the benefits individuals get from one another are strikingly different from each other which suggests that there are differentiated relationships among individuals that arise due to differences in the ability to monopolize resources. So in other words, it is competition among individuals influences the interactions and hence the relationship among individuals is based on the competitive regime (Aureli and de Waal 2000). However, escalation of conflict will lead to a detriment in the group cohesion and deprive individuals of its benefits. Thus there has to be a balance between costs and benefits in society and thus the risk of conflict has to be great enough so that valuable relationships are not damaged (de Waal 1996). Hence, the need for conflict resolution is expected. Reconciliation is the most common mechanism of conflict resolution which involves friendly interactions between two former opponents (de Waal and van Roosmalen 1979). Consolation is another mechanism for conflict resolution where a third individual approach and involves in friendly interactions with the loser of the conflict (de Waal and van Roosmalen 1979).

Reconciliation

Reconciliation is an affiliative interaction between two participants of an aggressive encounter (de Waal and van Roosmalen 1979). Although it was not initially accepted as a valid concept with a notion that animals lack such cognition (Aureli and de Waal 2000). However, it has been seen widely that reconciliation is present throughout the non-primate and primate species (Aureli et al. 2002, Cools et al. 2008, Cordoni and Palagi 2008, Fraser and Bugnyar 2011, McFarland and Majolo 2011a, Schino 2001). The major theory which describes the function of reconciliation is 'valuable relationship hypothesis' (de Waal and Aureli 1997, Kappeler and van Schaik 1992). It suggests that reconciliation repairs and restores relationships with group members who are keys for gaining maximum benefits by involving in affiliative interactions more often than others after an aggressive encounter (Cords and Aureli 2000, de Waal 1996, Koski et al. 2007, Koyama 2001, Majolo et al. 2009a, Silk et al. 2003). In summary, reconciliation will be targeted towards the individual who holds the maximum resources. This differentiation is pronounced between the sexes due to anisogamy where the competition for resources is different as proposed by Trivers (1972).

Female Competition

The most dominant hypothesis which has been put forward to explain female competition is Socioecological Theory (Wrangham 1980). The basic premises around which the model finds its underpinnings is the limiting resource for fitness in the females which is food (Wrangham 1980). The females have different needs to increase their fitness as they put effort to give birth and parental investment which has high nutritional demands and thus they compete for food (Trivers 1972). In species of macaques, where female is the non-dispersing sex, females compete for food and their sociality is dependent on the abundance and distribution of food. If the food is distributed evenly then the competition is expected to be low among the females and thus less aggression and less pronounced. In the case of high competition, the food is clumped and not everyone has equal access. Under these conditions, the dominance hierarchy is highly pronounced with high power differentials (known as steepness) among the females to monopolize resources (Gammell et al. 2003, Isbell et al. 1998, Koenig 2002, Sterck et al. 1997). Grooming, which is considered as the social currency is then directed towards the high ranking female to gain maximum access to the food monopolized by the dominant female (Seyfarth 1977). Under these conditions, reconciliation is highly differentiated. However, food is a resource that can be shared and thus the competition is of scramble type with less aggression (Clutton-Brock and Janson 2012, Isbell and Young 2002, Sterck et al. 1997, van Schaik 1989, Wrangham 1980).

Male Competition

The contrasting pattern is seen in the males where females are the dispersing sex and thus giving males fewer opportunities to form highly affiliative relationships among themselves (Dunbar 1991, Hamilton 1964, Kurland 1977, Trivers 1971). The reason for such a pattern is that males compete for females which are non-sharable resources, to maximize their fitness (Trivers 1972, Wrangham 1980). This depends on the number of receptive females in the group and the reliability of the signals advertising receptivity in females (Nunn 1999b, Engelhardt et al. 2005). It has been observed in various species of different lineages of macaques: *silenus-sylvanus*, *fascicularis*, and *sinica-arctoides* (Ostner and Schulke 2014).

Macaca fascicularis umbrosus

Long-tailed macaque (*Macaca fascicularis*), of *fascicularis* lineage, has the second-largest distribution after Rhesus macaques among all the non-human primates (Fooden 1995). The subspecies are usually differentiated into insular and continental (island-dwelling) populations (Fooden 1995). Thierry (2007) classified the species as moderately despotic and placed them in Grade 2 of macaque classification (Thierry 2007). Conflict resolution has been observed in the species (Aureli 1992). However, a lack of subsequent research on different populations under different ecological conditions has been the gap to validate the pattern of conflict resolution. *M. f. umbrosus* is an insular subspecies of long-tailed macaque residents of three islands of Nicobar in Andaman and Nicobar archipelago. The first study that was carried out to understand the distribution and ecology of *M. f. umbrosus* was in 2003 (Umapathy et al. 2003). After this in 2004, a massive tsunami decimated the populations of macaques which was recorded by Sivakumar (2010). However, known for their plasticity the macaques recovered from their population crash (Velankar et al 2016). Under these dynamic ecological conditions, however, there is a gap in the understanding and data on the sociality of these macaques with respect to competitive regimes.

The aim of my study was to provide an understanding of aggression and conflict resolution in the Nicobar long-tailed macaque (*M. f. umbrosus*) and add to the existing knowledge of the species.

Chapter 3:

Food and Females:
Female Social Relationships in Nicobar Long-Tailed Macaques

Chapter 3

Food and Females: Female Social Relationships in Nicobar Long-Tailed Macaques

Introduction

Sociality in females is more pronounced than males as they compete for a sharable resource i.e., food (Wrangham 1980, Trivers 1972). However, the extent of the sociality in females depends on the spatial availability of food resources. The socio-ecological model posits that it is the quality, availability, and distribution of food resources along with the presence of predators which shapes the relationships among females (Clutton-Brock and Janson 2012, Isbell and Young 2002, Sterck et al. 1997 van Schaik 1989, Wrangham 1980). The model suggests that female relationships are dependent on the availability of food and the presence of predators shapes the nature of social systems (Fig. 3.1 A & B).

This model has explained social relationships in macaque society based on the competitive regime prevalent within the group which can be of aggressive contest competition or non-aggressive scramble competition. The competition is of contest type with high rates of aggression if the high-quality food patch size is relative to the size of the group (Heesen et al. 2014). In other words, the potential for contest competition is high when food is monopolizable by a few individuals and less available for others (Isbell et al. 1998, Koenig 2002, Sterck et al. 1997). Here dominance hierarchy plays an important role in understanding the food-related conflict in females. Conditions with high rates of aggression and high power differentials

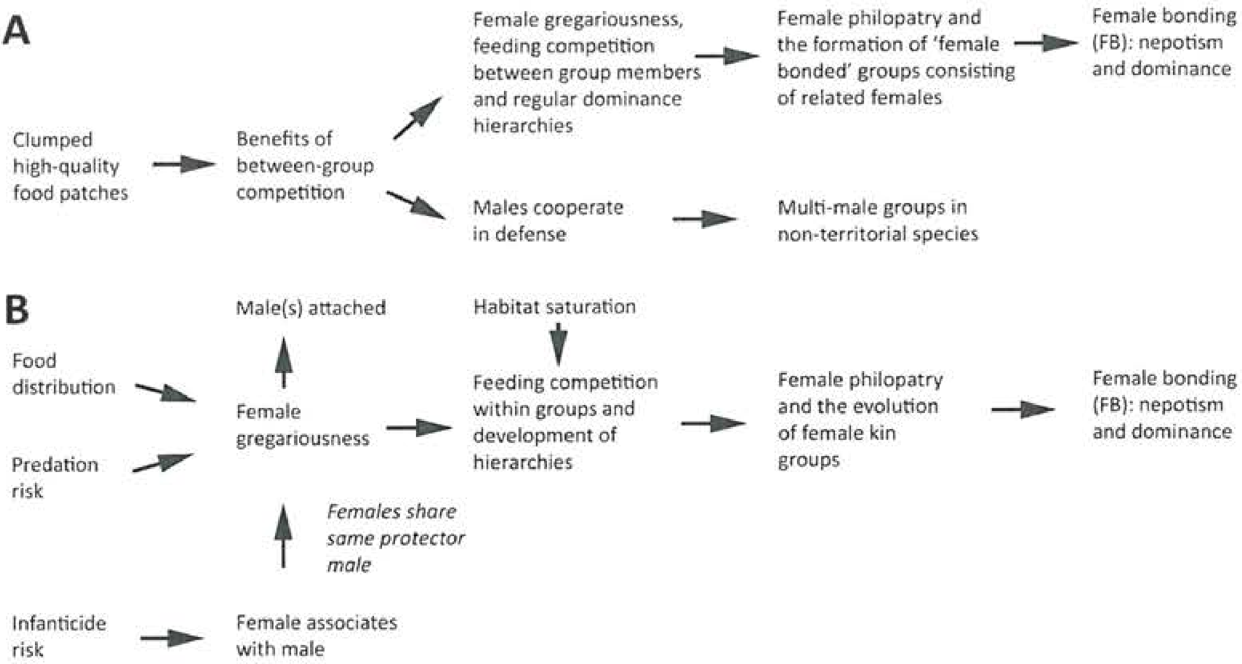


Figure 3.1 A. Flow diagram for evolution of female groups as explained by Wrangham (1980) B. Flow diagram of primate societies incorporating effects of male infanticide and habitat saturation as explained by Sterck et al. 1997 (Figure from Clutton-Brock and Janson 2012)

between similar-ranking individuals giving rise to female philopatry, highly linear dominance relationships and kin-based relations (Heesen et al. 2014, Janson and van Schaik 1988, Koenig 2002, Sterck et al. 1997, van Schaik 1989, Wrangham 1980). It has been observed that provisioning of food leads to high rates of aggression and monopolization of food due to the availability of high-quality in restricted amount for a very short time (Sinha et al. 2005). In bonnet macaque (*M. radiata*), it was seen that provisioning increases the aggression within the group and disrupts the sociality (Sinha et al. 2005). However, if the food is distributed uniformly, the linearity of the dominance hierarchy is substantially low and monopolizability of resources by a dominant female is substantially lower.

Grooming is considered as social currency which is exchanged for benefits from higher-ranking individuals (Seyfarth 1977). Seyfarth (1977) hypothesized that low ranking females direct their grooming towards the high ranking females to gain proximity, for infant

Network Analysis: In-degree and out-degree of affiliation and aggression among the females to find out whether affiliation was distributed according to the rank were measured. To further understand homophily in the group, the eigenvector centrality was determined which identifies how well an individual is connected to a well-connected individual. To further examine whether a high-ranking individual is the most connected individual, Pearson's correlation was performed between the individual eigenvector centrality scores and normalized David's scores. A sociogram was constructed based on the rate of affiliation and dominance rank of an individual for an overview of how affiliation is distributed among the males in the group. The calculations were performed on UCINET version 6 (Borgatti 2002), and NetDraw 2.158 (Borgatti 2002) was used to construct the sociogram.

Provisioning: 5 provisioning events were observed during the course of study. The lack of data did not permit the use of robust statistical methods.

Food-related aggression in the study group.

Results

Linearity and steepness values for the females were 0.040 and 0.52 respectively, which suggested a low monopolization of food resources. Female NI had the highest normalized David score (nDS) and ST had the lowest nDS score.

Table 3.1 Dominance hierarchy in females of the study group TR.

