Demography and birth seasonality in the Nicobar long-tailed macaque (*Macaca fascicularis umbrosus*)

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

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

The Nicobar long-tailed macaque (*Macaca fascicularis umbrosus*) is confined to the southern and central Nicobar archipelago. We have collected demographic and birth data for five groups of *M. f. umbrosus* to understand their group structure, demography and breeding seasonality. Group size, individuals in age–sex classes and age–sex ratio did not vary between the groups and years. The birth rate was neither associated with the number of adult females in the group nor with group size. The number of births in a month was positively correlated with rainfall, and about 71% of the births occurred during the rainy season, though, the number of births did not vary systematically among the months. Perhaps, higher availability of food resources in the wet season than the rest of the year may support lactation in females and provide food for the weaned infants. The similarity in some demographic traits between the Nicobar long-tailed macaque and other subspecies indicates that these traits may be conserved over evolutionary time, while for other traits, differences among subspecies may reflect the effect of local conditions and recent histories. This is the first report on demography and birth seasonality of this unique subspecies of the long-tailed macaque.

Keywords: Birth rate, demography, group size, population dynamics.

DEMOGRAPHIC characteristics are the evolutionary consequences of life history traits which fix in a population as they maximize individual reproductive output[1–3]. Demographic characteristics including group size, age and sex composition of the group, birth rate, mortality, migration frequency of individuals, and growth rate, change over time due to ecological constraints[4]. Predation pressure and intra-group competition over food are two major factors that determine the upper limit of the group size, which directly relates to the birth and survival rate of individuals[5,6]. In the long-tailed macaque, *M. fascicularis*, birth rate and early infant survival decreased with increase in group size due to over-optimal group size[7]. Contrary to this, group size positively correlated with the birth rate but no relation was found between the group size and infant survival in the Japanese macaque, *M. fuscata*[8]. Overall, the group size influences intra-group resource competition, which in turn affects the reproductive output of a group.

Age–sex composition also plays a major role in the reproductive output of a group. In macaques, reproductive success in females increases with increase in proportion of males (adult and sub-adult) in the group. This is due to increased immature survival because of better protection of immatures against infanticide by outer group males[9]. While birth rate decreased with increase in number of females in the group in lion-tailed macaque *M. silenus*[10] and *M. fuscata*[8], both birth rate and infant survival rate decreased in the Taiwanese macaque, *M. cyclopis*[11]. Thus, the reproductive success in females is also dependent on the intra-group feeding competition.

Birth seasonality refers to the regular fluctuation of births over a year[12]. In heterogeneous environmental regimes, seasonality affects behavioural ecology and reproduction in many ways including timing and the narrowness of the breeding peak[13,14]. Additionally, environmental stress may also affect birth seasonality[14]. Macaques exhibit various patterns of reproductive seasonality; from sharply discrete matings and births, to complete non-seasonality where matings and births are distributed throughout the year[15]. The Barbary macaque (*M. sylvanus*), Bonnet macaque (*M. radiata*), Rhesus macaque (*M. mulatta*), Japanese macaque (*M. fuscata*), Tibetan macaque (*M. thibetana*) and Formosan rock macaque (*M. cyclopis*) show discrete reproductive seasonality. *M. fascicularis*, *M. silenus*, Toque macaque (*M. sinica*), and Celebes macaque (*M. maurus*) give birth throughout the year with distinct birth peaks, and black crested macaque (*M. nigra*) and Tonkean macaque (*M. tonkeana*) are completely non-seasonal without any prominent peak[16].

M. fascicularis are widely distributed in the Nicobar, Bali, Jawa, Kalimantan, Lesser Sunda, Penninsular Malaysia and is largely confined to islands[17]. *M. f. umbrosus*, one of the 10 sub-species of *M. fascicularis*, is found on three offshore islands of the southern and central Nicobar archipelago including Great Nicobar, Little Nicobar and Katchal[18] of India. These islands were hit by massive earthquake followed by tsunami in 2004, which drastically reduced the population of macaques[19]. Velankar *et al.*[20] reported that the population is in the process of recovering from the crash even after 10 years. The recovery in population size may be dependent on adjustments or alterations in the life-history traits of the species, viz. birth rate, survival rate, emigration and immigration, as all these play a major role in regulating population growth. Since conservation and population management requires basic data on demographic structures and population dynamics, we present, in this article, the first ever data on the demography and birth seasonality of *M. f. umbrosus* in this small, isolated, and environmentally stressed population and set a platform for long-term monitoring of population dynamics.

