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Female Montane Slender Loris *Loris tardigradus nycticeboides* at Nuwara Eliya, Sri Lanka. Photo by C.A. Mahanayakage.

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EDITORIAL: WILL WE LOSE THE COUSINS WE DIDN'T KNOW WE HAD?

In the past two years our refined understanding confirmed the existence of two ape species in Southeast Asia that hadn't been known to scientists. First came the Gaoligong Hoolock Gibbon *Hoolock tianxing* Fan et al., east of the Irrawaddy-Nmai Hka River in the China-Myanmar border area (Fan et al. 2017). This was the second newly-recognised species in a decade (following Northern Yellow-cheeked Crested Gibbon *Nomascus annamensis* Van Ngoc Thinh et al. (2010). More surprising was a new great ape, Tapanuli Orangutan *Pongo tapanuliensis* Nurcahyo, Meijaard, Nowak, Fredriksson & Groves in Nater et al. (2017), confined to a small area of Batang Toru, south of Lake Toba in western Sumatra. On current taxonomy, this is one of just eight surviving hominid species on Earth. The last to be described was the Bonobo *Pan paniscus* Schwartz, in 1929. The last extant Asian hominid described was the Sumatran Orangutan *Pongo abelii* Lesson – in 1827.

We may never complete picture of how many hominids have gone extinct in the group's 13-million-year history; about one in nine described species survive. Sadly our Tapanuli cousin is at high risk of extinction now. With fewer than 800 left it is the rarest hominid, one whose range was probably once much wider in southern Sumatra. Nater et al. (2017) point to ongoing threats of road construction, illegal clearing of forests, hunting, killings during crop conflict, and trade, citing Wich et al. (2012, 2016). They also refer to a proposed hydroelectric development that could impact up to 8% of *P. tapanuliensis*'s habitat and split the range.

As a single, major threat, this deserves scrutiny. A Chinese state-run company, Sinohydro, has begun clearing forest for a large dam despite opposition by local communities, scientists, non-profit organisations, global citizens and international financial institutions. Critics note it has breached a range of company policies, government guidelines and international commitments (Anon., 2018), and ask to immediately halt all construction activities and restore damaged sites, reassess environmental and social impacts, and grant protected status to the entire Batang Toru forest complex.

The Tapanuli dam is considered to fall under China's vast Belt and Road Initiative, which is set to drive a whole slew of biodiversity losses (Lawton, 2018). Domestically, China is paying increasing attention to the idea of Ecological Civilisation. The question arises: will Ecological Civilisation stop at the borders? If extinction of one of our closest relatives is considered an acceptable cost, it's hard to be optimistic. But if civilisation is to be a long-term experiment, many prevailing ideas about development will need to be revised.

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PHOTOGRAPHIC RECORD OF THE ASSAMESE MACAQUE *Macaca assamensis* IN TRIPURA, NORTHEASTERN INDIA

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The Assamese Macaque *Macaca assamensis* (Mc-Clelland) is a relatively common primate of the Himalaya (west up to Kumaon in Uttarakhand) and adjacent areas including the northeastern (NE) states (Choudhury 2016). Its occurrence in the state of Tripura (Fig. 1) in NE India was doubted by many. Prater (1980), Mukherjee (1982), Mukherjee & Chakraborty (1992), Gupta (1994; 2000; 2001a; 2001b) and Majumder et al. (2015) did not report its occurrence in the state. Similarly, Corbet & Hill (1992) made no mention of Tripura, and the range map excluded not only Tripura but many other areas of known distribution in northeast India. Choudhury (2001), however, mentioned that it occurs in all the northeastern states of India (including Tripura). This was mainly based upon occurrence near Assam–Tripura border in North Tripura district (Choud-



Fig. 1. Location of observed Assamese Macaque in Tripura (as represented by the red dot).



Fig. 2. Alpha male of observed group. © Anwaruddin Choudhury



Fig. 3. Some members of the observed group. $\ensuremath{\mathbb{O}}$ Anwaruddin Choudhury

hury 2013); however, there was no photographic record. Srinivasulu & Srinivasulu (2012) also listed the species in Tripura but without any details or reference.

During my short visits (one day each) in October 1997 and April 2000, and seven days' field work in January 2008 I did not come across any *M. assamensis*. I again spent 20 days in January–February 2016. On 3 February 2016, some unidentified macaques were noticed in the trees near Udaipur–Amarpur main Road (I travelled through this road in 2008 also), roughly midway between the two towns in Gomati district (earlier part of South Tripura district). They were *Macaca assamensis*, of which there were no published records from interior areas. Subsequently I saw them on several other days in the same spot, c. 10 km before reaching Amarpur (23°30' N, 91°36.3' E; c. 100–130 m a.s.l.). Fig. 2 and Fig. 3 illustrate the first photographic evidence of *M. assamensis* from Tripura.

These were of the nominate subspecies, i.e., *M.* assamensis assamensis (McClelland) as indicated by their tail-length. The area is a reserved forest known as Boromura–Gandhari. There were at least 16 macaques in the group, which included one alpha male, one more adult male, two adult females with infant being carried, two adult females without infant and eight subadults/ juveniles. The habitat was tropical moist deciduous with some teak *Tectona grandis* L. f. plantations distributed therein. The macaques were observed mostly in mixed natural patches, and would flee upon detecting us.

Potential threats to the group observed include *jhum* or slash-and-burn shifting cultivation. Some tribes also kill primates for the pot. Other conservation concerns in nearby areas are clearing of forest, even inside reserved forests, for paddy cultivation and expansion of rubber cultivation. In some places land allotted to tribal people under the Forest Dwellers (Rights) Act are converted into rubber gardens.

Since the site is the only confirmed locality exclusively within Tripura, therefore it was recommended to the local forest administration to protect the area, may be as an 'eco-park', as in Tripura such eco-parks have protected several forest patches from destruction.

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6

PREVIOUSLY UNREPORTED POPULATION OF RHESUS MACAQUES *Macaca mulatta* IN CHIANG RAI PROVINCE, THAILAND: PRELIMINARY OBSERVATIONS

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ABSTRACT

Efforts to document the distribution of macaques in Thailand have been gradually improving over the past several years. Here we add to the growing database with a summary of a previously unreported population of Rhesus Macaque *Macaca mulatta* located at Wat Phrabuddhabat Pa Reau in Chiang Rai Province. This work is part of an on-going study addressing human-primate conflict and coexistence in Thailand. The Wat covers an area of about 53 ha consisting of forest and ponds surrounded by an agricultural/rural residential area. The macaques receive some provisioning by the monks, nuns, local residents and occasional tourists. We conducted observations of the macaques and queried the monks, nuns and local residents during 20-21 November 2015 and 22-23 July 2016. Those queried reported population sizes ranging between "100" and "2000" monkeys and 1-4 groups. Based on our observations, we identified at least two groups of approximately 55 and 44 monkeys. All individuals queried reported crop raiding and expressed concern over an "increasing" monkey population and need for effective population management. We plan to follow up with a more intensive survey of this population to better assess conservation concerns, human-primate interaction, and options for healthy coexistence.