Individuals	Rank Position	David Score (nDS)	Linearity	Steepness
NI	1	3.73	0.4	0.52
TE	2	1.08		
AU	3	0.03		
BY	4	-0.75		
RE	5	-1.6		
ST	6	-2.82		

Affiliation and Aggression: The rate of affiliation 0.275/focal hour (Mean ± SE = 0.279 ± 0.169)was higher than the rate of aggression 0.042/focal hour (Mean ± SE = 0.037 ± 0.064). Affiliation given was dependent on the affliation received (TauKr = 0.538, $P = 0.005$, N = 6, Permutations = 10000). Similarly, aggression given was dependent on aggression received (TauKr = 0.485, $P = 0.013$, N = 6, Permutations = 10000). Affiliation was strongly skewed towards the high ranking individuals (Double-Dekker MQRAP: $R^2 = 0.841$, $P < 0.05$, N = 29, perm = 2000).

Social Network: High-ranking females did not receive or give more affiliation than the subordinates (Table 3.2). Similarly, they did not receive or give higher rates of aggression (Table 3.2). Eigenvector centrality values for both aggression and affiliation did not correspond to high-ranking females showing that they did not impart higher tolerance (Table 3.2). The sociograms also depict a similar pattern (Fig 3.4).

Table 3.2 Social network metrics for females in the study group TR.

ID	Normalized Outdegree	Normalized Indegree	Eigenvector Centrality
		Aggression	
NI	0.318	0.046	0.619
TE	0.066	0.217	0.341
AU	0.145	0.145	0.389
BY	0.020	0.000	0.030
RE	0.079	0.246	0.577
ST	0.072	0.046	0.121
		Affiliation	
NI	0.355	0.300	0.534
TE	0.286	0.202	0.332
AU	0.091	0.217	0.250
BY	0.361	0.296	0.421
RE	0.348	0.486	0.537
ST	0.237	0.176	0.277

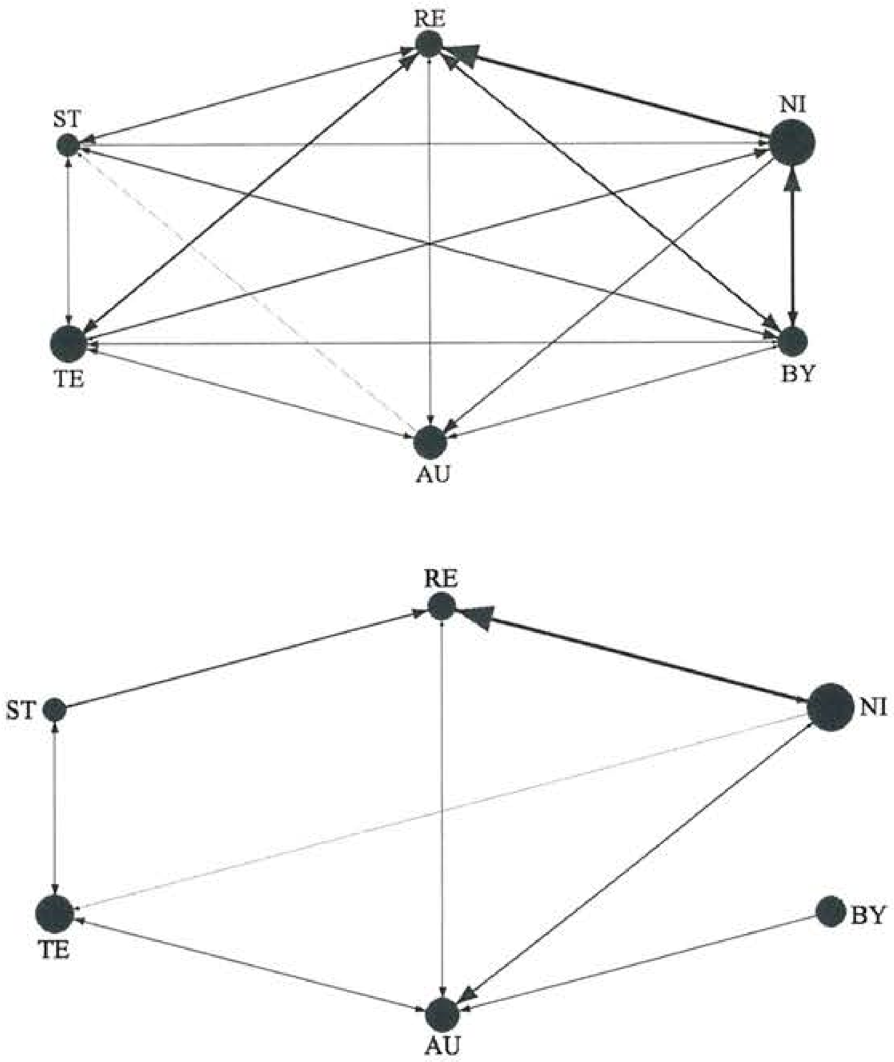


Figure 3.4 Sociogram depicting affiliation and aggression among females in the study group TR. Arrowheads are proportionate to tie strength (proximity). Sizes of the nodes are proportionate to the ascending order of rank position, with the highest-ranking individual represented by the largest node.

Grooming and Proximity: Grooming rate and proximity did not show any correlation (TauKr = 0.022, P = 0.141, N = 6, Permutations = 10000). In addition, the high-ranking females did not have higher eigenvector centrality values for proximity (Table 3.3). This shows that the dominant females did not exchange tolerance in exchange for grooming which was visible in the sociogram (Fig 3.5).

Table 3.3. Eigenvector centrality values for proximity among the females in the study group TR.

Rank	Individual	Eigenvector centrality
1	NI	0.435
2	TE	0.420
3	AU	0.437
4	BY	0.374
5	RE	0.425
6	ST	0.350

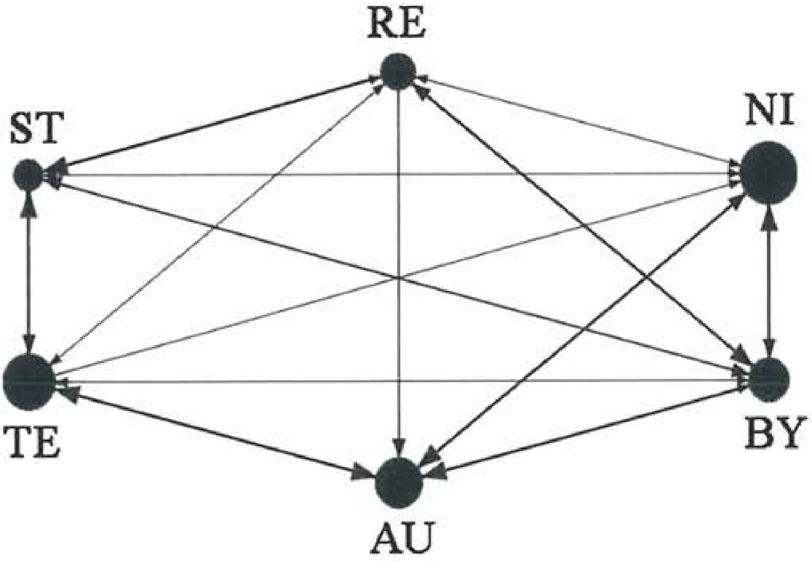


Figure 3.5 Sociogram for proximity network in female-female dyads of the study group TR. Arrowheads are proportionate to tie strength (proximity). Sizes of the nodes are proportionate to the ascending order of rank position, with the highest-ranking individual represented by the largest node.

Provisioning: In all the 5 provisioning events recorded, NI monopolized the highly valuable food available for a very short time as it was observed that NI gained the access to food all the five times and aggressively chased away all the females from the site of provisioning.

Discussion

M. f. umbrosus females in the group have less linear dominance hierarchy and low hierarchical steepness. The rate of aggression as well affiliation given is dependent on the amount of affiliation received which suggests that the females keep an account on the interactions they participate in. The grooming being the currency in social trade was not being exchanged for social tolerance although there was strong evidence of affiliation towards the high ranking females (Henzi and Barrett 1999). The high ranking females did not play a central role in the distribution of affiliation as it was found that neither the indegree nor the outdegree of affiliation or aggression was highest for the dominant females. Additionally, the top-ranking females did not have the highest eigenvector values which strengthen the fact that dominant females are not responsible for the distribution of either affiliation or aggression in the group.

Distribution of food shapes the relationship amongst the females by shaping the competitive regime in the group (Isbell and Young 2002, Wrangham 1980). This competition, on the other hand, is dependent on the resource holding potential of the dominant individual measured usually as dominance steepness (Gammell et al. 2003). As steepness is influenced by the local resource availability, it may vary among populations (Macdonald 2013). As per the socioecological theory, dominance hierarchies are steeper when food sources are clumped and thus easily monopolizable (Isbell and Young 2002). In *M. f. umbrosus* the steepness values are much lower (0.52) than previously found in *M. fascicularis* (0.98 and 0.85 in Balasubramaniam et al. 2012, Butovskaya et al. 1995, respectively). Hence, it is possible that tolerance near food resources is not a valuable commodity. Thus, low hierarchical steepness might account for the lack of a correlation between grooming rates and tolerance.

Besides, Seyfarth (1977) proposed grooming is usually directed towards the high-ranking female to gain access to food. This hypothesis has found support in the biological market principle where it is presumed that the grooming is used as social currency to exchange services from dominant individuals, for example, support in fights, access to infant and access to food (Henzi and Barrett 1999; Noë and Hammerstein 1994; Schino 2001). Seyfarth Model has been an influential model in explaining the directionality of grooming although it lacks a general consistency across different ecological conditions as seen in *M. fascicularis* (Gumert 2010). Although, dominance steepness values were not calculated in two other studies focused on rank-related grooming patterns in *M. fascicularis* (Gumert 2010, Wheatley 1999). Gumert (2010) explained the moderate role played by rank in the grooming network. Thierry (2007) classified macaques into four grades (Grade 1 to 4 in increasing order of tolerance) and considered *M. fascicularis* a Grade 2 species, which corresponds to a weakly despotic society. Gumert (2010) found partial evidence for rank-related grooming among individuals. The observations corresponded to Thierry's (2007) classification of long-tailed macaques (*Macaca fascicularis umbrosus*) as weakly despotic species which is hypothesized to exhibit moderate rank-related grooming. However in *M. f. umbrosus,* I found that rank-biased patterns of grooming can occur in *M. fascicularis* even when the conditions are not despotic due to the availability of food. Under these circumstances, grooming towards the dominant individuals may impart other benefits such as infant handling which might increase the survivability of the offsprings. This seems to be useful for a population that is recovering from a drastic decline after the 2004 tsunami (Velankar et al. 2016).

Top: An event of grooming in the study group,
Bottom: Dominant female NI feeding on the widely distributed mango

The inconsistency in rank dependent interactions was also seen in the social network analysis. The high-ranking females were not the key players in the social market place as they were not found to be the most central in the distribution of both aggression and affiliation. Thus, my study adds to the existing information on grooming patterns in *M. f. umbrosus* although it was restricted to a single group, yet the findings establish the baseline pattern of affiliation and aggression among the females.

Chapter 4:

Mates and Males:
Male Social Relationships in Nicobar Long-Tailed Macaques

Chapter 4

Mates and Males: Male Social Relationships in Nicobar Long-Tailed Macaques

---

Introduction

Social systems in primates are dependent on the interaction between the reproductive strategies of males and females (Wrangham 1980). The socioecological theory has been influential in explaining these social systems based on the availability of resources. Females compete for food and the distribution of food shapes the competition among the females which ultimately determines their reproductive success (Wrangham 1980). On the other hand, males compete for access to mating and availability of sexually-receptive females that influence the competition (Wrangham 1980). The strategies differ for both the sexes to ensure maximum fitness, in which males try to mate with as many females and thus compete with each other to gain maximum access to females. Thus, the competitive regime differs between the sexes based on the shareability of the resources, as contest competition is prevalent mostly in males as mates are non-sharable in nature (Kodric-Brown and Brown 1987). The competition between males depends on two conditions viz., male co-residency and synchronicity of female fertile phases. Male co-residency is useful for defense against group take over, territory defense, between-group competition and forming coalitions to interfere with mating against high-ranking males, which sometimes lead to rank-changing coalitions (Ostner and Schulke 2014).