Materials and methods

Data collection

This study was carried out from January 2013 to December 2015 in the Great Nicobar Biosphere Reserve, Great Nicobar Island, India (Figure 1). We selected five groups of Nicobar long-tailed macaques (LB, MG, PI, TR and MA) inhabiting areas in and around Campbell Bay village for the current study. Due to remoteness and inaccessibility of the habitat, frequent finding of groups and collecting data on different aspects from all these study groups was difficult. Data was collected on group size and group composition for four groups (LB and MG from March 2014 to March 2015, PI and TR from March 2013 to December 2015), birth data for all the five groups from January 2013 to December 2015, infant survival data for two groups (MG and TR) and inter-birth interval data for one group (TR).

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

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

Monthly rainfall data for six years from 2010 to 2015 of Nicobar Islands was obtained from the India Meteorological Department, Andaman Nicobar and Lakshadweep group of Islands, and Ministry of Earth Sciences (Government of India).

Data analysis

We combined the classes of sub-adult males, juveniles and infants into one category as immatures, while, for some analyses, adult males and adult females were put together as adult individuals. The age–sex ratio was computed and analysed for five categories: adult males (ADM), adult females (ADF), adult individuals (AD), immatures (IMM) and infants (INF). In a fission–fusion macaque society, temporary absence of the macaques from the main group is a common phenomenon[21], and hence, for group dynamics, an individual was considered to be part of a group only (or not) if it was present (or absent) for a continuous stretch of at least 15 days.

We calculated the mean group size and the number of individuals in each age–sex class (ADM, ADF and IMM) and age–sex ratio (ADM : ADF, AD : IMM, ADF : IMM and ADF : INF) for all the groups using the data collected in the month of March for each year.

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

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

Birth data collected from all the five groups were arranged month-wise. Mean monthly rainfall of each month was calculated from the rainfall data of six years (2010–2015). Pearson's product–moment correlation test was applied to check the relation between monthly births and mean rainfall data. All statistical analysis was done using SPSS 20 statistical software.
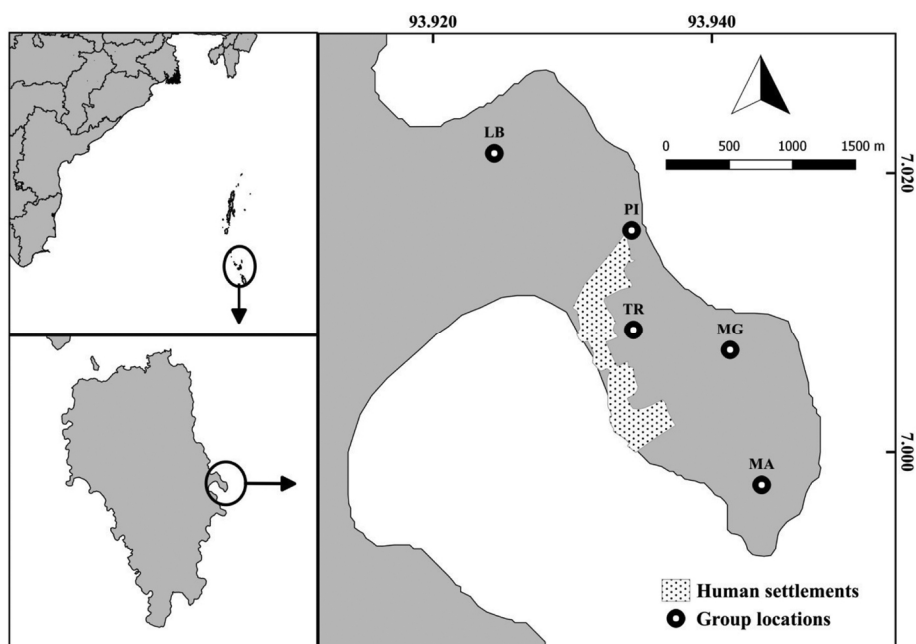
Figure 1. Group locations in the study site, Campbell Bay, Great Nicobar Island.