Keywords: conservation, human-primate conflict, population distribution, population management

INTRODUCTION

Assessing the distribution and status of nonhuman primate populations is essential for effective conservation and management of these species (Malaivijitnond et al., 2005; Lwanga et al., 2011; Kyes et al., 2013b). In Thailand, the pioneering work by Aggimarangsee (1992) and Malaivijitnond and colleagues (Malaivijitnond & Varavudhi, 2002; Malaivijitnond et al., 2005) has provided important data on macaque distribution throughout the country.

Currently, there are six species of macaques found in Thailand: Long-tailed Macaque *Macaca fascicularis*

(Raffles) (the most frequently observed species: Malaivijitnond et al., 2005); Stump-tailed Macaque *M. arctoides* (I. Geoffroy Saint-Hilaire); Assamese Macaque *M. assamensis* (McClelland); Northern Pigtailed Macaque *M. leonina* (Blyth); Sunda Pig-tailed Macaque *M. nemestrina* (Linnaeus); and Rhesus Macaque *M. mulatta* (Zimmermann) (and see Lekagul & McNeely, 1988; Malaivijitnond et al., 2005; Roos et al., 2014). Although the Rhesus Macaque is listed as Least Concern by the IUCN Red List (Timmins et al., 2008), in Thailand it has been reported in only 13 locations throughout the northeastern and western regions of the country during the past 40 years (Eudey,

Location Name	Province and Coordinates	Study period*	Reference(s)
1. Wat Pa Aranwiwek- Phusing	Nongkhai (N18º12'27.1" E103º50'00.5")	1998-2004	Malaivijitnond et al., 2005
2. Wat Pa Banpaun	Udon Thani (N18º00'47.3" E102º05'10.5")	1998-2004	Malaivijitnond et al., 2005
3. Wat Pa Phukon	Udon Thani (N17º54'54.9" E102º07'20.2")	1998-2004	Malaivijitnond et al., 2005
4. Wat Pa Nakham Noi	Udon Thani (N17º54'14.4" E102º10'03.8")	1998-2004	Malaivijitnond et al., 2005
5. Ban Sang School	Nongkhai (N17º51'27.4" E103º57'46.7")	1998-2004	Malaivijitnond et al., 2005
6. Wild Monkey Park	Nakhon Phanom (N17º39'29.8" E104º19'58.3")	1998-2004	Malaivijitnond et al., 2005
7. Wat Phattanajit	Nakhon Phanom (N17°26'08.5" E104°34'23.1")	1998-2004	Malaivijitnond et al., 2005
8. Wat Tham Pa Mak Ho	Loei (N17°14'05.6" E101°46'80.8")	1998-2004	Malaivijitnond et al., 2005
9. Wat Tham Sung	Loei (N17º04'51.5" E101º47'14.7")	1998-2004	Malaivijitnond et al., 2005
10. Kumpawapi Park	Udon Thani	1989, 1991	Aggimarangsee, 1992
11. Phu Khieo Wildlife Sanctuary	Chaiyaphum (N16º27' E101º38')	2000-2001	Borries, et al., 2002
	Chaiyaphum (N16º27'38.3" E101º39'22.2")	1998-2004	Malaivijitnond et al., 2005
12. Huai Kha Khaeng Wildlife Sanctuary	Uthai Thani	1973-1986	Eudey, 1980; 1991
13. Thung Yai Naresuan Wildlife Sanctuary	Tak	1973-1986	Eudey, 1980; 1991

Table 1. Reported distribution of *M. mulatta* in Thailand over the past 40+ Years.

*Presumed study dates. We have attempted to identify the dates of observation to the best of our understanding. Exact study dates are not always clearly specified in some papers.

1980, 1991; Aggimarangsee, 1992; Borries et al., 2002; Malaivijitnond & Varavudhi, 2002; Malaivijitnond et al., 2005) (see Table 1 and Fig. 1). Most of these identified Rhesus Macaque sites appear to be situated around Buddhist temples (*Wat*). Data on the population demographics at each site are limited at best.

Here we add to the growing database on Rhesus Macaque distribution in Thailand with a summary of our preliminary observations of a previously unreported population of Rhesus Macaques located at Wat Phrabuddhabat Pa Reau in Chiang Rai Province. This work is part of an on-going study addressing humanprimate conflict and coexistence in Thailand.

METHODS Study Area

Wat Phrabuddhabat Pa Reau is located in Northern Thailand at N20°10'52.6", E100° 03'32" (Fig. 1). It is located in Pa Reau Village, Ta Kow Pleak Sub-district, Mae Chan District, in the province of Chiang Rai. The Wat was established in 1979 and covers an area of 52.8 ha (0.53 km²) consisting mostly of deciduous forest, orchards, a large pond, and several smaller ponds. Within the Wat forest/grounds, there are a wide variety of natural food sources (e.g. *Ficus* spp., bamboo spp.) and cultivated fruit trees (e.g. lychee, mango). The Wat is surrounded by agricultural land 8



Fig. 1. Locations of *Macaca mulatta* populations in Thailand reported over the past 40+ years, including Wat Phrabuddhabat Pa Reau, Chiang Rai. Refer to Table 1 for location details. (Courtesy: Google Earth: 2015 Google; 2015 CNES / Astrium.)

(e.g. rice fields, pineapples and corn) and also rural residential areas (Fig. 2).

A local attraction at the Wat is the resident population of Rhesus Macaques that local residents, and occasional tourists, come to feed (Fig. 3). We first learned of a possible Rhesus population at Wat Phrabuddhabat Pa Reau in 2014 from a local village leader who participated in our annual field course in Conservation Biology & Global Health (Kyes et al., 2013a) in collaboration with Mae Fah Luang University that year. To help regulate feeding of the monkeys, there is a designated "feeding area" situated by the large pond that serves as a rest/recreation area where people can purchase bananas and corn to feed the monkeys (Fig. 4). The Buddhist monks and nuns also provide occasional provisioning with bananas and corn. In addition to feeding the monkeys, people also frequently come to this area to feed the fish (carp and catfish) in the large pond. Commercial fish food also is available for purchase.

Procedure

We conducted preliminary observations of the macaques at this site on two separate occasions: first during 20-21 November 2015 and again during 22-23 July 2016. We conducted brief walking surveys of the Wat area (using established roads/trails) and observed the monkeys during feedings by the Wat's nuns and



Fig. 2. Wat Phrabuddhabat Pa Reau and surrounding agricultural and rural residential areas. Yellow line indicates approximate Wat boundary. (Courtesy: Google Earth: 2015 Google; 2015 CNES / Astrium)



Fig. 3. Adult male Rhesus Macaque (*M. mulatta*) at Wat Phrabuddhabat Pa Reau (photo by R. Kyes).

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Fig. 4. Local residents feeding bananas to the Rhesus Macaques in the "feeding area" at Wat Phrabuddhabat Pa Reau (photo by R. Kyes).

visitors to obtain estimates of number of groups and approximate group size (via direct count).

We also queried several individuals in and around the Wat (monks, nuns, and local residents) regarding the status of the monkeys and possible conflict (similar to our previous/on-going work in Indonesia and Thailand: Kyes et al., 2011; R.C. Kyes et al., in press). Questions included: 1) How long have the monkeys been here? 2) How many groups/monkeys live here? 3) Is there any conflict with the monkeys? If yes, what kind of conflict and how do people deal with the conflict?