The degree of mate competition in males also depends on the number of fertile females available at a time in the group, which is determined by the synchronicity of the estrous cycle among the females and the reliability of fertility signals in the species (Nunn 1999b). In a seasonally breeding macaque, for example, *M. radiata*, females synchronize their estrous phases hence, the potential for contest competition is low and thus, it is difficult for the dominant male to monopolize the mating share and thus hierarchy is more relaxed (Singh et al. 2011). The other determining factor for mate competition is the reliability of the fertility signals by the females of the species which has been described by the graded-signal hypothesis (Nunn 1999b). The hypothesis suggests that the degree of fertility signals in the females is a probabilistic indicator of the stage of fertility. Swelling in the anogenital region has been found to be a signal of fertility and the degree of swelling determines the stage of fertility (Nunn 1999b). However, the sexual swelling has not been found to be reliable to assess fertility in females, for example, in species like Assamese macaque (*M. assamensis*) and long-tailed macaque (*M. fascicularis*) (Engelhardt et al. 2005, Fürtbauer et al. 2011).

Dominant female NI exhibiting sexual swelling.

Interestingly, macaque species show a wide variation in male-male relationships among lineages (Ostner and Schulke 2010). Phylogenetically, macaques can be classified into three distinct lineages: *Silenus-sylvanus* lineage, *fascicularis* lineage and *sinica-arctoides* lineage (Thierry 2007). The male relationships vary significantly among the lineages.

Relationship among the specific males is achieved by stable, reciprocated and equitable interactions and when these relations are well differentiated, they are termed as bonds (Silk

1992). This choosing of favorable individuals for specific interaction is known as homophily (Lazarsfeld and Merton 1954). These bonds are well-differentiated and do not depend on kin relatedness (Carnes et al. 2011, Nunn 1999b, Ostner and Schulke 2014, Willems et al. 2013). Studies on different species have shown variation in the affiliative bonding among different lineages (Ostner and Schulke 2014). The underlying principle of the variation in bonding among males is the degree of synchronicity in fertile phases of females and the reliability of sexual swellings, which determines the availability of females and shapes the competition among males (Carnes et al. 2011, Nunn 1999b, Ostner and Schulke 2014). Species of *silenus-sylvanus* lineage except for Barbary macaques (*M. sylvanus*) that show strong seasonal peaks of reproductive availability of females and they exhibit reliable fertility signals (Berghänel et al. 2010, 2011, Kaumanns and Singh 2012, Krishna et al. 2006, Kumara et al. 2010, Thierry 2007, Young et al. 2013b). The males in such situations do not form differentiated bonds among themselves. On the other hand, species in *sinica-arctoides* lineage show no seasonality or reliable fertility signals and thus differentiated as well as equitable male bonds (Kaumanns and Singh 2012, Krishna et al. 2006, Singh et al. 2010, Thierry 2007). Species of *fascicularis* lineage shows moderate seasonality but less reliable fertility signals (Dubuc et al. 2009, Engelhardt et al. 2005, O'Neill et al. 2004, Maestripieri and Roney 2005). In these species, it has been found that the males will interact differentially with other males although these relations are not found to be equitable (Ostner and Schulke 2014). Thus, it is interesting to understand the various reproductive strategies employed by *M. f. umbrosus* (Pal 2018). The low synchronicity in the fertile phases was recorded in long-tailed macaque females at Great Nicobar Island i.e., there was a specific number of receptive females at a particular season (Pal 2018). Although females showed fertility signals, they were not reliable (Pal 2018). Hence, the patterns of reproductive behavior in the subspecies followed the species-level pattern, which led me to predict that:

(a) males will show affiliation among themselves although the affiliation will not be reciprocated and equitable.

(b) the affiliative interactions will not be differentiated i.e, some individuals will not be more favored for affiliation.

(c) dominance hierarchy will be moderately linear with moderate steepness values with a moderate rate of aggression and affiliation.

I further explored the data on a group of Nicobar long-tailed macaque (TR group at Great Nicobar Island) to verify these predictions. During the study, a takeover event was observed and the effects of such migration were evaluated on the hierarchy of the group.

Analysis

A total of 41 affiliative interactions and 48 aggressive/submissive interactions among the males were recorded in the focal animal sampling. I calculated the overall rate of affiliation (dividing the total number of affiliative interactions per focal hour), mean affiliation among males (total affiliation episodes among males divided by the number of males), rate of aggression considering the same residency period for the 5 males as they stayed in the group throughout the study period. Data are reported as a mean and standard error unless stated otherwise.

I used 85 aggressive encounters from *ad libitum* and focal samples to construct a dominance hierarchy structure using normalized David's score (nDS) values with DomiCalc software (de Vries et al. 2006, Schmid and de Vries 2013). I calculated hierarchical linearity using DomiCalc software using unbiased Landau's Index. I also calculated the steepness of the hierarchy using linear regression with the rank position of each individual as an independent variable and David scores as a dependent variable. The analysis was performed using "compete" package version 0.1 (Curley 2017) on R 3.4.3 (R Core Team, 2017).

To investigate whether the rate of affiliation given was dependent on the rate of affiliation received, I performed Kendall's TauKr matrix correlation between the matrices of affiliation given and affiliation received (Hemelrijk 1990, Hemelrijk et al. 2003, Hemelrijk et al. 2005, Hemelrijk et al. 2008).

Rank-related Differentiation: To check whether the affiliation distribution was differentiated and skewed towards the high-ranking individuals, I performed double Dekker semi-partialing multiple regression quadratic assignment procedure (MRQAP) which corrects for the autocorrelations between the variables *viz.*, rank and affiliation (Dekker et al. 2007). I performed linear mixed model (LMM) to test whether the rate of affiliation was biased towards the rank or identities of the individuals. Two sets of the model were run: (a) full model with identities of actor and receiver, as well as of dyad considered as random effects with affiliation rate and normalized David's score values being the dependent variable and the response variable respectively. (b) A null model considering only random effects to see whether affiliation was influenced by random effects only. I compared the full model with a null model using ANOVA to explain which model fits better to explain grooming distribution. To estimate the effect size, regression coefficient values were used with 95% confidence intervals. LMM was performed using the package "lme4" version 1.1-21 (Bates et al. 2015) on R 3.4.3.

Network Analysis: Affiliation in a group can be better understood with social networking analysis which has proven to be an important tool to understand interactions and relationships (Barrett et al. 2012, Brent et al. 2011, Croft et al. 2008, Flack et al. 2006; Kanngiesser et al. 2011, Sueur et al. 2011a, Whitehead 2008, Xia et al. 2012). I performed a social network analysis of affiliative interactions and calculated the degree or strength and eigenvector centrality to determine relationships among the individuals in a group.

I used SOCPROG 2.7 (Whitehead 2007) for the calculation of network measures and NetDraw 2.158 (Borgatti 2002) to visualize the grooming networks with the node (point denoting each individual) sizes representing ascending rank order. Thickness of edge (connections of the nodes) represents the strength of ties (total bouts of grooming).

Male Migration: I described the social conditions that changed after the immigration event of adult male FY was observed in the group, which overthrew the reigning dominant male. The difference in mating rates before and after the takeover was analyzed using the paired t-test.

Results

Affiliation and Rank: The mean affiliation rate was 0.946 ± 0.718_{SE}/h (N = 5) and the rate of affiliation given was related to the rate of affiliation received (Linear regression: R^2 = 0.882, P = 0.018, N = 41), although, the rates were not equitable in nature (Matrix correlations: Mantel's Z = 2.011, P = 0.079, N= 5, perm = 10000).

There were moderate linearity and steepness values among the males with two individuals having proportionately more wins than losses (FY and KU) (Table 4.1).

Table 4.1 Hierarchy in the males of study group TR

Individuals	Rank Position	Normalized David Score (nDS)	Linearity	Steepness
FY	1	3	0.65	0.79
KU	2	0.98		
BE	3	-0.31		
HK	4	-0.94		
AI	5	-2.73		

Affiliation was not favored towards the high-ranking individuals thus showing a lack of differentiated interactions based on rank (Double-Dekker MQRAP: R^2 = 0.002, P = 0.40, N = 40, perm= 2000). Rank (nDS) did not influence the affiliation (Table 4.2).

Table 4.2 A linear mixed model to test whether affiliative interaction was dependent on rank or identities of the individual (random effects)

	Estimate ± Standard Error	T	P
Intercept	0.246 ± 0.078	3.17	0.001
Rank (nDS)	-0.004 ± 0.015	-0.317	0.751
Null model vs. Full Model :	$\chi^2 = 0.098$, p = 0.755, df = 5		

The high-ranking male did not have the highest values for strength and eigenvector centrality showing that affiliation was not biased towards the high-ranking individuals (Table 4.3) which were also depicted in the sociogram (Fig 4.1). It shows that the dominant males did not play a significant role in the distribution of aggression in the group.

Table 4.3 Eigenvector centrality values for male affiliation network in the study group

Rank	ID	Strength	Eigenvector Centrality
1	FY	0.27	0.132
2	KU	1.35	0.551
3	BE	1.11	0.463
4	HK	1.66	0.632
5	AI	0.53	0.255

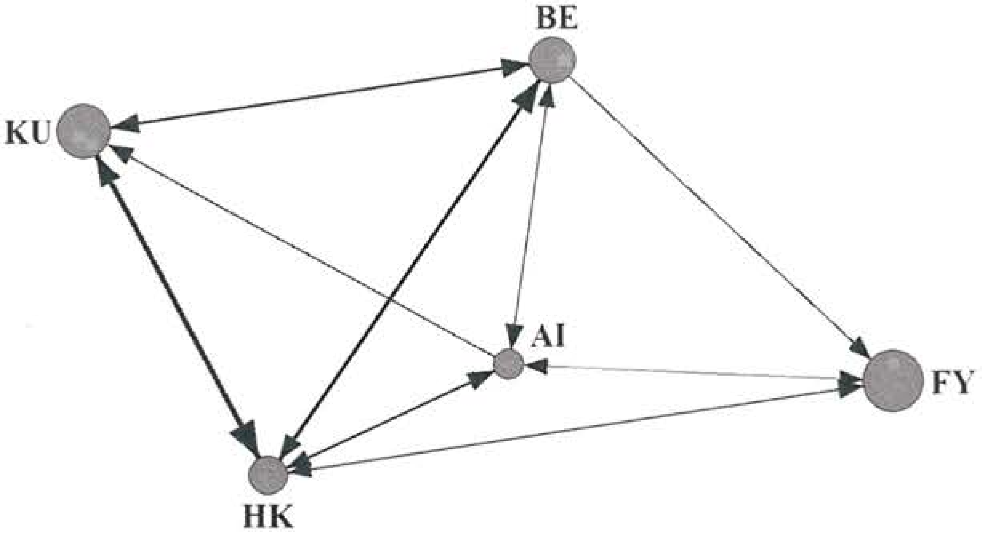


Figure 4.1 Affiliation network for the males in the study group TR. The size of the nodes is proportional to the rank of the individual. Arrowheads and width of the edges (the connection between the nodes) are proportional to the rate of affiliation among the nodes.

There was no correlation between the nDS values and eigenvector centrality values (Pearson's correlation coefficient = -0.259, $P = 0.643$, N = 5).