Table 1. Variation in group size and age–sex individuals between group years ($N = 10$) in the study groups ($N = 4$)

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

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

Table 2. Age–sex ratio of study groups ($N = 4$) between group-years ($N = 10$)

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

INF, Infant.

Ethical note

The study was approved by the ethical committee of Sálim Ali Centre for Ornithology and Natural History (Coimbatore). Permission to carry out this study was granted by the Andaman and Nicobar Forest Department (Permit No. CWLW/WL/134/566). All research activity conducted for the study complied with appropriate institutional Animal Care, Use Committee, laws and guidelines of the Ministry of Environment, Forest and Climate Change, Government of India.

Results

The mean group size of LB, MG, PI and TR were 39, 40, 79 and 16.67 respectively (Table 1) differed significantly (Kruskal–Wallis $H = 246.07$, $P = 0.01$ indicating that the group size varied more across groups than within the groups across the years). However, the size in the case of each group did not differ over the years (Table 1). Similarly, the number of adult males, adult females and immature individuals also did not change over the years. The overall adult male to adult female ratio in the population over the years was $1 : 2.05$. Although this ratio did not vary significantly over the years in either of the groups, the smallest TR group showed more variation than the other groups over the years (Table 2). The age–sex ratios for other classes were almost similar in all groups over the years (Table 2).

A total of 69 births were recorded in the four main study groups, of which 25 were males and 44 were females. The mean birth rate was 0.49 per adult female

per year (range: 0.32–0.70) with maximum in MG (0.70) in 2014 and minimum in PI (0.32) in the year 2013 (Table 3). We treated each group-year as an independent data point for further calculations. The birth rate (Table 3) was neither associated with the number of adult females in the group ($r = 0.33$, $N = 10$, $p = 0.94$) nor with the group size ($r = 0.15$, $N = 10$, $p = 0.68$). The mean annual survival rate of immatures was 0.79 ($N = 65$ animal-years) (Table 4). The mean inter-birth interval in TR group females was 14.75 months with a considerable variation ranging from 9 to 23 between individuals ($N = 8$ females; Table 5).

A total of 92 births were recorded in all the five study groups, which comprised of 33 males and 59 females (Figure 2). Births were distributed throughout the year, though, 13.04% of the births were recorded in July and November, whereas 3.26% were recorded in February

Table 3. Births ($N = 69$) observed and the calculated birth rate in four study groups

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

Table 4. Immature survival rate in each group ($N = 2$)

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

Table 5. Inter-birth interval for TR group females

Female ID	Inter-birth interval (months)
AU 1	17
AU 2	9
AU 3	12
BY 1	18
BY 2	15
BY 3	10
PM 1	23
RE 1	14
Mean (±SD)	14.75 (±4.59)

and April. About 70.65% of the total births were recorded in the wet season (May–November). The number of adult females and the number of births did not vary systematically over the months ($\chi^2 = 0.56$, d$f = 11$, $P = 0.99$ and $\chi^2 = 7.65$, d$f = 11$, $P = 0.75$ respectively). The number of births in a month was positively correlated with total rainfall in that month ($r = 0.621$, $N = 12$, $p = 0.03$; Figure 3).