RESULTS

Based on responses from the individuals queried (n=12, including monks, nuns, and local residents),

the monkeys have lived in the Wat forest for at least 40 years: at least as long as anyone interviewed can remember. Presumably, the monkeys are a remnant population of larger population that would have existed in what was once a more expansive forest area. As the forest habitat decreased over the decades (due to agricultural expansion), the monkeys would have become restricted to the remaining forest fragment protected at the Wat.

Individuals also reported population sizes ranging between "100" and "2000" monkeys, and estimates of 1-4 groups. Based on our observations, we identified at least two groups (Group 1 and Group 2) with group sizes of approximately 55 and 44 monkeys respectively (based on direct counts during feeding). We also observed what appeared to be an all-male group of six young adult/sub-adult males. Although our preliminary observations did not allow sufficient time for "high confidence" counts of group sizes or estimates of composition, we did obtain our best estimates with Group 1 during a morning feeding. This group of 55 monkeys was composed of three adult males (one shown in Fig. 3), 13 adult females, two sub-adult males, three sub-adult females, 24 juveniles and 10 infants. Again, we consider these estimates to be preliminary counts generated during a short observation period.

In response to the question of conflict, all individuals reported crop raiding by the monkeys. One individual (local farmer) mentioned that the crop raiding has become so severe that he decided to change his entire agricultural production from pineapples to coffee. We observed active crop raiding in a corn field as well as a pineapple field located along the Wat border (Fig. 5). The monks also reported that the monkeys often destroyed the Wat property by ripping shingles off the roofs of the buildings.

Local residents reported using electric fencing along the perimeter of their pineapple fields to guard their crops (also see Fig. 5). They also used sling shots and firecrackers to scare the monkeys away. There were no reports of aggressive behaviour being directed toward people by the monkeys. We observed only a brief stare threat by an adult female directed toward a woman during a feeding event. All individuals queried expressed growing concern over an "increasing" monkey population and the need for effective population management.

DISCUSSION

The confirmation of an existing Rhesus Macaque population at Wat Phrabuddhabat Pa Reau in Chiang Rai Province adds to the current database on Rhesus Macaque distribution in Thailand and brings the number of known sites with Rhesus Macaque populations to 14. These findings also extend the observed existing range of Rhesus Macaques in Thailand close to the country's northern border. The identification of this previously unreported population is significant in that Rhesus Macaque populations in Thailand are now considered relatively rare (Malaivijitnond et al., 2007). Thus the discovery of any existing Rhesus Macaque



Fig. 5. Rhesus Macaques sitting at the edge of a pineapple field adjacent to the forest boundary at Wat Phrabuddhabat Pa Reau where crop raiding is a frequent occurrence (photo by R. Kyes).

population deserves special attention and careful consideration on how best to ensure successful management and conservation.

Rhesus Macaques in Thailand (like many primate species around the world) are being impacted by a number of anthropogenic pressures including habitat loss and urbanization, resulting in confinement to forest fragments, decrease in genetic heterogeneity, and increasing interaction and conflict with humans. Issues of hybridization (via release of pet macaques of other species) also pose a threat to the genetic integrity of the remaining natural Rhesus Macaque populations in Thailand. This is a serious conservation concern that has been studied and discussed by Malaivijitnond et al., (2005) and Malaivijitnond et al., (2007). From our preliminary observations, we believe the Rhesus Macague population at Wat Phrabuddhabat Pa Reau is likely a pure species population: an assumption based on the characteristic morphological appearance of the monkeys. Obviously, genetic assessment will be required for positive determination.

Perhaps the greatest concern for the long-term sustainability of the Wat Phrabuddhabat Pa Reau macaque population is how to ensure the healthy coexistence between the people and the monkeys. The on-going conflict with the monkeys was a serious issue for the people we spoke with. The conflict was impacting their daily activity and economic welfare. This was perhaps most evident from the farmer who switched to coffee production having managed pineapple crops for several years in fields adjacent to the Wat forest. Clearly, this was a significant change with considerable financial investment (and risk) - and a direct result of the on-going conflict. For the monkeys, venturing out of the Wat grounds presents risks such as being shot by a slingshot and the potential of being wounded or killed.

Despite the nuisance and conflict with the monkeys, all individuals we spoke with were concerned about the welfare of the monkeys and appreciated the need for an effective population management program. The first question we were asked by almost every individual we met was, "Are you here to help sterilize the monkeys?" The consensus among everyone we spoke with is that there are too many monkeys, the population is growing and the conflict is increasing. Further, they were unanimous in their desire to have an effective population management plan for the monkeys. As such, we plan to follow up on these preliminary observations with a more intensive survey of this population, including health assessment and genetic analysis, to better assess the conservation concerns, levels of human-primate interaction, and population management options for the healthy coexistence between the monkeys and local residents.

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HABITAT SUITABILITY MODEL FOR THE MONTANE SLENDER LORIS IN THE HAKGALA STRICT NATURE RESERVE, SRI LANKA

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ABSTRACT

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Geographic Information Systems (GIS) and remote sensing are powerful analysis and decision-making tools used in a spectrum of applications in many different fields. The Montane Slender Loris *Loris tardigradus nycticeboides* is an Endangered primate subspecies, found only in the mountain rainforest region of Sri Lanka. This study attempts to validate the applicability of the 'habitat suitability model' on the Montane Slender Loris located in the Hakgala Strict Nature Reserve (HSNR), in the central highlands of Sri Lanka, using GIS and remote sensing techniques. The main objectives are to map the habitat suitability factors, along with related topographic data through GIS, and to reveal the possibility of using spatial and geographical features for effective analysis to identify suitable habitats of the Montane Slender Loris in the HSNR. The study reveals available habitat for the species is critically small, accounting for only 4.3% of the protected land area, suggesting improved management may be needed to ensure the future survival of the loris in the HSNR.

Keywords: Conservation, Geographic Information Systems, Habitat suitability, Montane Slender Loris

INTRODUCTION

It is widely recognized that the main threats to species persistence include habitat loss and fragmentation. Conservationists must take into account the species' living patterns to make educated conservation plans for them. Ecological Niche Modelling (ENM) has been developed to include suitable habitat and species range estimates for consideration in conservation (Chefaoui et al., 2005; Gaubert et al., 2006; Guisan et al., 2006). This technique can provide information for protectedarea prioritization and protected-area network design (Margules & Austin, 1994; Rondinini et al., 2005; Sánchez-Cordero et al., 2005) and identify the effects of habitat disturbance on species distribution (Banks et al., 2005; Sánchez-Cordero et al., 2005; Rhodes et al., 2006). Interpretation involves understanding the analysis method, types, mechanisms and effects of biotic interactions that affect a species' distribution (Kearny, 2006; Soberón, 2007). The ecological niche is a set of environmental variables which favours a species' distribution and maintains a viable population (Grinnell, 1917). The biogeographic distribution of a species is based on abiotic and biotic conditions as well as geographical accessibility (Soberón & Peterson, 2005). ENM-based predictions of suitable living areas for a species (Guisa & Thuiller, 2005; Peterson & Kluza, 2003) can help guide conservation priorities (Loiselle et al., 2003). Ecological studies in Sri Lanka have produced a body of knowledge about the habitat requirements and threats of the Montane Slender Loris *Loris tardigradus nycticeboides* (Hill, 1942; Mahanayakage, 2013; Gamage et al., 2015). Methods and channels capable of bringing this knowledge into the field of practical forestry and nature conservation are needed.