Aggression and Rank: The rate of aggression was 0.993 ± 0.791$_{\text{SE}}$/h. The percentage of high intensity aggression (chase and charge) (Percentage = 14.583 %, N = 7) and contact aggression (grab and bite) (Percentage = 4.167 %, N = 2) were low. Rate of aggression was exchanged among the individuals (Matrix correlations: TauKr = 0.308, $P = 0.049$, N = 5, perm = 10000). However, there was no relation between rate of aggression given and rank of the individual (Double-Dekker MQRAP: $R^2 = 0.041$, $P = 0.0153$, N = 20, perm = 2000). Rank had no influence on strength or eigenvector centrality of aggression in the group explaining that high ranking individuals do not hold important positions in the distribution of aggression among the males in the group (Table 4.4 and Fig 4.2)

Table 4.4 Eigenvector centrality values for male aggression network in the study group

Rank	ID	Strength	Eigenvector Centrality
1	FY	0.16	0.16
2	KU	1.58	1.83
3	BE	0.83	1.15
4	HK	0.74	0.96
5	AI	1.48	1.84

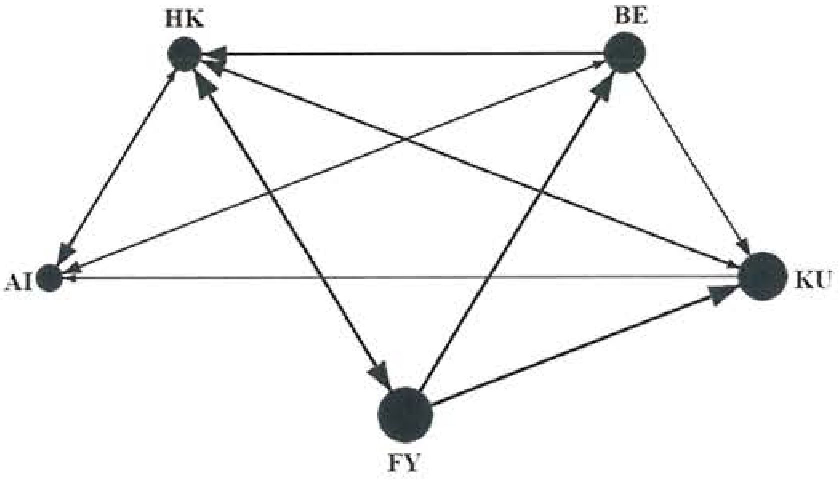


Figure 4.2 Aggression network for the males in the study group TR. The size of the nodes is proportional to the rank of the individual. Arrowheads and width of the edges (the connection between the nodes) are proportional to the rate of aggression between the nodes.

Male Migration: The outer group male, later named as FY replaced the alpha male of the group RY on 14 October 2013 thus changing over the rank. The changeover was violent, and the former alpha male RY sustained severe injuries and died on March 2014. Subsequently, the mating rates changed significantly from pre-takeover to post-takeover period ($t = 4.88$, df $=54$, $P < 0.001$). It was observed that FY participated in 77.78 % of mating whereas RY was not observed to take part in any mating. The rank changeover event was eventually followed by males emigrating from the group, and by November 2015 all the males emigrated from the group and the group was single-male multi-female with FY monopolizing all the mating.

Discussion

In Nicobar long-tailed macaque, the rate of affiliation, although being high, was not reciprocated equitably among the individuals. The rate of affiliation given was dependent on the rate of affiliation received but it was independent of the rank of the individuals. Hinde (1976) mentions that - if there is a sense of recognition among the individuals, then, every interaction will influence how future interactions may take place between the individuals. In other words, preferring specific individuals for specific interactions (homophily) is common among the individuals (Lazarsfeld and Merton 1954). The rate of affiliation given by the males was influenced by the rate at which they received affiliation. This showed that there is a sense of recognition among the individuals towards the affiliation received. However, this differentiation was not based on the hierarchical status of the individuals. Both aggression and affiliation rates were independent of the rank of the individuals.

The recognition of individuals was not dependent on their ranks but identities. This result was further substantiated when the high-ranking males did not take the central positions in the affiliation network or did not give and receive higher affiliation. Instead, centrality values were slightly skewed towards the lower-ranking males. Thus, rank-related social bonding and differentiated relationships based on rank among the males in the group was not found.

Adult male KU touching genital of dominant male FY as an affiliative gesture.

Differentiation of relationships and bond formation is perhaps the unit of sociality in primates which are reciprocal, equitable and stable through time (Silk 2002). The strongest bonds are the ones that follow all the conditions and there will be no bond if there is no differentiation. There was a differentiation among the males regarding the identities of the individuals as some of the relations were stronger than the others in Nicobar long-tailed macaque. However, there was no equity in the payoffs between the interactions in these relations. In the study population, the females show low synchronicity although they have mild peaks and lack reliable fertility signals. Therefore, under these circumstances, the contest potential is high as it is easier to monopolize the females (Pal 2018). This resembles the patterns found in the *fascicularis* group (Dubuc et al. 2009, Engelhardt et al. 2005, O'Neill et al. 2004, Maestripieri and Roney 2005). Under such circumstances, it has been seen that males have frequent affiliative interactions and coalitions; however, no differentiation or equitability has been found (Hill 1994). The affiliation rate was high 0.946 ± 0.718_{SE}/h (N = 5) and was higher than the grooming rates found in males in the species of the same lineage *Macaca fuscata* (0.38 ± 0.20_{SD}) (Horiuchi 2005) and *M. cyclopis* (0.05 ±

0.04_{SD}) (Lin et al. 2008). Males favor certain individuals for interactions in Nicobar long-tailed macaque. *Fascicularis* group species are expected to show male-male bonding which will be intermediate to the silenus-sylvanus group and sinica-arctoides group (Ostner and Schulke 2014), where the former does not form strong affiliative bonds because of high synchronicity in the fertile phases but the latter group has been seen to maintain strong affiliative bonds due to the low synchronicity (Ostner and Schulke 2014). This is in congruence with the moderate linearity (0.65) and steepness values (0.79) which suggests that the hierarchy is not strong and opportunities for affiliation are high, as the high rate of affiliation found in our study ($0.946 \pm 0.718_{SE}$/h).

The lack of seasonality in the females and absence of reliable fertility signal also led to high rates of aggression in the group ($0.993 \pm 0.791_{SE}$/h) and the rate of aggression received was matched with the rate of aggression given. However, most of the aggression was not directed from the high-ranking individual towards the low ranking individual and the highest-ranking male FY was not found to be the most aggressive individual. This may be because of the fact that the group size is the smallest in the area and the group faces the average number of between-group encounters ($0.47 \pm 0.37_{SD}$) (Pal et al. 2018). In such a situation, it may be imperative for the top-ranking male to maintain affiliation and less aggression with the males of the group in order to guard the males from extra-group mating (Girard-Buttoz et al. 2014).

Sudden immigration of outer males changes the social organization and has drastic changes in the group (Kumar et al. 2001, Singh et al. 2006). It was seen in the study group that when an immigrating male FY took over the highest rank in the group, it changed the dominance hierarchy of the group and acquired the monopoly of mating in the group, whereas the overthrown male RY lost his share of the most critical resource for fitness as a male.

In conclusion, the study explains the relationship among males in a group of Nicobar long-tailed macaques and provides an understanding of the social and resource constraints that underpin these relations. The results are in partial agreement with the predictions as there was a differentiation in the interactions, but they were not balanced; which is consistent with the previously found results in the *fascicularis* group of macaques (Ostner and Schulke 2014). Perhaps, it seems that the pattern of affiliation is conserved among different classes of macaques and is influenced by within-group competition.

THE BEST FRIENDSHIPS ARE THOSE THAT HAVE SURVIVED THE TEST OF TIME, CONFLICT AND CHANGE.

Karen Salmansohn

Chapter 5:

Conflict Resolution in Nicobar Long-Tailed Macaques

Chapter 5

Conflict Resolution in Nicobar Long-Tailed macaques

Introduction

When the competition for food or mate is of contest type (due to lack of resources or clumping of resources) the interactions among the individuals are aggressive to maximize the monopolization of resources (Trivers 1972). This leads to physical aggression which is costly to the individuals involved in fights as they face physical injury, renewed aggression, high anxiety and damage to social relationships (Aureli et al. 2002, McFarland and Majolo 2011a, b). Hence to reduce these costs, mechanisms exist among the individuals to engage in behavior which diffuses the tension between the individuals and restores relationships. Together these mechanisms are broadly termed as conflict resolution (de Waal and van Roosmalen 1979, Aureli et al. 2002).

Conflict resolution through affiliation is also known as 'reconciliation' (de Waal and van Roosmalen 1979). Reconciliation is any friendly interaction within minutes after a fight between the former opponents involved in the fight. It has now been observed among various taxa to resolve conflicts among the opponents and various hypotheses have been put forward to explain the role of reconciliation. Reconciliation reduces the stress after an aggressive encounter, stabilizes the heart rate and reduces self-directed behavior which is an indicator of anxiety (Aureli and Smucny 2000, Smucny et al. 1997). In addition, reconciliation patterns are variable and differentiated among the individuals in the group.

Top: Individuals fighting for food,
Bottom: Reconciliation (embrace) among former opponents

One major hypothesis explaining this variation in reconciliation is valuable-relationship hypothesis which suggests that reconciliation patterns will be based on the quality of relationships in the group (Aureli et al. 1989, de Waal and Yoshihara 1983, Kappeler and van Schaik 1992). The basis of this value to every other individual they interact with. This was furthered by Cords and Aureli (2000) who suggested that the quality of any relationships is based on the value it holds for the partners with clear fitness returns, compatibility among the partners and security in the relationship. The predictions of the hypothesis have been observed in both primate and non-primate species (Aureli et al. 2002, Cools et al. 2008, Cordoni and Palagi 2008, Fraser and Bugnyar 2011, McFarland and Majolo 2011a, Schino 2000).

The strength of relationships have been usually tested through the grooming interactions among the individuals in a dyad as grooming is considered the most important social interaction as alleviates stress (Aureli et al. 1999, Schino et al. 1988, Wittig et al. 2008), maintains hygiene (Hutchins and Barash 1976, Tanaka and Takefushi 1993, Zamma 2002) and acts as a social currency (Barrett et al. 1999). It has been postulated that other social measures like the directionality of grooming, dominance hierarchy, kin relations, and sociality can have a significant impact on reconciliation among dyads which is usually calculated as a conciliatory tendency (CT) (Arnold and Aureli 2010, de la O et al. 2013). CT is the propensity of individuals to involve in a friendly interaction after a fight to reconcile among them which differs between and within dyads, groups, and species (Thierry et al. 2008, Veenema et al. 1994).

Studies on conflict resolution in *M. fascicularis* have mostly been carried out in the captive environments except for a study by Aureli (1992). He found that reconciliation and redirection of aggression were major post-conflict behaviors in the species and reconciliation was considerably less when the aggressive conflict was about the food. This was the first study that explained the patterns of conflict resolution in the wild long-tailed macaque. The difference in the competitive regimes has set differences in the way males and females to interact with each other. Females compete over food which is sharable in nature and hence the competition is lower than that of males who compete for non-sharable resource i.e., mates (Trivers 1972). Hence, social relationships are stronger among females than in males. Hence according to the valuable relationship hypothesis females are thus expected to have a higher conciliatory tendency than males.

Aureli et al. (2002) found that the pattern of conflict resolution in captive long-tailed macaques was similar to the wild populations. This also assisted Thierry (2007) to classify long-tailed macaque in Grade 2 which suggests that they are less tolerant. If socioecological conditions influence the competitive regime in males and females, then the difference in the reconciliation between the sexes is expected. In this chapter, I discuss the basic patterns of aggression and the socioecological conditions that influence the aggression, the patterns of conflict resolution which would provide validity to conflict resolution patterns under different conditions, the social conditions under which reconciliation operates and compared it between the sexes.