Discussion

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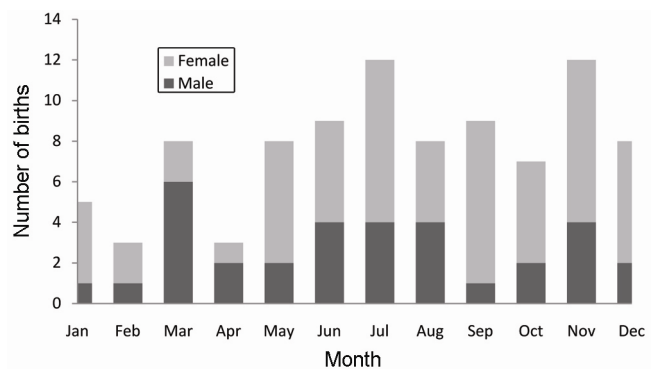

Figure 2. Distribution of births in each month in all groups ($N = 92$, males = 33, females = 59).
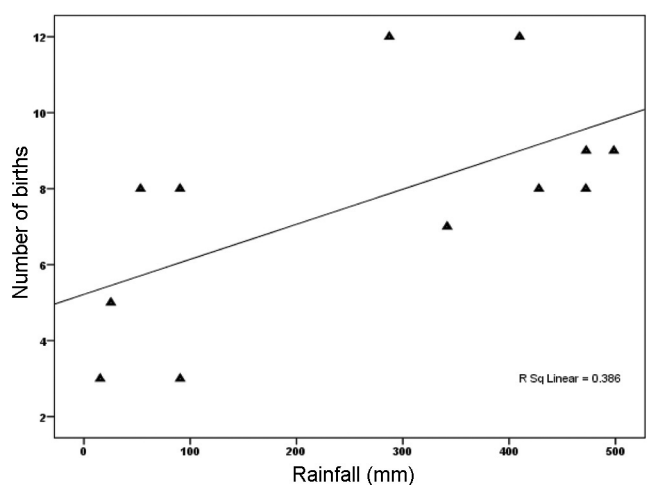

Figure 3. The relationship between number of births in a month and mean monthly rainfall.

Macaques live in a largely female philopatric society where females stay in their natal groups and males migrate[22]. Frequent inter-group male migration makes the demographic structure very dynamic[4]. Although adult females do migrate, such instances are rare; nevertheless minimum changes in the number of adult females in study groups between the years may reflect female philopatry in macaques. Conversely, variation in the number of immatures other than age–sex individuals causes the maximum observed variation in the macaque groups. This may be due to the variation in birth rate, high immature mortality and non-natal migration of sub-adult males in macaques[10].

There are optimal demographic sex ratios in each macaque species, which support maximum reproductive output, growth and stability in the population[17]. Although the number of adult females to males in *M. f. umbrosus* (1 : 2.05) is similar to that in *M. f. fascicularis*[23] (1 : 2.10), the immature to adult female ratio was higher in *M. f. umbrosus* (1 : 1.55) than in *M. f. fascicularis* (1 : 1.25). The variation in age–sex ratio between these sub-species may be the result of variation in the local ecological conditions and recent histories.

Neither the per capita group size, nor the per capita number of females was related to birth rate and the birth rate did not differ between the groups, suggesting that the reproductive output of female Nicobar long-tailed macaques did not vary across groups. However, the birth rate in *M. f. umbrosus* (0.49) was lower than that in *M. f. fascicularis* (0.63)[24], though the inter-birth interval and infant survival rate were similar in the two subspecies[25]. Our preliminary findings on demographic parameters of long-tailed macaques show a large consistency between the subspecies, which may be signifying the species-specific conservative nature of traits[4].

Births occurred throughout the year suggesting a non-seasonal breeding pattern in *M. f. umbrosus*, though larger number of births occurred in the wet season than in the dry season. *M. f. fascicularis* showed a May–July birth peak in peninsular Malaysia[26], whereas the population in northern Sumatra showed two birth peaks in July, and September–October[12]. The introduced *M. f. fascicularis* population in Anguar Island, Micronesia, showed marked birth peak during January–April[27]. In frugivorous macaques, breeding pattern strongly depends on seasonal fruit peak which is directly dependent on seasonal rainfall[12]. Hence, phenology of fruiting trees (timing of fruit) of different geographical regions with even similar vegetal characteristics may differ with rainfall variation of that region[26], which can explain the variation in birth pattern in long-tailed macaques. The relatively higher number of births in *M. f. umbrosus* during the rainy months may be due to the high availability of food resources[13], which may support lactating females and provide food to the weaned infants.