The Montane Slender Loris, classified by the IUCN Red List as Endangered (Nekaris, 2008), is a primate inhabiting the mountain region of central Sri Lanka (Gamage et al., 2015). Gamage et al. (2015) highlighted that the Montane Slender Loris is an extreme habitat specialist found only in the montane evergreen forests in the Nuwara-Eliya area (Fig. 1). Furthermore, their occupancy modelling study revealed that Montane Slender Loris occupancy was closely associated with altitude, canopy height and canopy connectivity: the best habitat being taller-canopy (height >4m) montane evergreen forests between 1,600 and 2,100 m above sea level (asl) with good canopy connectivity (Gamage et al., 2015). The study confirmed that Montane Slender Loris is an extremely rare and critically threatened species in Sri Lanka, and identification of suitable habitats is one of the key aspects of Montane Slender Loris conservation (Gamage et al., 2015).

Several species distribution modelling tools, with broad ecological applications, have been used in the past (Peterson, 2003). These models were developed based on biophysical and environmental factors to predict the distribution of a species according to a predetermined set of ecological conditions found to be preferred by that species. These methods are very sensitive to species sample size and habitat distribution patterns (Wisz et al., 2008). Using the above-mentioned tools, the objective of this study was to predict and locate potential new Montane Slender Loris habitats in Hakgala Strict Nature Reserve (HSNR), which could potentially contain viable populations of lorises that should be protected.

METHODS Study area

This study was conducted in the HSNR in Sri Lanka, a potentially-important habitat for Montane Slender Loris in a mountainous region. This site is situated in the Nuwara Eliya and Badulla districts, and is one of the three Strict Nature Reserves in Sri Lanka, all under the Department of Wildlife Conservation's jurisdiction, and is the only such reserve in the wet zone, where our study was based. Areas with eucalyptus/pine plantations and encroachments were omitted from this study. The HSNR covers an area of 11.42 km², ranging in an altitude between 1,650 m to 2,178 m asl (Fig. 1).

Data collection

This survey was conducted in March 2015. Information was collected as point data. The representativeness of a sample obtained by simple random sampling makes it reasonable to make generalisations from the results of the sample back to the population (Kearny, 2006). Hence, we made 100 random sampling points in the study area where suitability factors were measured. With this technique, each point of the population has an equal chance of being selected. ARC GIS 10 Random Point Generator



Fig. 1. Random Sampling Points in the Hakgala Strict Nature Reserve.

was used to generate random points in the selected study area as shown in Fig. 1.

Generated data points were imported to Google Earth. According to a terrain profile of the area, a track was created connecting approximately 10 nearby points. Walking along each track was attempted during the visit, but on some days this was not possible due to difficulties in manoeuvring through the fallen trees. The search was conducted by walking along navigational tracks created for sampling data points, as presented in Fig. 2. Randomly created data points were imported to GPS. A Trimble Juno SB GPS helped to navigate the random points. Canopy height of each point was measured using a laser Range Finder (TruPulse 200L, Lasertech, Colorado, USA), and the canopy connectivity was measured using photographs of each random point, captured using a digital camera (Sony COOLPIX P 900) at 1 m height from the ground. Initially, a captured image was converted into a greyscale image using Adobe Photoshop. The canopy cover percentage was calculated using black and white pixels in each picture. Since there were more than 100 photographs taken, manual calculation of black and white pixels was a time-consuming process. Therefore, the canopy connection percentage of each image was calculated using a self-developed software application in the NET platform. Canopy connectivity was measured as a percentage where the dark area was considered as the where the light is not passing and calculated it as the area of canopy.

Modelling procedure

We used loris species occurrence records in which frequent sightings of 25-30 loris were observed. The locations were marked with GIS, categorised by environmental (bioclimatic) factors, and analysed using the maximum entropy distribution modelling approach (Peterson, 2003) to identify areas of potential occurrence of Montane Slender Loris in HSNR. In the current predictions generation, we used the freeware MaxEnt, version 3.3.3 (Phillips et al., 2004). Using ArcGIS, we generated the estimates of species presence probability, varying from 0 (lowest) to 1 (highest). MaxEnt uses the values of user defined points selected randomly from 10,000 points and constructs an index of habitat suitability falling between 0 and 1. Our sample points totalled 10 (Phillips et al., 2004). Even though sample size was small, the variables could be tested by examining cross-correlations (Pearson correlation coefficient, r>7) among them, based on 100 localities of species occurrence records randomly generated from the area (following Fielding & Bell, 1997). Furthermore, the difference between high,



Fig. 2. The navigational tracks for sampling points.



Fig. 3. Predicted potential suitable habitat for Montane Slender Loris in Hakgala Strict Nature Reserve, Sri Lanka; A – Digital elevation model; B – Height distribution; C – Canopy cover distribution; D – Habitat suitability map of Montane Slender Loris.

medium, and low potential was defined as subsets of a species potential presence in the predicted area variable space corresponding to geographic locations defined by actual or potential habitat preferences of the species (Gromley et al., 2011).

RESULTS

To construct the habitat suitability map for Montane Slender Loris in HSNR, five key-feature datasets, or data layers were used: HSNR study area, base map imagery, elevation data (Fig. 3A), canopy height (Fig. 3B), and canopy connectivity (Fig. 3C). As per the elevation map, the whole of HSNR provides a suitable elevation range for the Montane Slender Loris. However, the canopy cover (canopy connectivity) maps illustrate that only slightly over 25% of the HSNR provides suitable habitat for Montane Slender Loris. Nevertheless, the canopy height map shows 60% of the HSNR is covered with canopy of over 4 m height, which is reportedly the preferred canopy height for Montane Slender Loris (Gamage et al., 2015). Habitat suitability for Montane Slender Loris in the HSNR, assessed using Multi Criteria Decision Analysis (MCDA),

helped to identify additional geographical areas that have potentially suitable habitats for Montane Slender Loris (viz. elevation data, canopy height, and canopy connectivity).

The GIS-based analysis demonstrated the optimal locations where potentially suitable habitats exist, considering the effects of elevation, canopy height and canopy connectivity. It showed that high-potential areas cannot be found in areas with low canopy cover or in areas of higher elevation. The MaxEnt model successfully predicted potentially suitable habitats for Montane Slender Loris, i.e. 98% success rates at logical process training. The most suitable habitat for Montane Slender Loris was predicted in the highest canopy area where we observed 25 lorises (Figs. 3B & 3D), and its distribution was quite fragmented. The MaxEnt model's internal Jackknife test of variable importance indicated that 'Height distribution and canopy distribution' were the two most significant predictors of Montane Slender Loris habitat distribution.

According to this model, as shown in Fig. 3D, it is estimated that there exists approximately a 49-hectare (0.5 km²) land area in HSNR with very high potential habitat suitability for Montane Slender Loris, followed by an 848-hectare (8.5 km²) with medium potential habitat suitability, and a 60-hectare (0.6 km²) with low potential habitat suitability. Furthermore, the model clearly highlighted that Montane Slender Loris habitats in the HSNR are highly fragmented.