Analysis

I enumerated the proportion of each individual who participated in aggression as a victim and aggressor. I then performed a Pearson's correlation test to find the relation between Normalised David Scores (nDS) and aggression proportion to understand whether high ranking individuals initiated more aggression. I performed a Generalised Linear Model to evaluate whether the context, type of aggression (contact and non-contact) and kind of dyad (Male-Male, Male-Female, Female-Male, and Female-Female) had an impact on the PC affiliation.

Composite Sociality Index (CSI): I computed Composite Sociality Index for each dyad of the group, based on Silk et al. (2006) equation with a modification where I used affiliation frequency instead of approach frequency to understand overall sociality based of affiliation and not based approach alone.

$$dCSI = \frac{\frac{G_{ij}}{G} + \frac{A_{ij}}{A}}{2}$$

where G_{ij} and A_{ij} are frequencies of grooming and affiliation for the dyad comprising of *i* and *j* while *G* and *A* are the total frequency of grooming and affiliation for all the dyads. The greater the value of *dCSI*, the stronger is the relationship between individuals *i* and *j*.

Directional Consistency Index (DCI): To measure asymmetry in the distribution of affiliation among the members of a dyad, I calculated DCI and approaching after van Hooff and Wensing (1987):

$$DCI = \frac{H - L}{H + L}$$

where H is the number for times affiliation was directed towards the more favoured individual and L is the number of time affiliation was directed towards the less favoured individual in a dyad.

Conciliatory Tendency (CT): I paired the MC samples with the PC samples based on the criterion mentioned above. I calculated the number of attracted pairs (pairs of samples where affiliation was solely found in PC or found in PC earlier than it was found in MC), dispersed pairs (pairs of samples where affiliation was found solely in MC or found earlier in MC than in PC) and neutral pairs (where no affiliation was found in either PC or MC). I then used the formula by Veenema et al. (1994) to calculate the conciliatory tendency of each dyad and for the overall group:

$$CT = \frac{Attracted\ Pairs - Dispersed\ Pairs}{Attracted\ Pairs + Dispersed\ Pairs + Neutral\ Pairs}$$

I used GEE (Generalised Estimation Equation) which is an extension of Generalised Linear Model dealing with correlated response data which are produced by repeated measures. The method used quasi-likelihood estimation instead of the Akaike Information Criterion (AIC) values (Cui 2007, Pan 2001). The lower values of quasi-likelihood under the independence model criterion (QICC) for a particular model suggest the best fitting model. I used GEE to investigate whether the rank difference (absolute difference in the Normalised David Score between the members of a dyad), dCSI and DCI influenced the CT among the dyads.

Results

A total of 83 PC samples were collected and it was found that the proportion of aggressor and victim roles differed for females and males. NI had the highest aggressor to victim ratio among the females and FY had the highest ratio among males (Table 5.1).

Table 5.1 Aggression proportion and normalized David's Score Values (nDS) among the individuals of the study group TR

		nDS	Aggression Proportion
Females			
	NI	3.73	0.736
	TE	1.08	0.333
	AU	0.03	0.382
	BY	- 0.75	0.25
	RE	- 1.6	0.25
	ST	- 2.82	0
Males			
	FY	3	0.963
	KU	0.98	0.167
	BE	- 0.31	0.2
	HK	- 0.94	0
	AI	- 2.73	0.5

There was a significant relation between the nDS and proportion of aggression in females (R = 0.959, $P = 0.002$, N = 6) suggesting that high ranking individuals initiated more aggression in females. However, in case of males this relationship was not present (R = 0.500, $P = 0.391$, N = 5).

PC Affiliation: 4 models were run to find what influences the PC affiliation and it was found that combination of aggression type and the type of dyad (male: male, female: female, male: female, female: male) (Table 5.2). Parameter estimates for the best model results showed that for intercept (female to female aggression dyad) propensity for PC affiliation decreased (Table 3). Aggression type when increases from non-contact to contact type increase the tendency for PC affiliation in the group (Table 5.3). In addition, for a male to female aggression dyad, PC affiliation increased (Table 5.3).

Table 5.2 The best candidate models for PC affiliation

Model	df	AIC	ΔAIC	Model Weight
Agg + Type	5	97.9	0.0	0.66
Agg + Type + Context	11	100.2	2.33	0.21
Agg	2	101.1	3.25	0.13
Agg + Type + Dyad	46	136.1	38.2	0.00

Agg = Aggression type (contact and non-contact), Type = Type of dyad (Male : Male, Female : Female, Female : Male, Male : Female), Context = Context of fight, Dyad = Dyad identity (unique dyad with aggressor and victim pair)

Table 5.3 Parameters estimates for the best model

Parameter	Estimate	Std. Error	Walds χ^2	P
Intercept	-1.01	0.38	6.92	<0.01*
Agg	1.74	0.63	7.72	<0.01*
Female to Male	-0.56	0.82	0.46	0.49
Male to Female	-1.47	0.74	3.90	0.048*
Male to Male	1.14	0.76	2.23	0.13

Agg = Aggression type (contact and non-contact)

Conciliatory tendency: Overall conciliatory tendency for the group was found to be 5.6. For males, the value of CT (30) was lower than the CT value of females (76). GEE results show that the model with the cumulative effect of DIC and DNDS was the best model which explained conciliatory tendency among the males (Table 5.4). Parameters estimate shows that DIC influenced the conciliatory tendency among the males (Table 5.5)

Table 5.4 The 4 best candidate models for the conciliatory tendency among the males

Model	K	QIC	ΔQIC	Weight
CCT ~ DIC + DNDS	3	16.0	0	0.356
CCT ~ DCSI + DNDS	3	16.5	0.47	0.281
CCT ~ DIC + DCSI	3	17.1	1.07	0.208
CCT ~ DIC + DCSI + DNDS	4	17.7	1.67	0.155

CCT= Corrected Conciliatory Tendency, DIC = Directional Consistency Index, DNDS = Differences among normalised David's Scores, DCSI = Dyadic Composite Sociality Index

Table 5.5 Parameter estimates for the best model influencing CCT among males

Parameter	Estimate	Std. Error	Walds χ^2	P
Intercept	-0.20	0.07	0.08	0.774
DIC	0.93	0.44	4.52	0.034*
dNDS	-0.01	0.02	0.36	0.549

DIC = Directional Consistency Index, DNDS = Differences among normalised David's Scores

In females, the best model with DIC had the lowest QIC value (Table 5.6) although none of the parameters significantly influence the conciliatory tendency (CT) among the females in the group.

Table 5.6 The 4 best candidate models for the conciliatory tendency among the males

Model	K	QIC	ΔQIC	Weight
CCT~ DIC	2	17.8	0.00	0.380
CCT ~ DCSI	2	18.1	0.32	0.325
CCT ~ DNDS	2	19.7	1.83	0.152
CCT~DII+DNDS	3	20.8	2.97	0.086

CCT= Corrected Conciliatory Tendency, DIC = Directional Consistency Index, DNDS = Differences among normalised David's Scores, DCSI = Dyadic Composite Sociality Index

Discussion

The study explains why the individuals in a group of wild Nicobar long-tailed macaque involve aggression when it is detrimental to their social living. The study provides evidence of reconciliation in Nicobar long-tailed macaque. Consolation was not found in the study group, where a third individual usually ameliorates the anxious situation by providing affiliation to the victim after an aggressive encounter. Results also expand the validity of understanding conflict resolution in different ecological conditions and subspecies. The study finds contact aggression has a direct relationship with PC affiliation, and PC affiliation is dependent on aggression type and type of dyad. Aggression type when shifts from non-contact to contact, it increases the chances of PC affiliation.

M. fascicularis have low conflict resolution and are classified as intolerant species after inducting in Grade 2 (Thierry 2007). The CT value found in the study (5.6) is in congruence with Thierry's classification (2007). The CT value is close to Rhesus macaques (*Macaca mulatta*) and Japanese macaques (*Macaca fuscata,* Thierry et al. 2008) where only 5 % of conflicts are resolved. Thus, the values are in accordance with values found in other despotic species such as *M. mulatta*, and *M. fuscata* which are classified as Grade 1 macaque with high levels of intolerance marked by a steep dominance hierarchy. The value of CT in our study was higher than that of tolerant macaques, for example, Tonkean macaques (*Macaca* *tonkeana*) and crested macaques (*Macaca nigra*) where almost 50% of the conflicts are reconciled (Thierry et al. 2008). It corresponds to the gradation as these macaques are known for higher tolerance and less linear dominance hierarchy and ranked Grade 4 in Thierry's classification (2007). These results also suggest that CT in my results also corresponded to the phylogeny of the macaques as Rhesus and Japanese macaques share the same lineage to that of long-tailed macaque.

The PC affiliation was significantly related to the type of aggression that took place between individuals which means that individuals participated more in affiliative interactions if the aggression remained of the non-contact type which is considered as less severe. This is intuitive because if the severity is high the damage to a relationship is more and the less is the opportunity to repair it. This is also in congruence with valuable relationship hypothesis which suggests that the PC affiliation is more towards the relationships which are valuable to a particular individual (Aureli et al. 1989, de Waal and Yoshihara 1983, Kappeler and van Schaik 1992). The female to female aggression tends to decrease the propensity in the PC affiliation, however, no change of PC affiliation was detected for the male to male aggression. This was an interesting finding as the females are usually known to compete for resources and thus form stable bonds when the resources are abundant. The dominance hierarchy and competition for food is significantly lower in the study group than what is expected from the species which ideally should make females form better bonds and should lead to higher PC affiliation according to valuable relationships hypothesis (Aureli et al. 1989, de Waal and Yoshihara 1983, Kappeler and van Schaik 1992).

Dominance hierarchy is an indicator of competition for resources and it changes between species as well as sexes because of difference in resource reliance (Emlen and Oring 1977, Schulke and Ostner 2012). Results of the study using information theory (GEE) shows that in males, rank distance (DNDS) and directionality of affiliation (DIC) influenced CT;

where it was found that CT is higher when the rank distance is lower and DIC is higher suggesting that CT is favoured towards the males with whom affiliation is higher. The males in the group TR form bonds which can be considered as valuable relationships (Chapter 4). Hence, CT among the males was based on a valuable relationship hypothesis. The CT values for male-male aggression were similar (30%) to Rhesus macaques (Petit et al. 1997) showing that CT values also corresponded to the lineage of the macaques. In females, CT was higher (76) which is higher than males and it is expected as females are more social among themselves than males. However, none of the parameters influenced the CT in the group as there was no significant impact of DIC, DNDS, and DCI on the CT in the group. However, lack of further parameters did not enable us to verify the influencing factor for the CT among the females and is an avenue for further research including data on kin relationships.

Hence, the study provides the basic pattern of PC affiliation in *M. f. umbrosus* and compares the patterns between sexes which compete over different resources. It also adds to the validity of conflict resolution between different species/subspecies (phylogeny) and under diverse ecological conditions showing that overall CT is close to the value found in the *fascicularis* lineage and the conflict resolution follows the valuable relationship hypothesis.

Chapter 6:

Summary

Chapter 6

Summary

"Peace is not the absence of conflict, it is the ability to handle conflicts by peaceful means." – Ronald Reagan

This quote from a former US President finds its core in the understanding of conflict, aggression and conflict management in animal societies. In group-living animals, choices are made to maximize individual fitness in an evolutionary sense. Such decisions are made to gain maximum advantage from group-living without losing a major share of any valuable resources. Macaques are such group-living primates that live in a matrilineal, female philopatric group where the members compete to maximize their fitness, leading to constant competition among themselves, which eventually leads to aggression. However, they are also known to reside in a highly cohesive group where cooperation imparts its benefits for the members. That being said, not all species have the same approach to aggression and cooperation. Thierry (2007) classified macaques into four grades based on tolerance, Grade 1 being the least tolerant and Grade 4 being the most tolerant. High tolerance towards other individuals is related to a high aggression rate, strict dominance hierarchy, and less conflict mitigation.