Birth rate in most macaque species ranges between 0.29 (*M. silenus*)[28] and 0.78 (*M. cyclopis*)[11], and the birth rate of *M. f. umbrosus* (0.49) falls in the middle range. Immature survival rate of many of the macaque species ranges between 0.52 (*M. sinica*)[29] and 0.96 (*M. silenus*)[10] and *M. f. umbrosus* (0.79) showed an intermediate immature survival rate. However, inter-birth intervals of these macaques can be grouped under two ranges, one is between 13.85 (*M. cyclopis*)[30] and 15.60 (*M. fuscata*)[31] months where the *M. f. umbrosus* (14.75) falls, and the second is between 19.30 (*M. sinica*)[16] and 30.00 (*M. silenus*)[32] months. Although many of the macaque species inhabit evergreen forests, the life history traits vary highly, especially birth rate and inter-birth interval. Phylogenetic background and current ecological factors of a species determine the life history traits which in turn influence the demographic characteristics[33], including the reproductive output[34].

M. f. umbrosus faces both anthropogenic pressures like habitat fragmentation and habitat loss, and natural disturbances like tsunami, cyclones, El Nino events, all of which have a negative impact on these macaques[20]. High degree of similarity of demographic traits of *M. f. umbrosus* with other subspecies shows that these traits are quite conservative, though a few traits appear to be influenced by local conditions and recent history.

1. Chapman, C. A. and Rothman, J. M., Within-species differences in primate social structure: evolution of plasticity and phylogenetic constraints. *Primates*, 2009, **50**, 12–22.
2. Cords, M. and Chowdhury, S., Life history of *Cercopithecus mitis stuhlmanni* in the Kakamega Forest, Kenya. *Int. J. Primatol.*, 2010, **31**, 433–455.
3. Singh, M., Kumara, H. N., Kavana, T. S., Erinjery, J. J. and Kumar, S., Demography and reproductive output in langurs of the Western Ghats, India. *Primates*, 2016, **57**, 501–508.
4. Dittus, W., Demography: a window to social evolution. In *Macaque societies: A Model for the Study of Social Organization* (eds Thierry, B., Singh, M. and Kaumanns, W.), Cambridge University Press, Cambridge, 2004, pp. 87–116.
5. Wrangham, R. W., An ecological model of female-bonded primate groups. *Behaviour*, 1980, **75**, 262–300.
6. van Schaik, C. P., Why are diurnal primates living in groups? *Behaviour*, 1983, **87**, 120–144.
7. van Schaik, C. P., van Noordwijk, M. A., de Boer, R. J. and den Tonkelaar, I., The effect of group size on time budgets and social behaviour in wild long-tailed macaques (*Macaca fascicularis*). *Behav. Ecol. Sociobiol.*, 1983, **13**, 173–181.
8. Takahata, Y. *et al.*, Does troop size of wild Japanese macaques influence birth rate and infant mortality in the absence of predators? *Primates*, 1998, **39**, 245–251.
9. Ryan, S. J., Starks, P. T., Milton, K. and Getz, W. M., Intersexual conflict and group size in *Alouatta palliata*; A 23-year evaluation. *Int. J. Primatol.*, 2007, **29**, 405–420.
10. Kumar, A., Birth rate and survival in relation to group size in the lion-tailed macaque, *Macaca silenus. Primates*, 1995, **36**, 1–9.
11. Hsu, M. J., Lin, J. F. and Agoramoorthy, G., Effects of group size on birth rate, infant mortality and social interactions in Formosan macaques at Mt Longevity, Taiwan. *Ethol. Ecol. Evol.*, 2006, **18**, 3–17.
12. van Schaik, C. P. and van Noordwijk, M. A., Interannual variability in fruit abundance and reproductive seasonality in Sumatran

long-tailed macaques (*Macaca fascicularis*). *J. Zool.*, 1985, **206**, 533–549.

13. Brockman, D. K. and van Schaik, C. P., Seasonality and reproductive function. In *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates* (eds Brockman, D. K. and van Schaik, C. P.), Cambridge University Press, Cambridge, 2005, pp. 269–306.