DISCUSSION

These results provide information for future species management planning and will help to locate new habitat locations and determine the extent of those areas. This study revealed that the habitat distribution patterns for threatened and endangered species such as the Montane Slender Loris can be modelled with MaxEnt, using a small number of occurrence records and environmental variables, like previous studies (Hoffman et al., 2008). This method has been proven to perform better than other modelling approaches (Ortega-Huerta & Townsend, 2008). MaxEnt estimates the probability distribution of a species' presence data, based on environmental variables, even using small sample sizes of up to six specified localities. The potential habitat distribution map for Montane Slender Loris can aid in planning land use management around its existing populations, discover new populations, identify top-priority survey sites, and set priorities to restore its natural habitat for more effective conservation. More research is needed to determine whether the existing protected areas adequately cover suitable habitats for Montane Slender Loris.

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POPULATION SIZE AND DISTRIBUTION OF THE CAPPED LANGUR *Trachypithecus pileatus* (Blyth, 1843) IN MADHUPUR NATIONAL PARK, BANGLADESH

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ABSTRACT

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We studied the population size and distribution of the Capped Langur *Trachypithecus pileatus* in Madhupur National Park, Bangladesh, from February to October 2015. Altogether, we recorded 99 individuals. We found 98 individuals from 12 groups and one isolated adult male. The group size ranged from 4 to 14 (mean 7.62 \pm 3.2) individuals; 48.5% were adults and 51.5% were non-adults. The ratio of adults to non-adults was 1:1.06, and the adult sex ratio of males to females was 1:2.69. We recorded most (61.5%) of the groups within the park boundaries in undisturbed dense forest with a high diversity of food plants and a high canopy layer.

Keywords: group composition, group size, sex ratio

INTRODUCTION

Bangladesh has a comparatively poor forest cover (1.4 million hectares) accounting for only 11% of the country's land area (FAO, 2010). There are three species of colobines in Bangladesh: the Capped Langur Trachypithecus pileatus (Blyth), Phayre's Langur T. phayrei (Blyth), and the introduced Northern Plains Sacred Langur Semnopithecus entellus (Dufresne). In Bangladesh, the Capped Langur is found in dense forest and bamboo patches of both moist deciduous and mixed evergreen forests (IUCN Bangladesh, 2015). In the early 1970s and 1980s it occurred in Gazipur District to Jamalpur, Sherpur, Netrokona and Mymensingh under Mymensingh Division to the forests in Sylhet and Chittagong Divisions. At present, there are only a small number of individuals left in the Mymensingh Division while the remaining populations are only present in the mixed-evergreen forests of Sylhet and Chittagong Divisions (Khan, 2015). This species is also found in northeastern India, northwestern Myanmar, Bhutan and southern China (Srivastava, 1999). It is assessed as nationally Endangered (IUCN Bangladesh, 2015) and globally Vulnerable (Das et al., 2008). Populations of this species face a range of threats, particularly to their habitat, with the most severe stemming from human alteration to the forests (Das et al., 2008). Some major causes are jhum cultivation, plant monocultures, timber and firewood harvests, and other development, resulting in a loss of trees in which this species feeds, travels and sleeps (Das et al., 2008). Also, these langurs are subject to trade for their meat and other body parts, and as pets (Molur et al., 2003).

A few studies have reported on the population status of this species in Bangladesh (Gittins, 1980; Feeroz, 2001) and India (e.g. Kumar & Solanki, 2008; Biswas et al., 2009), and there is some information on its activity patterns, diet and reproductive behaviour in Madhupur National Park and other areas in Bangladesh (e.g. Green, 1981; Islam & Hussain, 1982; Stanford, 1987; 1991; Kabir, 2006; Das et al., 2008; Mandal & Kabir, 2014). The Madhupur National Park is under severe pressure due to the harvesting of fuelwood and dry leaf litter for cooking, grazing of livestock, illicit tree felling, and fire hazards (Khan, 2010). Large numbers of people (~60,000) live in this area, and the demand for fuelwood, timber, building materials, and land to cultivate exerts heavy pressure on the remaining forest (Hossain et al., 2004). An estimate from more than a decade ago showed that over 70% of the Shal Shorea robusta Gaertn. forest is now either degraded or encroached upon (Nishat et al., 2002). The underlying key causes to the destruction of langur habitat are high population pressure and weak forest management. In this study, we investigated the population status and distribution of the Capped Langur in Madhupur

National Park. The aim was to determine the population size and number of groups living in the national park, including group and age-sex composition.

METHODS Study area

The study was carried out in the Madhupur National Park, Tangail (Fig. 1) from February to October 2015. The Madhupur forest is the largest tropical moist deciduous forest (24,150 ha) in Bangladesh, a portion (8,436 ha) of which is protected as the Madhupur National Park. The national park is in the northern part of the Bhawal-Madhupur Shal forest tract (24° to 25°15'N and 90° to 91°E, about 20m asl), some 50km south of the Garo Hills of the Meghalaya State of India, and about 150km north of Dhaka, the capital of Bangladesh. Geologically it is a terrace from one to ten metres above the adjacent floodplains. The soils of the tract have developed largely on Madhupur clays, which are nutrient poor and somewhat acidic, and red or brown in colour. The forest ranges from dense stands of trees to areas with sparse stands, including some scrub forests and human settlements. The topography includes numerous depressions with gentle slopes intercepting the ridges. The climate is moderate with warm weather from March to October and a recorded maximum temperature of 34.8°C in April. The minimum was 13.3°C recorded in February. The highest rainfall was recorded in July and lowest in March.

The Garo people are one of the largest indigenous communities (approximately 100,000 to 130,000 people) (Islam, 2008). They live in the northeastern part of Bangladesh with the highest presence in the Gazipur, Mymensingh, Netrokona, Tangail, Sherpur, Jamalpur and Sylhet districts (Muhammed et al., 2011). Two tribal clans, the Koch and the Mande (Garo), who are dependent on these forests, live in the Madhupur tract (Rahman et al., 2010). The Koch are among the earliest peoples of Bangladesh, while the Mande have their main centre of dispersal in the Garo hills in India (Rahman et al., 2010). Bengali-speaking people, who used to live along the fringes of the extensive forests, have entered in large numbers and cleared most of the forests (Rahman et al., 2010). Bengalis have developed stable agro-horticulture systems in the west (Rahman et al., 2010). Due to anthropogenic disturbances, the landscapes and ecosystems of most of the tract have changed drastically in the last 30 years, triggering the loss of invaluable biodiversity in the area (Rahman et al., 2010).

Shal (Shorea robusta Gaertn.) is the dominant tree species. The other common trees are Palash Butea monosperma (Lam.) Taub., Haldu Adina cordifolia (Roxb.) Benth. & Hook.f. ex B.D.Jacks., Shidah Jarul Lagerstroemia parviflora Roxb., Bazna Zanthoxylum rhetsa DC., Hargoja Dillenia pentagyna Roxb., Koroi Albizia spp., Menda Litsea monopetala (Roxb.) Pers., Kushum Schleichera olosa (Lour.) Merr., Udhal Sterculia villosa Roxb., Bahera Terminalia beliirica (Gaertn.) Roxb., Kurchi Holarrhena antidysenterica (Roth) Wall. ex A.DC., Haritaki Terminalia chebula Retz., Pitraj Aphanamixis polystachya (Wall.) R.Parker, Shorea Streblus asper Lour., Sonalu Cassia fistula L., Assar Grewia microcos L. and Amlaki Phyllanthus emblica L. (Rashid, 2003).