Long-tailed macaques are classified as Grade 2 macaques which are intolerant species and thus expected to have high competition, strong hierarchy, low affiliation, and low conciliatory tendencies. However, it differs between the sexes as females form a strict dominance hierarchy with more aggression and less affiliation based on clumped food resources found in my study area. In such a case, it is expected that affiliation and especially grooming is directed towards high ranking females to gain access for food.

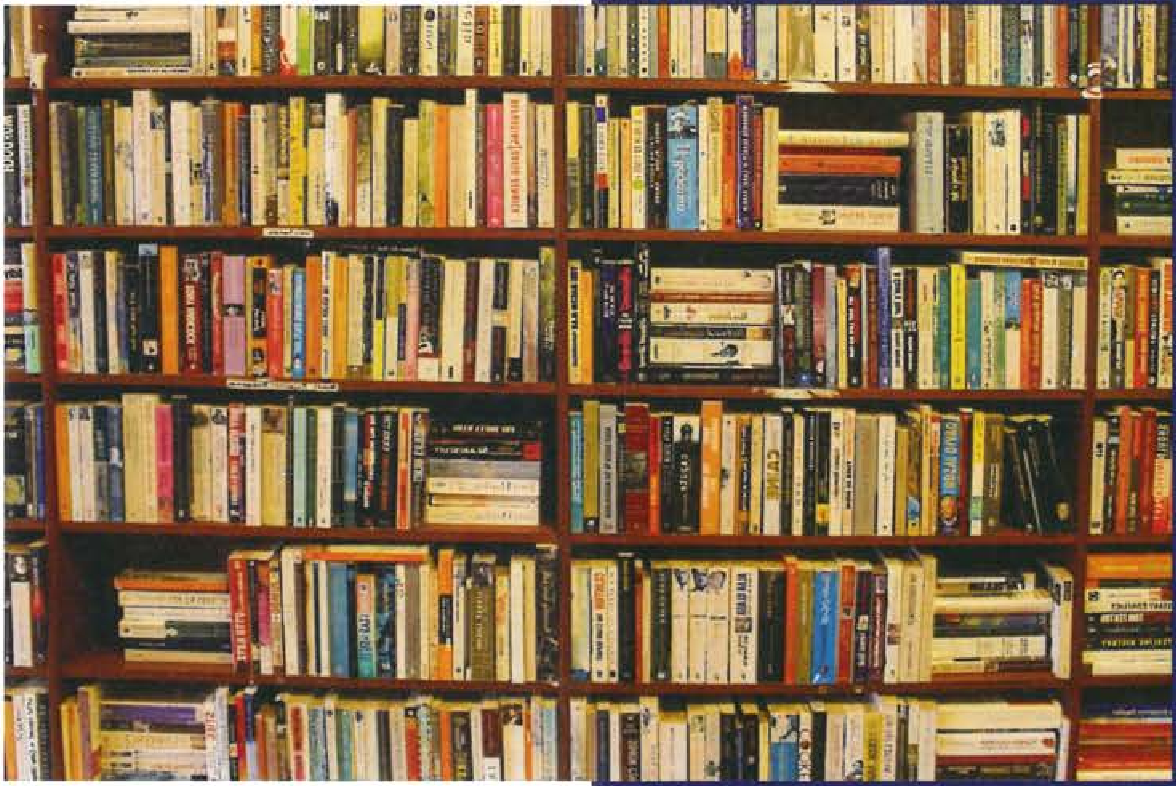
A strong dominance hierarchy with high linearity and steepness in females indicates high competition among the females for food. This pattern was absent in the study with a moderately strong hierarchy, possibly due to the avoidance of competition for food. This, in turn, suggests that food distribution is uniform and abundant for each individual of a small group, which is the foundation of the socioecological theory. Furthermore, low competition in the group allows females to form close bonds and exchange affiliative behaviors as recorded in the study. Low monopolization is depicted by low steepness values and under such a regime, subordinate females do not use grooming as currency to gain access to food from dominant females.

Grooming can also be used to exchange other services in return for example infant handling and support during fights. The females in the study group did not exchange grooming for accessing food as the dominant females did not play a major role in the affiliation. However, the direction of grooming towards the high ranking females could be to gain access to infants for maximizing survivability and better survival rate of the immature individual. High numbers of immature individuals are important in a population, which is recovering from a drastic dip in the number as in the case of the study group. However, in a situation where a high-quality food was available for a small time and for minimal quantity as in case of provisioning, it was observed that the dominant female monopolized all the food and aggressively kept the food away from other females.

On the other hand, males are expected to have higher aggression, lower affiliation and lower conciliatory tendencies than females, which was observed in the group. The bonding among males based on reciprocity of affiliation is expected to be a function of the lineage based on the female reproductive phase and less reliable fertility signals. In *M. f. umbrosus* females, reproductive phases are moderately synchronized and have less reliable fertility signals, hence competition for females was moderately low. Resultantly, the rate of affiliation among males was observed to be high, although the exchange of affiliation was inequitable. Also in such a competitive regime, the monopolizability of mates is moderately strong and it was observed in the study group where the dominant males did not enjoy biased affiliation towards themselves. Besides, high ranking males did not play a significant role in the distribution of affiliation or aggression. *M. fascicularis* males show differentiated bonding without equity, which was reflected in the study. Additionally, bonding was independent of rank effect as expected in the species. In other words, males of the group exhibited species level social characteristics. Male immigration caused a change in dominance hierarchy and mating was monopolized by the male who overthrew the former alpha male.

As found in various taxa, reconciliation was the most common form of conflict resolution in the group which repairs the relationships. Females being more social than males reconciled more than males. The conciliatory tendency (CT) is variable among the macaque species and found to be high in despotic macaque societies. The CT was found to be similar to other despotic species like Rhesus and Japanese macaque. CT also differs among the members of the group and in my study it was influenced by the type of dyad (male: male, female: female, male: female, female: male) and type of aggression (from non-contact to contact). There was no evidence of consolation found in the study group.

Therefore, my study shows that aggressions in female *M. f. umbrosus* follow the socioecological theory and are less aggressive than other subspecies due to the availability of resources. Males follow the species trait of aggression depending on the female receptivity. The study provides the baseline information on the conflict resolution in the previously understudied *M. f. umbrosus* and shows that the patterns of conflict resolution could a conserved trait within the lineage. My study shows that there is "peace without the absence of conflict" in the study group TR.



REFERENCES

References

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

Ardrey, R. A. (1967). *The Territorial Imperative.* London: Collins

Arnold, K., Fraser, O. N., and Aureli, F. (2010). Postconflict reconciliation. In: Campbell, C. J Fuentes, A., MacKinnon, K. C., Bearder, S. K., Stumpf, R. eds. *Primates in Perspective*, London: Oxford University Press. 2nd edition, pp. 608–25.

Aureli, F. (1992). Post-conflict behaviour among wild long-tailed macaques (*Macaca fascicularis). Behavioral Ecology and Sociobiology*, 31: 329–337.

Aureli, F., Cords, M. and van Schaik, C. P. (2002). Conflict resolution following aggression in gregarious animals: a predictive framework. *Animal Behaviour*, 64: 325–343.

Aureli, F. and de Waal, F. B. (2000). *Natural Conflict Resolution.* University of California Press.

Aureli, F., Preston, S. D. and de Waal, F.B. (1999). Heart rate responses to social interactions in free-moving rhesus macaques (*Macaca mulatta*): a pilot study. *Journal of Comparative Psychology*, 113: 59.

Aureli, F. and Smucny, D. A. (2000). The role of emotion in conflict and conflict resolution. In: Aureli, F. and de Waal, F.B. eds. *Natural Conflict Resolution*, University of California Press, pp.199–224.

Aureli, F., van Schaik, C. P. and van Hooff, J. A. (1989). Functional aspects of reconciliation among captive long-tailed macaques (*Macaca fascicularis*). *American Journal of Primatology*, 19: 39–51.

Bates, D., Maechler, M., Bolker, B. and Walker, S. (2015). *lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1–7. 2014.*

Barthélemy, M., Barrat, A., Pastor-Satorras, R. and Vespignani, A. (2005). Characterization and modeling of weighted networks. *Physica a: Statistical Mechanics and its Applications*, 346: 34-43.

Barrett, L., Henzi, S. P., & Lusseau, D. (2012). Taking sociality seriously: the structure of multi-dimensional social networks as a source of information for individuals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367: 2108-2118.

Balasubramaniam, K. N., Dittmar, K., Berman, C. M., Butovskaya, M., Cooper, M. A. et al. (2012). Hierarchical steepness, counter-aggression and macaque social style scale. *American Journal of Primatology*, 74: 915-925.

Bejder, L., Fletcher, D. and Bräger, S. (1998). A method for testing association patterns of social animals. *Animal Behaviour*, 56: 719–725.

Berghänel, A., Ostner, J., Schröder, U. and Schülke, O. (2011). Social bonds predict future cooperation in male Barbary macaques, *Macaca sylvanus*. *Animal Behaviour*, 81: 1109–1116.

Berghänel, A., Schülke, O. and Ostner, J. (2010). Coalition formation among Barbary macaque males: the influence of scramble competition. *Animal Behaviour*, 80: 675–682.

Borgatti, S. P. (2002). NetDraw: Graph visualization software. *Harvard: Analytic Technologies*.

Brent, L. J., Lehmann, J. and Ramos-Fernández, G. (2011). Social network analysis in the study of nonhuman primates: A historical perspective. *American Journal of Primatology*, 73: 720–730.

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

Carnes, L. M., Nunn, C. L. and Lewis, R. J. (2011). Effects of the distribution of female primates on the number of males. *PLoS ONE*, 6: e19853.

Clutton-Brock, T.H. and Janson, C.H. (2012) Primate socioecology at the crossroads: past, present and future. *Evolutionary Anthropology*, 21: 136–150.

Cools, A. K., van Hout, A. J. M. and Nelissen, M. H. (2008). Canine reconciliation and third-party-initiated postconflict affiliation: do peacemaking social mechanisms in dogs rival those of higher primates? *Ethology*, 114: 53–63.

Cordoni, G. and Palagi, E. (2008). Reconciliation in wolves (*Canis lupus*): new evidence for a comparative perspective. *Ethology*, 114: 298–308.

Cords, M. and Aureli, F. (2000). Reconciliation and relationship qualities. In: Aureli, F. and de Waal, F. B. eds. *Natural Conflict Resolution*, University of California Press, pp. 177–198.

Croft, D. P., James, R. and Krause, J. (2008). *Exploring Animal Social Networks*. Princeton University Press.

Cui, J. (2007). QIC Program and Model Selection in GEE Analyses. *The Stata Journal*, 7: 209–220.

Curley, J. P. (2016). *compete: Analyzing Social Hierarchies: R package version 0.1.*

David, H. A. (1987). Ranking from unbalanced paired-comparison data. *Biometrika*, 74: 432-436.

David, H. A. (1988). *The Method of Paired Comparisons*, London: Charles Griffin & Co.

