Social Organization, Behavior and Phylogeography of *Macaca fascicularis umbrosa* on the Nicobar Islands, India

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TABLE OF CONTENTS

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Executive Summary

In India, data on the unique endemic subspecies, Nicobar Long-tailed Macaque *Macaca fascicularis umbrosus* was limited to status reports from short surveys. The subspecies is endemic to three islands in the Nicobar group of Andaman and Nicobar archipelago *viz.*, Great Nicobar, Little Nicobar and Katchal. Previous studies on these macaques suggest that their population decreased significantly after the 2004 Tsunami. Large parts of the habitat of the macaque were affected. Further, the inhabited islands have been isolated for long and this could potentially result in inbreeding within, and genetic isolation among populations. The consequence of this would be high genetic distance between, populations resulting in a strong genetic structure. Phylogeography utilizes standing patterns of genetic variation to explain historical events such as migrations and demography over space and time. Thus we initiated a study to document phylogeography, ecology, social organisation and behaviour of *M. f. umbrosus* in the Nicobar Islands, which would help in understanding the ecology and evolutionary history of this species. The study was conducted from January 2013 to January 2016.

POPULATION: We recorded the encounter rate of *M. f. umbrosus* groups per kilometre in Great Nicobar (effort 119.55 km), Little Nicobar (effort 14.09 km) and Katchal (effort 78.50 km) was 0.30, 0.35 and 0.48 respectively, with the mean group size of $39.83 \pm 17.47_{SD}$ in Great Nicobar and $43.50 \pm 26.15_{SD}$ in Katchal. The group encounter rate was found to be higher in 2014 (0.37) than in 2006 (0.10) or even 2000 (0.23). The highest encounter rate was observed in Katchal (0.48 against 0.30 of Great Nicobar) which is probably due to abandoned plantations. Encounter rate of *M. f. umbrosus* obtained during the present study was compared with previous studies using GLM and it was found to be significantly higher (Walds $Z = 3.11$, $P = 0.002$), indicating an increase in macaque population after sharp decline reported during the 2006 study. The population increased at an intrinsic rate (r) of 0.12, 0.14 and 0.17 in Great Nicobar, Little Nicobar and Katchal respectively from 2006 to 2014. Although statistically not significant, the mean group size declined from $36.12 \pm 7.07_{SD}$ in 2000 to $26.75 \pm 28.23_{SD}$ by 2006, and increased to $41.30 \pm 20.02_{SD}$ by 2014. Percent adult males and females per group increased from 9.87 and 43.63 in 2000 to 23.36 and 48.13 by 2006, and decreased to 14.30 and 31.00 by 2014

respectively. Conversely, percent immature per group decreased from 46.75 in 2000 to 28.50 by 2006, and increased to 54.60 by 2014. The number of adult females to adult males has significantly decreased from 4.74 in 2000 to 2.06 by 2006 and 2.32 by 2014. The immature to adult female ratio significantly decreased from 1.09 in 2000 to 0.59 by 2006 and increased to 1.89 by 2014. Results showed that the population has recovered from a drastic decline caused by the tsunami, but it cannot be ascertained whether it has reached stability in group size and composition because of the altered group structure. The number of males per female has increased and this may be due to lack of space to disperse and increased population density in these islands probably has resulted in lesser number of females per male.

GROUP DYNAMICS: We selected five macaque groups in Great Nicobar Island to study the group dynamics and birth seasonality (group identity: LB, MG, PI, TR and KM). The variation in group size between the years was highest in group-PI 5.35_{SD}, where it was lower in group-TR 1.70_{SD}. The variation in the number of adult males in the group-TR was highest 1.25_{SD} and lowest was in the group-LB 0_{SD}, conversely the variation in the number of adult female and immature in group TR was lowest (0.94_{SD} and 0.47_{SD} respectively), where as it was highest in group-PI (2.05_{SD} and 5.44_{SD} respectively). The high variation in the number of immature is due to the high mortality rate of immature and non-natal migration perhaps has caused the maximum observed variation in these groups than other age-sex individuals. However, the variation in the group size, number of adult males, number of adult female and immature in each of the study groups between the years did not vary significantly. No change in adult female number signifies the female philopatry in the species. The variation in adult male to adult female ratio, adults to immature ratio, and adult female to the immature ratio between the years and groups did not vary significantly. This suggests that the sex ratios were maintained in each group to optimize reproductive output. The mean birth rate was $0.49 \pm 0.06_{SD,}$ and ranged between $0.40\pm 0.07_{SD}$ and $0.58\pm 0.12_{SD.}$ The birth rate did not vary between the groups. However, correlation test sowed number of births in the group was highly correlated with the group size ($r = 0.960$, N = 10, p = 0.000) and number of females in the group ($r = -0.884$, $N = 10$, $p = 0.001$). The positive relation between birth rate and group size may be due to the benefit of group foraging. On the other hand, increased number of female increases the intra-group female competition for food, which perhaps affects the birth rate negatively. The mean survival rate of immature was $0.79 \pm 0.03_{SD}$. The mean inter-birth interval in the study group was $14.75 \pm 4.59_{SD}$ months. Although

inter-birth interval varied from 9 to 23 months between the females, but the variation was not significant. Although, the number of births in different months did not differ, the number of births was positively correlated with the rainfall (r=0.621, N=12, p=0.03), and 70.65% of births occurred in rainy season (July to December). Perhaps, higher availability of food resources in the rainy season than in the rest of the months may support lactation in females and provide food for weaned infants, which increase the reproductive output and infant survivability in these macaques.