Data collection

We carried out surveys for 36 days, totaling 432 hours. We conducted two-day surveys from dawn to dusk every two weeks using the line-transect method (Brockelman & Ali, 1987). We made nine transects (Table 1, Fig. 1) in and around the forest. The length of the total transects were 85km. The transects were established to avoid areas with spiny Calamus sp. (north and south of transect 3), which were practically difficult to establish given the limited time available for fieldwork. The lowland areas inside the forest are used for seasonal crop cultivation by the local people, which were also avoided during the study period. Some patches of the park area are used for pineapple, banana, arum cultivation and some areas (south of the highway) are used for monoculture plantations (Acacia sp.), and these areas were avoided while setting up the transects. The Kathalia Canal connects to the Banna River and runs through the transect 2 from east (transect 6) to west, and on both sides of the canal there are open paddy fields. Moreover, as the Capped Langurs live in the higher canopy, it is possible to observe them easily from the transects.

We repeatedly surveyed the transects, recording group size and age/sex class of all individuals and any disturbances due to human activities such as settlements, grazing, logging, agriculture, hunting and poaching. We classified the langurs into four age categories: adult, sub-adult, juvenile and infant, based on the morphological differences described by Stanford (1991). We recorded the sex only of adults. We differentiated the groups based on their group size, composition, locations and visible markings of members (injury, abnormalities or other characteristic features) as described by Hasan et al. (2013). We recorded the GPS locations of each group using a Garmin eTrex 20.



Fig. 1. Madhupur National Park and location of transect lines established during the study.

RESULTS Population size

We recorded 98 Capped Langurs in 12 groups and one solitary adult male (Table 2). We observed this isolated adult male near Rasulpur Mazar (Fig. 2). We observed it several times taking food such as bread, bananas, and biscuits from the local people and tourists. Local people reported that it regularly visited Rasulpur, at intervals of 3–5 days to take food from the people. No other langurs were observed taking food from people. We also saw this individual in other parts of the Beribaid forest beat.

We observed the largest sub-population (62.6%) of Capped Langurs in the Beribaid beat of the

Transect no.	Length (km)	Location	Group recorded	Frequency of transect walks
1	8.65	Rasulpur – Pochismail	5,6,7,8,9,10	12
2	1.11	Joloi rest house – Biman Bahini Camp	-	13
3	7.83	National Park Gate – Dokhola	3,4,11,12,13	7
4	8.66	Dokhola – Pochismail	-	5
5	0.59	Joloi resthouse – Garo Village	-	10
6	2.1	Rasulpur Bazar – Razabari	1,2	11
7	1.6	Rasulpur Bazar – Harinatala Village	-	12
8	0.55	Harinatala Village	-	8
9	0.67	Kathalia Village	-	7



Fig. 2. A solitary adult male Capped Langur, Madhupur National Park.

Jatiya Uddan Range (Table 2, Fig. 3). Beribaid is an undisturbed dense forest with a high diversity of food plants and a high canopy layer. The Tangail-Mymensingh highway passes through this beat, and there is a regular transit of forest officers and staff, who prevented the Garo people from hunting.

We did not record the Capped Langur in the peripheral zone of the north-western side of the Dokhola beat of the national park, which has fragmented forest with low tree density and canopy cover. Moreover, there was also high hunting pressure due to settlements of Garo people in this area. The Garo have a history of hunting the langurs for food. This behaviour contrasts with that of the Bengali people (other local people, the majority of whom are Muslims) who do not hunt or consume the langurs. Local people informed us that the Garo people hunted and consumed the langurs opportunistically. Moreover, during our work we observed Capped Langur fleeing when they saw Garo people. Out of 12 groups, we recorded ten groups within the national park boundaries. During winter, when food is scarcer, two of the groups outside of the park moved from natural forest to human settlements (villages of Harinatala and Kathalia of Muktagacha upazila), near the eastern boundary of the national park. These villages are not

Group No.	Location	Sighting date	GPS Location	AM	AF	J	Ι	Total
1.	Kathalia	Aug. 13	N24°40.734′ E90°09.049′	1	3	2	-	6
2.	Rasulpur Mazar	Apr. 23	N24°41.227′ E90°08.263′	1	-	-	-	1
3.	Beribaid	Sep. 30	N24°40.904′ E90°08.08′	1	7	6	-	14
4.	Beribaid	Aug. 13	N24°40.812′ E90°08.014′	2	2	1	1	6
5.	Beribaid, Jaloi Cottage (south) (tailless adult-female)	May 14	N24°41.156′ E90°08.079′	1	4	3	3	11
6.	Dokhola beat	Jul. 24	N24°41.010′ E90°07.531′	1	2	5	2	10
7.	Beribaid, BimanBhahini Camp	Jul. 24	N24°40.575′ E90°07.506′	1	1	2	-	4
8.	Beribaid, Jaloi Cottage (north)	Apr. 3	N24°40.497′ E90°07.386′	1	1	5	-	7
9.	Beribaid, Mahua cottage	Jun. 4	N24°40.460′ E90°07.373′	1	4	3	-	8
10.	Beribaid	Jun. 5	N24°40.362′ E90°07.251′	1	4	5	2	12
11.	Rasulpur – Lohoria road 2 (west)	Jul. 23	N24°41.353′ E90°07.099′	1	2	1	1	5
12.	Lohoria beat (east side)	Jul. 24	N24°41.446′ E90°06.179′	1	3	4	1	9
13.	Rasulpur – Lohoria road 1 (east)	Jul. 23	N24°41.441′ E90°06.178′	1	2	2	1	6
Total				13	35	40	11	99
%				13.1	35.4	40.4	11.1	100

Table 2. Sighting records of Capped Langurs in Madhupur National Park.

AM: Adult Male, AF: Adult Female, J: Juvenile, I: Infant



Fig. 3. Number of Capped Langurs across Madhupur National Park.

part of the ethnic community. The local people of these villages do not hunt the langurs but they chase them when the langurs raid crop fields or fruit plants. Of the groups in the park, we recorded three (25%) in the undisturbed deep forest area, and other groups (75%) near the park's east-central boundaries (Fig. 4).

Group size and composition

Group sizes ranged from 4 to 14, with an average of 7.62±3.2. We recorded the largest group (group no. 3) in Beribaid, the smallest group (group no.7) in Biman Bahini Camp area (Beribaid beat) (Fig. 5). The forest of Biman Bahini area was fragmented and had low dense canopy layer. We found non-adult individuals (sub-adult, juvenile and infant) to slightly outnumber the adults among the 99 Capped Langurs (51.5% to 48.5%). The mean ratio of adults to non-adults was 1:1.06 (Table 3). In each group, juveniles outnumbered other age groups. Most of the individuals in each group were juveniles. The number of adult females was similar to the number of juveniles, and the number of adult males was similar to that of infants.

Age-sex composition

We found that most of the groups (91.7%) had a single adult male and only one group (Beribaid, group no. 4, Table 3) had two adult males. Of the single-adult-male groups, we found most (83.3%) to be single-male multi-female groups and only 16.7% of the groups to be single-male single-female. When data from all

groups were combined, we found 27.1% adult males and 72.9% adult females, at a ratio of 1: 2.69 (Table 3).