Dekker, D., Krackhardt, D. and Snijders, T. A. (2007). Sensitivity of MRQAP tests to collinearity and autocorrelation conditions. *Psychometrika*, 72: 563-581.

de la O, C., Mevis, L., Richter, C., Malaivijitnond, S., Ostner, J. and Schülke, O. (2013). Reconciliation in Male Stump-tailed Macaques (*Macaca arctoides*): Intolerant Males Care for Their Social Relationships. *Ethology*, 119: 39–51.

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

de Waal, F. B. (1996). Conflict as negotiation. *I*n: McGrew, W. C., Marchant, L. F. and T. Nishida, eds. *Great Ape Societies*, pp. 159–172

de Waal, F. B. and Aureli, F. (1997). Conflict resolution and distress alleviation in monkeys and apes. In: Carter, C. S., Lederhendler, I. I. and Kirkpatrick, B. eds. *The Integrative Neurobiology of Affiliation*. MIT Press, pp. 317-328.

de Waal, F. B. and van Roosmalen, A. (1979). Reconciliation and consolation among chimpanzees. *Behavioral Ecology and Sociobiology*, 5: 55–66.

de Waal, F. B. and Yoshihara, D. (1983). Reconciliation and redirected affection in rhesus monkeys. *Behaviour*, 85: 224–241.

Dubuc, C., Brent, L. J., Accamando, A. K., Gerald, M. S., MacLarnon, A. et al. (2009). Sexual skin color contains information about the timing of the fertile phase in free-ranging *Macaca mulatta. International Journal of Primatology*, 30: 777–789.

Dugatkin, L. A. (1997). *Cooperation among animals: an evolutionary perspective*. Oxford University Press, on Demand.

Dunbar, S. B., Koretz, D. M. and Hoover, H. D. (1991). Quality control in the development and use of performance assessments. *Applied Measurement in Education*, 4: 289-303.

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: 195–204.

Emlen, S. T. and Oring, L. W. (1977). Ecology, sexual selection and the evolution of mating systems. *Science*, 197*:* 215-223.

Flack, J. C., Girvan, M., de Waal, F. B. and Krakauer, D. C. (2006). Policing stabilizes construction of social niches in primates. *Nature*, 439: 426.

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

Fraser, O. N. and Bugnyar, T. (2011). Ravens reconcile after aggressive conflicts with valuable partners. *PLoS One*, 6: e18118.

Fürtbauer, I., Mundry, R., Heistermann, M., Schülke, O., and Ostner, J. (2011). You mate, I mate: macaque females synchronize sex not cycles. *PLoS One*, 6: e26144.

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. *Animal Behaviour*, 66: 601–605.

Girard-Buttoz, C., Heistermann, M., Rahmi, E., Agil, M., Fauzan, P. A., and Engelhardt, A. (2014). Costs of mate-guarding in wild male long-tailed macaques (*Macaca fascicularis*): physiological stress and aggression. *Hormones and Behavior*, 66: 637-648.

Goodall, J. (1986). *The Chimpanzees of Gombe: Patterns of Behavior.* Cambridge: Harvard University Press, Belknap Press.

Gumert, M. D. (2010). Dominance and reciprocity in the grooming relationships of female longtailed macaques (*Macaca fascicularis*) in Indonesia. In: Gursky-Doyen, S and Supriatna, J. eds. *Indonesian Primates*. Springer Science and Business Media, pp. 309-341.

Hajra, P. K., Rao, P. S. N. and Mudgal, V. (1999). *Flora of Andaman and Nicobar Islands*. Botanical Survey of India.

Hamilton, W. D. (1964). The genetical evolution of social behaviour. II. *Journal of Theoretical Biology*, 7: 17-52.

Hanneman, R. A. and Riddle, M. (2005). *Introduction to social network methods*. University of California Riverside.

Heesen, M., Rogahn, S., Macdonald, S., Ostner, J. and Schülke, O. (2014). Predictors of food-related aggression in wild Assamese macaques and the role of conflict avoidance. *Behavioral Ecology and Sociobiology*, 68: 1829–1841.

Hemelrijk, C. K. (1990a). A Matrix Partial Correlation Test used in Investigations of Reciprocity and Other Social Interaction Patterns at Group Level. *Journal of Theoretical Biology* 143: 405-420

Hemelrijk, C. K. (1990b). Models of and tests for, reciprocity, unidirectional and other social interaction patterns at a group level. *Animal Behaviour* 39: 1013-1029

Hemelrijk, C. K., Wantia, J. and Daetwyler, M. (2003). Female co-dominance in a virtual world: Ecological, cognitive, social and sexual causes. *Behaviour* 140: 1247-1273

Hemelrijk, C. K., Wantia, J. and Gygax, L. (2005). The construction of dominance order: comparing performance of five different methods using an individual-based model. *Behaviour* 142: 1043-1064

Hemelrijk, C. K., Wantia, J. and Isler, K. (2008) Female dominance over males in primates: Self-organisation and sexual dimorphism. *PLoS ONE* 3: e2678

Henzi, S. P. and Barrett, L. (1999). The value of grooming to female primates. *Primates*, 40: 47–59.

Hinde, R. A. (1976). Interactions, relationships and social structure. *Man*, 11: 1–17.

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

Hutchins, M. and Barash, D. P. (1976). Grooming in primates: implications for its utilitarian function. *Primates*, 17: 145–150.

Isbell, L. A., Pruetz, J. D. and Young, T. P. (1998). Movements of vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*) as estimators of food resource size, density and distribution. *Behavioral Ecology and Sociobiology*, 42: 123–133.

Isbell, L. and Young, T. (2002). Ecological models of female social relationships in primates: similarities, disparities and some directions for future clarity. *Behaviour*, 139: 177–202.

Janson, C. H. and van Schaik, C. P. (1988). Recognizing the many faces of primate food competition: methods. *Behaviour*, 105: 165-186.

Kanngiesser, P., Sueur, C., Riedl, K., Grossmann, J. and Call, J. (2011). Grooming network cohesion and the role of individuals in a captive chimpanzee group. *American Journal of Primatology*, 73: 758–767.

Kappeler, P. M. and van Schaik, C. P. (1992). Methodological and evolutionary aspects of reconciliation among primates. *Ethology*, 92: 51–69.

Kaumanns, W. and Singh, M. (2012). Social relationships among lion-tailed macaque (*Macaca silenus*) males in differently structured social units. *Current Science*, 102: 1451-1455

Kodric-Brown, A. and Brown, J. H. (1987). Anisogamy, sexual selection and the evolution and maintenance of sex. *Evolutionary Ecology*, 1: 95–105.

Koenig, A. (2002). Competition for resources and its behavioral consequences among female primates. *International Journal of Primatology*, 23: 759–783.

Koski, S. E., de Vries, H., van den Tweel, S. W. and Sterck, E. H. (2007). What to do after a fight? The determinants and inter-dependency of post-conflict interactions in chimpanzees. *Behaviour*, 144: 529-556.

Koyama, N., Nakamichi, M., Oda, R., Miyamoto, N., Ichino, S. and Takahata, Y. (2001). A ten-year summary of reproductive parameters for ring-tailed lemurs at Berenty, Madagascar. *Primates*, 42: 1-14.

Krebs, D. L. and Miller, D. T. (1985). Altruism and aggression. *The Handbook of Social Psychology*, 2: 1–71.

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: 377–386.

Kummer, H. (1978). On the value of social relationships to nonhuman primates: a heuristic scheme. *Social Science Information*, 17: 687–705.

Kumar, A., M., Singh, M., Kumara, H. N., Sharma, A. K. and Bertsch, C. (2001). Male migration in lion-tailed macaques. *Primate Report*, 59: 5–18.

Kurland, J. A. (1977). *Kin selection in the Japanese monkey*. Karger Publishers.

Lazarsfeld, P. F. and Merton, R. K. (1954). Friendship as a social process: A substantive and methodological analysis. *Freedom and Control in Modern Society*, 18: 18–66.

Lin, T. J., Agoramoorthy, G., Huang, C. C. and Hsu, M. J. (2008). Effects of troop size on social relations among male Formosan macaques, *Macaca cyclopis*. *Zoological Studies*, 47: 237-246.

Lorenz, K. (1967). *On Aggression.* Methuen, London:

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: 571-584.

Maestripieri, D. and Roney, J. R. (2006). Evolutionary developmental psychology: Contributions from comparative research with nonhuman primates. *Developmental Review*, 26: 120–137.

Majolo, B., Ventura, R., and Koyama, N. F. (2009). A statistical modelling approach to the occurrence and timing of reconciliation in wild Japanese macaques. *Ethology*, 115: 152-166.

McFarland, R. and Majolo, B. (2011a). Exploring the components, asymmetry and distribution of relationship quality in wild Barbary macaques (*Macaca sylvanus*). *PLoS One*, 6: e28826.

McFarland, R. and Majolo, B. (2011b). Reconciliation and the costs of aggression in wild Barbary macaques (*Macaca sylvanus*): a test of the integrated hypothesis. *Ethology*, 117: 928–937.

Micheletta, J., Engelhardt, A., Matthews, L. E. E., Agil, M., and Waller, B. M. (2013). Multicomponent and multimodal lipsmacking in crested macaques (*Macaca nigra*). *American Journal of Primatology*, 75: 763-773

Morris, D. (1967). *The Naked Ape.* New York: Bantam

Newman, M. E. (2003). The structure and function of complex networks. SIAM Review 45:167–256.

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*: 1–11.

Nunn, C. L. (1999). The number of males in primate social groups: a comparative test of the socioecological model. *Behavioral Ecology and Sociobiology*, 46: 1–13.

O'Neill, A. C., Fedigan, L. M. and Ziegler, T. E. (2004). Relationship between ovarian cycle phase and sexual behavior in female Japanese macaques (*Macaca fuscata*). *American Journal of Physical Anthropology*, 125: 352–362.

Ostner, J. and Schülke, O. (2014). The evolution of social bonds in primate males. *Behaviour*, 151: 871–906.

Pabla, T.S. (2018). *History of Great Nicobar Island The History of Great Nicobar Island The Ascent: Andaman and Nicobar Islands, India*, Notion Press, Chennai.

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

Pan, W. (2001). Akaike's information criterion in generalized estimating equations. *Biometrics*, 57: 120–125.

Petit, O., Abegg, C. and Thierry, B. (1997). A comparative study of aggression and conciliation in three cercopithecine monkeys (*Macaca fuscata, Macaca nigra, Papio papio*). *Behaviour*, 134: 415–432.

Schino, G. (2001). Grooming, competition and social rank among female primates: a meta-analysis. *Animal Behaviour*, 62: 265–271.

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: 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: 1097–1105.

Schulke, O. and Ostner, J. (2012). Ecological and social influences on sociality. In: Mitani, J. C, Call, J., Kappeler, P. M., Palombit, R. A. and Silk, J. B. eds. *The Evolution of Primate Societies*, pp.195–219.

Seyfarth, R. M. (1977). A model of social grooming among adult female monkeys. *Journal of Theoretical Biology*, 65: 671–698.

Silk, J. B. (2002). The form and function of reconciliation in primates. *Annual Review of Anthropology*, 31: 21–44.

Silk, J. B., Alberts, S. C. and Altmann, J. (2003). Social bonds of female baboons enhance infant survival. *Science*, 302: 1231-1234.

Silk, J. B., Altmann, J. and Alberts, S. C. (2006). Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behavioral Ecology and Sociobiology*, 61: 183–195.

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: 515.

Singh, M., Jeyaraj, T., Prashanth, U. and Kaumanns, W. (2011). Male–male relationships in lion-tailed macaques (*Macaca silenus*) and bonnet macaques (*Macaca radiata*). *International Journal of Primatology*, 32: 167-176.