14. Janson, C. and Verdolin, J., Seasonality of primate births in the relation to climate. In *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates* (eds Brockman, D. K. and van Schaik, C. P.), Cambridge University Press, Cambridge, 2005, pp. 307–350.

15. van Schaik, C. P. and Brockman, D. K., Seasonality in primate ecology, reproduction, and life history: an overview. In *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates* (eds Brockman, D. K. and van Schaik, C. P.), Cambridge University Press, Cambridge, 2005, pp. 3–20.

16. Bercovitch, F. B. and Harvey, N. C., Reproductive life history. In *Macaque Societies: A Model for the Study of Social Organization* (eds Thierry, B., Singh, M. and Kaumanns, W.), Cambridge University Press, Cambridge, 2004, pp. 61–83.

17. Gumert, M. D., The common monkey of Southeast Asia: Long-tailed macaque populations, ethnophoresy, and their occurrence in human environments. In *Monkeys on the Edge: Ecology and Management of Long-tailed Macaques and their Interface with Humans* (eds Gumert, M. D., Fuentes, A. and Engel, L. J.), Cambridge University Press, Cambridge, 2011, pp. 3–44.

18. Umapathy, G., Singh, M. and Mohnot, S. M., Status and distribution of *Macaca fascicularis umbrosa* in the Nicobar Islands, India. *Int. J. Primatol.*, 2003, **24**, 281–293.

19. Sivakumar, K., Impact of the tsunami (December 2004) on the long tailed macaque of Nicobar Islands, India. *Hystrix It. J. Mamm.*, 2010, **21**, 35–42.

20. Velankar, A. D., Kumara, H. N., Pal, A., Mishra, P. S. and Singh, M., Population recovery of Nicobar long-tailed macaque *Macaca fascicularis umbrosus* following a tsunami in the Nicobar Islands, India. *PLOS ONE*, 2016, **11**(2), e0148205; doi:10.1371/journal.pone.0148205.

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

22. Thierry, B., Social epigenesis. In *Macaque Societies: A Model for the Study of Social Organization* (eds Thierry, B., Singh, M. and Kaumanns, W.), Cambridge University Press, Cambridge, 2004, pp. 267–294.

23. van Noordwijk, M. A. and van Schaik, C. P., Male migration and rank acquisition in wild long-tailed macaques. *Anim. Behav.*, 1985, **33**, 849–886.

24. van Noordwijk, M. A. and van Schaik, C. P., Competition among female long-tailed macaques, *Macaca fascicularis*. *Anim. Behav.*, 1987, **35**, 577–589.

25. van Schaik, C. P., Netto, W. J., van Amerongen, A. J. J. and Westland, H., Social rank and sex ratio of captive long-tailed macaque females (*Macaca fascicularis*). *Am. J. Primatol.*, 1989, **19**, 147–161.

26. Kavanagh, M. and Laursen, E., Breeding seasonality among long-tailed macaques, *Macaca fascicularis*, in Peninsular Malaysia. *Int. J. Primatol.*, 1984, **5**, 17–29.

27. Poirier, F. E. and Smith, E. O., The crab-eating macaques (*Macaca fascicularis*) of Angaur Island, Palau, Micronesia. *Folia Primatol.*, 1974, **22**, 258–306.

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

29. Dittus, W. P. J., Population dynamics of the toque monkey, *Macacasinica*. In *Socioecology and Psychology of Primates* (ed. Tuttle, R. H.), Mouton, The Hague and Paris, Mouton, 1975, pp. 125–152.

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

31. Fooden, J. and Aimi, M., Systematic review of Japanese macaques, *Macaca fuscata* (Gray 1870). *Fieldiana Zool.*, 2005, **104**, 1–198.

32. Kumar, A., The Ecology and Population Dynamics of the Lion Tailed Macaque (*Macaca silenus*) in South India, 1987, Ph D dissertation, Cambridge University.

33. Chapman, C. A. and Rothman, J. M., Within species differences in primate social structure: evolution of plasticity and phylogenetic constraints. *Primates*, 2009, **50**, 12–22.

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