DISCUSSION

We recorded 12 social groups along with one old solitary male in the study area. Old solitary males have also been reported for Hanuman Langurs Semnopithecus entellus (Dufresne) in India (Rajpurohit et al., 2004). We observed most of the groups within the high canopy layer in dense forest where the forest staff and officers patrol regularly. The Capped Langur avoided the forest area adjacent to the Garo settlements. This might be because the Garo people hunt the Capped Langur, consuming them as food during special occasions and even opportunistically (Naher et al., 2017). Garo aged between 15 and 25, who are mostly illiterate, are the most likely agegroup to engage in hunting (Naher et al., 2017). The Garo community of the northern part of the country participates in group hunting during the winter (Naher et al., 2017). Rhesus Macaques Macaca mulatta (Zimmermann) have apparently been wiped out from the Shal forest of north Bengal due to over-hunting (IUCN Bangladesh, 2015). Hunting for medicinal purposes and artifacts for socio-cultural practices and religious and cult ceremonies are the primary causes of population decline in Assam (Biswas et al., 2009) and Arunachal Pradesh (Kumar & Solanki, 2004, 2008) in India. Hunting, poaching and habitat destruction are

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Fig. 4. Distribution of Capped Langurs in Madhupur National Park.



Fig. 5. A group of Capped Langurs at Beribaid Forest Beat.

Group No.	Sighting area	AM	AF	AM:AF	Adult	Non-adult	Adult to non-adult	Total
1.	Kathalia (human habitation)	1	3	1:3	4	2	2:1	6
2.	Rasulpur Bazar	1	-	1:0	1	-	-	1
3.	Beribaid	1	7	1:7	8	6	1.33:1	14
4.	Beribaid	2	2	1:1	4	2	2:1	6
5.	Beribaid, Jaloi Cottage (south)	1	4	1:4	5	6	1:1.2	11
6.	Dhokhola range	1	2	1:2	3	7	1:2.33	10
7.	Beribaid, Biman Bhahini Camp	1	1	1:1	2	2	1:1	4
8.	Beribaid, Jaloi Cottage (north)	1	1	1:1	2	5	1:2.5	7
9.	Beribaid, Mahua Cottage	1	4	1:4	5	3	1.66:1	8
10.	Beribaid	1	4	1:4	5	7	1:1.4	12
11.	Rasulpur – Lohoria Road 2	1	2	1:2	3	2	1.5:1	5
12.	Lohoria beat (east side)	1	3	1:3	4	5	1:1.25	9
13.	Rasulpur – Lohoria Road 1	1	2	1:2	3	3	1:1	6
Total		13	35		48	51		99
Mean				1:2.69			1:1.06	

Table 3. Age-sex	ratio of	Canned	andur	aroune in	Madhunur	National Park
Table S. Aye-sex	Tallo OI	Cappeu L	_anyu	yroups in	iviauriupur	National Fair.

frequent in the adjacent forest areas of Pakke Wildlife Sanctuary (Kumar & Solanki, 2004).

Human disturbance, especially hunting pressure, evidently affects group sizes of Capped Langur. The langurs were scarcer and group sizes were smaller in areas where there was hunting, trapping or large numbers of ethnic people. Hunting, environmental constraints and human interference are also believed to affect the composition and group size of macaques in India (Kumar & Solanki, 2008). The size and composition of social groups of Capped Langur vary geographically, depending on habitat type and the abundance, distribution and quality of food (Stanford, 1991; Kumar & Solanki, 2008; Regmi & Kandel, 2008). Different group sizes have been recorded in Bangladesh and India. In Bangladesh, Islam & Hussain (1982) recorded an average of 6.4 individuals, Green (1978) and Stanford (1987) respectively recorded seven individuals and seven to nine individuals in Madhupur forest. In India, Mukherjee (1978) recorded group sizes ranging from seven to 13 individuals in Assam, Mukherjee (1982) reported five to six individuals in Tripura, Gupta (1994) recorded an average of 5.7 individuals in Tripura, and Choudhury (1995) recorded five to 15 individuals in Assam.

Our findings showed mostly single adult male groups, but there were also one group with two adult males and one solitary male. Kabir (2002) did not find any multi-male groups in Bangladesh. Nearly 90% of the Capped Langur groups were single-male, multi-female in Arunachal Pradesh, India (Kumar & Solanki 2008). Biswas et al. (2009) found Capped Langurs living in single-male (38.6%), two-male (30.6%) and multi-male bisexual groups (22.6%), along with an all-male group (4%) and solitary males (4%).

The sex ratio of the Capped Langur groups we recorded was female biased, which was also observed by Chopra et al. (2013). Chopra et al. (2013) further reported a large variation in the sex ratio among different habitat types and for different years.

Although the Capped Langur occupied all habitat types inside and outside of the national park, they were mainly concentrated in the peripheral region of the dense forest, and foraged only in the higher canopy layer and areas of human habitation other than human settlements. They primarily fed on immature leaves from a wide variety of trees. They also fed on fruits, buds, shoots and seeds. In Pakke Wildlife Sanctuary of Arunachal Pradesh in India, they occupied all habitat types inside and outside the sanctuary, but the tropical evergreen and semi-evergreen, deciduous forests with trees such as *Ficus benghalensis* L., *F. racemosa* L., *Bombax ceiba* L., *Altingia excelsa* Noronha, *Gmelina arborea* Roxb. and *Morus macroura* Miq. have been found to be important in influencing the distribution of Capped Langurs in the region (Kumar, 2006), and the availability of food trees may be a limiting factor (Joseph & Ramachandran, 2003).

At Madhupur, the groups of Capped Langurs were distributed in a very limited area in the park. Moreover, local people informed us that in the past (almost 30 years ago), they were distributed throughout the park and forest area, but gradually their population dwindled and the remaining langurs are now concentrated in a very restricted area, mainly due to disturbance from the Garo people and habitat destruction. The opportunity to acquire more food (agricultural field, homestead vegetable and fruit garden) influenced the Capped Langurs to forage and live in human settlements during the winter months.

Habitat destruction due to illegal logging, firewood collection and encroachment of land for seasonal crop plantation are the main challenges for Capped Langur conservation. Rules and regulations of Bangladesh Wildlife (Security and Conservation) Act 2012 should be implemented effectively to stop the illegal logging and encroachment of land and hunter activities. Attempts should be made by educating, motivating and involving people under the eco-development strategy with aims to bring a reduction in the dependency of local people on the resources of the park, and thus lead to habitat improvement and overall conservation. Attenuation of habitat and reduction of food plants and shelter trees have led to the incursion of primates into human habitation resulting in primate-human conflict. Reconciliation between the two is possible if local communities and government agencies evolve a partnership to conserve the habitats, with critical support from NGOs and independent researchers.

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MOTHER-INFANT INTERACTIONS IN A WILD POPULATION OF *Macaca nemestrina* (Linnaeus)

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ABSTRACT

Until now, mother-infant relationships have not been studied in a wild population of the Southern Pig-tailed Macaques *Macaca nemestrina*. We observed six mother-infant dyads from April 2016 to September 2016 in the Segari Melintang Forest Reserve, Peninsular Malaysia using focal sampling methods from the perspectives of both individuals. We hypothesized that as infant age increased, the same important mother-infant behaviours, previously observed to change in captive pig-tailed macaque mother-infant studies, would also change over time in field conditions. We expected that as the infant ages, mothers would decrease their rates of restraint and retrieval, and increase their rates of punishment. Two separate generalized linear mixed models (GLMM) of mother permissive behaviour and mother-infant contact duration as the outcome variables each showed infant age as the sole significant predictor variable indicating that as infant age increased, maternal behaviours changed as expected above, and mother-infant contact duration decreased. Mothers' interactions with other group members appeared influenced by mothers' associations with their offspring: adult females and juveniles were significantly more likely to be within 1-5 m proximity of mothers as infant age increased. Our data show that mother permissive behaviour, mother-infant contact duration, and proximity are crucial elements to consider when examining wild Southern Pig-tailed Macaque mother-infant relationships and infant independence, similar to what has been observed in captive settings.