Sinha, A., Mukhopadhyay, K., Datta-Roy, A. and Ram, S. (2005). Ecology proposes, behaviour disposes: Ecological variability in social organization and male behavioural strategies among wild bonnet macaques. *Current Science*, 89: 1166–1179.

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. 35-40.

Smucny, D. A., Price, C. S. and Byrne, E. A. (1997). Post-conflict affiliation and stress reduction in captive rhesus macaques. *Advances in Ethology*, 32: 157.

Sterck, E. H., Watts, D. P. and van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, 41: 291–309.

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: 703–719.

Symons, D. (1974). Aggressive Play and Communication in Rhesus Monkeys (*Macaca mulatta*). *Integrative and Comparative Biology*, 14: 317–322.

Tanaka, I. and Takefushi, H. (1993). Elimination of external parasites (lice) is the primary function of grooming in free-ranging Japanese macaques. *Anthropological Science*, 101: 187–193.

Thierry, B. (2007). Unity in diversity: lessons from macaque societies. *Evolutionary Anthropology*, 16: 224–238.

Thierry, B., Aureli, F., Nunn, C. L., Petit, O., Abegg, C. and de Waal, F. B. (2008). A comparative study of conflict resolution in macaques: insights into the nature of trait covariation. *Animal Behaviour*, 75: 847–860.

Trivers, R. L. (1971). The evolution of reciprocal altruism. *The Quarterly Review of Biology*, 46: 35-57.

Trivers, R. L. (1972) Parental investment and sexual selection. In: Campbell, B. ed., *Sexual Selection and The Descent of Man*. Chicago: Aldine pp.136-179.

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: 281–293.

van Hooff, J. A. R. A. M., and Wensing, J. A. B. (1987). Dominance and its behavioral measures in a captive wolf pack. In: H. Frank ed., *Perspectives in vertebrate science, Vol. 4. Man and wolf: Advances, issues and problems in captive wolf research*. Dordrecht, Netherlands: Dr W Junk Publishers. pp. 219-252.

van Schaik, C. P. (1989) The ecology of social relationships amongst female primates. In: Standen, V. and Foley, R. eds. *Comparative Socioecology: The Behavioral Ecology of Humans and Other mammals*, Blackwell, pp. 195–218.

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

Veenema, H. C., Das, M. and Aureli, F. (1994). Methodological improvements for the study of reconciliation. *Behavioural Processes*, 31: 29–37.

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: e0148205.

Watts, D. P. (2006). Conflict resolution in chimpanzees and the valuable-relationships hypothesis. *International Journal of Primatology*, 27: 1337–1364.

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

Whitehead, H. (2007). Socprog 2.3 (for MATLAB 7.4). *Halifax, Canada: Dalhousie University*.

Whitehead, H. (2008). *Analyzing animal societies: quantitative methods for vertebrate social analysis*. University of Chicago Press.

Willems, E. P., Hellriegel, B., and van Schaik, C. P. (2013). The collective action problem in primate territory economics. *Proceedings of the Royal Society B: Biological Sciences*, 280: 20130081.

Wittig, R. M., Crockford, C., Lehmann, J., Whitten, P. L., Seyfarth, R. M. and Cheney, D. L. (2008). Focused grooming networks and stress alleviation in wild female baboons. *Hormones and behavior*, 54: 170–177.

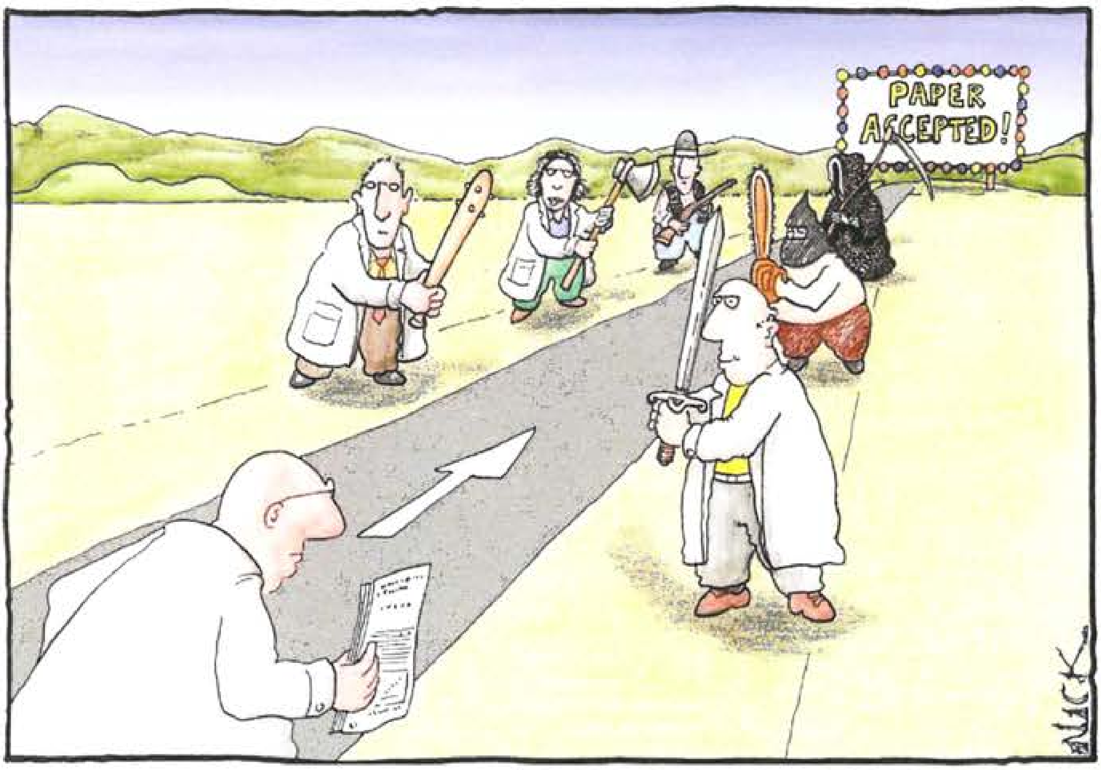
Wrangham, R. W. (1980). An Ecological Model of Female-Bonded Primate Groups. *Behaviour*, 75: 262–300.

Wrangham, R. W. and Peterson, D. (1996). *Demonic Males*. Boston: Houghton Mifflin.

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: 569–579.

Young, H., Griffin, R. H., Wood, C. L. and Nunn, C. L. (2013). Does habitat disturbance increase infectious disease risk for primates? *Ecology Letters*, 16: 656–663.

Zamma, K. (2002). Grooming site preferences determined by lice infection among Japanese macaques in Arashiyama. *Primates*, 43: 41–49.



PUBLICATIONS

Ethology Ecology & Evolution, 2018
https://doi.org/10.1080/03949370.2018.1459866

Taylor & Francis
Taylor & Francis Group

Between-group encounters in Nicobar long-tailed macaque (*Macaca fascicularis umbrosus*)

ARIJIT PAL[1,2], HONNAVALLI N. KUMARA[1,*], PARTHA SARATHI MISHRA[1,3], AVADHOOT D. VELANKAR[1,2] and MEWA SINGH[4,5]

[1] *Conservation Biology Department, Sálim Ali Centre for Ornithology and Natural History, Coimbatore 641108, India*
[2] *Manipal University, Manipal 576104, India*
[3] *Bharathiar University, Coimbatore 641046, India*
[4] *Biopsychology Laboratory and Institution of Excellence, University of Mysore, Mysore 570006, India*
[5] *Organismal Biology Unit, Jawaharlal Nehru Centre for Advance Scientific Research, Bangalore 560064, India*

Received 19 December 2017, accepted 12 March 2018

Group living primates often participate in between-group encounters to defend monopolizable resources. Participation in an encounter is influenced by the density and abundance of resources and the relative fighting ability of groups. We studied between-group encounters in three groups of Nicobar long-tailed macaques (*Macaca fascicularis umbrosus*) in the Great Nicobar Island, with one group, TR, being the focal study group to measure the influence of these factors on between-group encounters. Encounters varied from mutual tolerance to aggressive fights, with females participating less aggressively than males. Sleeping site and vegetation cover were the primary influences on the nature of interaction in the areas where home range overlapped. The initiation and intensity of an encounter were influenced by relative group size. The focal group (TR) was the smallest of the three groups in the area and it actively avoided confrontation with the other two groups (MG and PI), resulting in a lower observed encounter rate than expected. Both the frequency and aggressiveness of encounters was influenced by the number of females cycling and the number of males present in the study group. Inasmuch as encounters were influenced by the number of females and the distribution of food, rather than geography, we conclude that encounters serve to defend food resources and mates rather than that they are examples of territoriality.

KEY WORDS: aggression, intergroup encounters, mate defense, resource defense.

INTRODUCTION

The between-group encounters are a regular phenomenon in group living primates (Cheney 1987). The nature of between-group encounters, however, is influenced

---

[*] Corresponding author: Honnavalli N. Kumara, Sálim Ali Centre for Ornithology and Natural History, Coimbatore 641108, Tamil Nadu, India (E-mail:honnavallik@gmail.com).

Changes in behaviour following a 'rank changeover by challenge' in the Nicobar long-tailed macaque (*Macaca fascicularis umbrosus*)

Arijit Pal[1,2], Honnavalli N. Kumara[1,*], Avadhoot D. Velankar[1,2], Partha Sarathi Mishra[1,3,4] and Mewa Singh[4,5]

[1]Sálim Ali Centre for Ornithology and Natural History, Coimbatore 641 108, India
[2]Manipal Academy of Higher Education, Manipal 576 104, India
[3]Bharathiar University, Coimbatore 641 046, India
[4]Biopsychology Laboratory and Institution of Excellence, University of Mysore, Mysuru 570 006, India
[5]Organismal Biology Unit, Jawaharlal Nehru Centre for Advance Scientific Research, Bengaluru 560 064, India

A rank changeover is a sexual strategy by primate males to gain access to reproductive females. We observed one such event in the Nicobar long-tailed macaque (*Macaca fascicularis umbrosus*) at the Great Nicobar Island, India. In the three and half months of the post-rank changeover period, the home range reduced significantly while there was no change in the intensity of range use and day range length. The sleeping sites in the post-rank changeover period were confined to the centre of the home range. The overall mating rate and aggressive mating approach by males increased significantly during the post-rank changeover period. The females developed sexual swelling and started soliciting the immigrated males within two weeks after the rank changeover event. During this period no female conceived, which suggests that they used situation-dependent receptivity with deceptive swelling as a counter strategy to avoid male aggression for copulation.

Keywords: Between-group encounters, grid use, Nicobar long-tailed macaque, rank changeover, reproductive behaviour.

IN many group-living species, dominance rank or status is a good predictor of mating success in both males and females[1]. This relation is strong among males in the species that mate polygynously[2]. Although the influence of social rank on mating success varies, a top rank can help a male to monopolize mating resources[3]. 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 emigration of the previous dominant male[4]. 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 an aggressive challenge by the outer males[5,6]. van Noordwijk and van Schaik[7] 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 a top rank male and outer group male, where 44% rank changeover occur events after opportunistic invade of outer group male when the resident male left the group or was injured[8].

A sudden change in the social organization of a group has immense impact on its members[9,10]. 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[9,10]. After being defeated, the former dominant male may leave the group immediately[8,10], or stay with the group as a subordinate individual[5,11,12]. The new alpha male may be involved in agonistic interactions to establish dominance over the other group members[13,14]. The new dominant male tries to increase reproductive access by initiating mating with adult females of the group[12]. 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 forced mating with a female[15] and probable infanticide[16–18] to attain reproductive success. In response, the females may also adopt various counter-strategies such as group defence to protect themselves from sexual

---

*For correspondence. (e-mail: honnavallik@gmail.com)