TIME AVTIVITY BUDGET: Study of the way organisms interact with their environment is essential to understand the ecology of that organism. Monitoring activity budget of an animal is the easiest way to understand the interdependence of animal and its environment. Our study aimed at generating baseline information regarding activity patterns, feeding ecology and home-range estimation of this species. We selected a group TR with 21 individuals for this study. The group was followed from dawn (0600 hrs) to dusk (1800 hrs). During this, we recorded the major activities using instantaneous scan sampling. We recorded the geo-coordinates of the visually approximated group centre using handheld GPS for every 30 minutes. A total of 4628 individual scans were collected from October 2013 till December 2015. Although the time spent on each activity varied significantly (Kruskal – Wallis $\chi^2 = 53.96$, df = 5, P <0.001), the time spent on each activity between dry and wet season did not vary. The study group was observed to feed on 26 major food items of which 12 were introduced by humans and 14 were of native origin. The relative frequency of introduced species in feeding was significantly higher ($Z = 27.93$, $P < 0.01$) than native species. Macaques also relied significantly more on plant resources than on animal or human waste origin resources ($Z = 19.78$, $P < 0.01$). Among plant resources, macaques fed fruits significantly ($Z = 15.38$, $P < 0.01$) more than flowers, stem and leaves. A total of 803 group locations (Dry N = 330, Wet N = 473) was collected during the study period, which is spread over 66 grid cells. Of the 66 grids, only six grids were used for > 7 % of the observations. Number of grid cells and intensity of grid cell use by the group between seasons did not vary significantly. The study group being partially commensal spent more time feeding on food resources from the orchards and plantations, which may result in acquisition of low cost high energy food resulting in increased time for resting. The study group being in human dominated landscape, adapted to food resources available in human habitation, which resulted in increased human-macaque conflict in the region. Coconut, Banana and Guava are cultivated by local

people for economic gains and resulting loss due to monkeys has increased human- macaque conflict.

MALE TAKEOVER: Takeover is an effective sexual strategy of primate males to gain reproductive success by accessing females. Takeover male employs various strategies to acquire prime position and maximize reproductive fitness, which incur costs on group members. To reduce these costs, group members adopt various counter strategies. We observed a takeover event in *M. f. umbrosus* at Great Nicobar Island on 14 October 2013 where a male (FY) from other group overthrew a resident alpha male (RY) of the group TR. We compared habitat use and reproductive behaviour of the study group before and after takeover event. The home range size (number of grids used) between pre and post takeover period differed significantly, whereas the intensity of grid use remained same. Use of sleeping sites (pre-N = 11 and post- N = 9) as well as the intensity of use of sleeping sites, did not differ between pre and post-takeover. The day range length in pre ($999.18 \pm 225.52_{SD}$) and post ($981.87 \pm 200.16_{SD}$) takeover also did not differ. Such post-takeover changes in habitat use may be adopted as a strategy to avoid between-group interactions. The rate of between group interactions did not differ between pre and post-takeover respectively (N= 20). The aggressive between-group interactions in post-takeover period (N= 4, 0.005/h) were lesser than in the pre-takeover (N= 6, 0.017/ h). Mating initiation by males, sexual coercion and the overall mating rate increased significantly during the post-takeover period. Although, females initially avoided the immigrated male and subsiquently they started soliciting him within two weeks after developing sexual swelling. Number of matings per hour was higher in females as a counter strategy to minimize aggression and sexual coercion from takeover male. The sexual coercion by male differed significantly between pre and post-takeover. During the receptive period, no female was conceived, and the post-takeover first conception date of six females ranged between 11 and 51 weeks, with mean $30.6 \pm 16.3_{SD}$ weeks from the day of the takeover. This suggests that females use situation dependent receptivity with deceptive swelling as a counter strategy to avoid sexual coercion. Individuals of different age-sex classes and reproductive stages adopt different counter strategies to maximize inclusive fitness. Such interplay of strategies and counter-strategies results in both group and individual level changes in behaviour of macaques.

PHYLOGEOGRAPHY: Genomic DNA was isolated from 105 faecal samples of *M. f. umbrosus*, of which, 56 samples gave positive PCR amplification. Thirty one samples were sequenced for the D-loop region of mtDNA. Out of these, 21 samples were from Katchal, six samples from Great Nicobar, and four samples from Little Nicobar. Two samples from Great Nicobar, three from Katchal and one from Little Nicobar were sequenced for the 12s and 16s ribosomal gene of mtDNA. We downloaded sequences of two sub-species from NCBI (National Centre for Biotechnology Information) to examine the phylogenetic relationships. The *M. f. fascicularis* subspecies is distributed throughout the South Asian countries and is genetically structured and has several sister groups. The Indonesian group is paraphyletic and occurs in more than one clade. This may be due to with translocation of the species onto the islands. The Nicobar macaques are in a separate group (unique) and are sister to the Javan group. Sequence data of 2100 bp from the four mtDNA genes (D-Loop and 12s rRNA, 16s rRNA and tRNA) support the position of the Nicobar macaques being closest to the Javan group. The results from study of phylogeography suggest that the Nicobar macaques are unique and are sister to the Javan group. The three populations on the three islands of Nicobar are genetically different. As predicted, the Great and Little Nicobar populations are genetically more similar than either of them is to the Katchal population, which could be the effect of spatial distance and colonization.

In a nutshell, although the population of M. f. umbrosus in Nicobar Islands are highly susceptible to catastrophic events like tsunami, the population has shown a greater recovery following the population crash during the 2004 tsunami. The life history traits and feeding ecology showed that the species is highly adaptable to changing environmental conditions. Emigration and immigration of individuals between the groups are a regular phenomenon in the sub-species. M. f. umbrosus is genetically closer to the Javan group than the Indonesian group. Due to their generalist nature, they frequented to villages in the post-tsunami period and adapted to live in the human dominated landscape, which has lead to human-macaque conflict in these islands which is a concern for macaques.