Keywords: dyadic relationships, maternal behaviour, permissive, proximity

INTRODUCTION

In primates, infant dependence on the mother is prolonged compared with most other animals, and the later stages of the mother-infant relationship can vary greatly in terms of maternal permissive behaviours and physical contact, both between and within species living in different settings (Kaufman & Rosenblum, 1969). Physical contact and maternal permissive behaviour have been viewed as critical components of the dyadic mother-infant relationship and significant factors in the attenuation of the bond (Kaufman & Rosenblum, 1969), which gradually leads to increased infant independence.

This study focuses on a wild group of Southern Pig-tailed Macaques *Macaca nemestrina* (Linnaeus). Like other members of this genus, Southern Pig-tailed Macaques live in multi-male multi-female groups that are female-philopatric, where females remain in their natal groups while males leave at sexual maturity (Thierry, 2004). Thierry (2004) places Southern Pigtailed Macaques into the Grade Two category on his four-grade scale of macaque species based on speciestypical patterns of aggression and reconciliation. Grade Two species are characterized by high rates of aggression, high levels of despotism, and relatively low rates of reconciliation (Thierry, 2004). Group size varies between 20 and 80 individuals (Caldecott, 1986), and the dominance hierarchy is stable (Oi, 1990). To date, little is known about this species' mother-infant interactions in the wild, but maternal behaviour has occasionally been studied in captivity.

Captive pig-tailed macaques' mothering styles vary between individuals in measures of maternal protectiveness, rejection and warmth (Maestripieri, 1998). Aggression by other adults and previous maternal experience are both important in shaping

the captive Southern Pig-tailed Macague mothering style (Maestripieri, 1998). Captive Southern Pig-tailed Macague mothers affiliated more with their infants if the mothers experienced hostility from other group members (Maestripieri, 1998). Upon caregivers' attempts to force separation of infants from their mothers, infants were extremely vocal and clung to the mothers; once reunited, all signs of stress and vocalizations ceased (Jensen & Tolman, 1962). Separation increased infant-directed behaviour of the mother, and the infant became less likely to separate from the mother during the early stages of the reunion (Jensen & Tolman, 1962). Mother-infant separation led to more differences in infants' physiology and sleep patterns than did peer separation (Boccia et al., 1989). Lower-ranked mothers categorized in the first two grades in Thierry's (2004) four-grade scale were found to be protective, frequently retrieving infants and restricting infant interactions. In captivity, primiparous pig-tailed macaque mothers often neglected their firstborn (Maestripieri et al., 1997).

In the captive environment, pig-tailed macaque mothers initiated the LEN (Lips forward, Ears back and Neck extended) face, a frequent facial expression in this species (Oettinger et al., 2007; also known as "Pucker" face), when distance between them and their infants increased (Maestripieri, 1996). Infants who received more LEN faces from their mothers did not spend as much time in contact with them compared to infants who received fewer LEN faces (Maestripieri, 1996). Because of this apparent correlation the LEN face was suggested as a means of maternal encouragement of infant independence (Maestripieri, 1996).

Rosenblum and Kaufman (1968) designed two studies to compare captive Southern Pig-tailed Macaque mother-infant behaviours with those of other macaque species. They focused on maternal permissive behaviours in Bonnet Macagues Macaca radiata (É. Geoffroy Saint-Hilaire) and Southern Pigtailed Macaques. A female's permissiveness as a mother was measured by scoring three maternal behaviours that tend to change during infant development: restraint of the infant by the mother, retrievals of the infant by the mother, and finally punitive behaviours directed from the mother to the infant (Rosenblum & Kaufman, 1968). Rosenblum and Kaufman (1968) set out to characterize the extent to which a female could be viewed as more or less permissive (both as an individual, and across time) by scoring restraint, retrievals, and punitive behaviours she engages in and how these change as her infant ages. Generally, mothers are expected to restrain and retrieve more and punish less when an infant is younger. As the infant ages, mothers are expected to decrease rates of restraint and retrieval and increase rates of punishment. Their results highlighted physical contact as a critical component in the mother-infant social relationship. In their study, Bonnet Macagues spent a significant amount of time in contact with other members in their group, while Southern Pig-tailed Macagues were not in physical contact with others except when engaged in grooming and mating. Varying contact patterns in adult Southern Pig-tailed and Bonnet Macagues may greatly influence the mother-infant dyadic relationship, and by extension, the social development of the infant (Rosenblum & Kaufman, 1968). Infants of both species initiated breaks in contact early in their lives (Kaufman & Rosenblum, 1969). Mother and infant behaviours were collected separately and scored to reveal the progression of mother-infant interactions over 15 months, which showed a distinct drop in time of maximum separation bouts in Southern Pigtailed Macagues, while the Bonnet Macagues seemed to remain at a constant maximum time (Kaufman & Rosenblum, 1969).

In another mother-infant study comparing captive Southern Pig-tailed, Stump-tailed M. arctoides (É. Geoffroy Saint-Hilaire) and Rhesus M. mulatta (Zimmermann) Macaques, Southern Pig-tailed motherinfant pairs spent more time in contact than did Rhesus and Stump-tailed pairs (Maestripieri, 1994). Additionally, Southern Pig-tailed mother-infant pairs showed a gradual decrease over the weeks in the percentage of time spent in contact. Southern Pigtailed Macaque mothers were more protective than were Rhesus mothers and did not encourage infant independence as much as Rhesus mothers did. Maestripieri (1994) observed mothers self-scratching in all three species, which he attributed to maternal anxiety. In all three species, the rate of mother scratching while the infant was away decreased as the infant aged. The greater protectiveness observed in Southern Pig-tailed Macague mothers compared with Rhesus Macaque mothers may be related to the rate of infant development and the infant's vulnerability in its environment (Maestripieri, 1994).

The setting in which a mother raises her young can influence mother-infant interactions. In a study that compared Southern Pig-tailed Macaque mother-infant pairs in two different captive environments, groupraised mothers and infants spent more time in ventral contact and less time completely separated than did caged infants (Wolfheim et al., 1970). Nakamichi et al. (1990) compared individually-housed Long-tailed

Macagues M. fascicularis (Raffles) and socially-housed macague mother-infant pairs from other species. As individually-housed Long-tailed Macague infants aged, body contact between mother and infant, maternal holding, and infant suckling decreased, while mothers showed increased aggression towards their infants. In a comparison of wild and captive Rhesus Macague mother-infant pairs, Berman (1980) attributed slight differences in protective behaviours to environment type rather than differences between infants. She found captive mothers were more protective and less encouraging of infant independence than their wild counterparts. In both environments, Rhesus Macague mothers maintained contact and proximity to infants in the early stages of infant development. Gradually, the mother and infant spent more time out of contact, until a point when the infant was primarily responsible for maintaining contact and proximity to the mother, with an increase in maternal rejections. After several years, captive rhesus mother-infant interactions shifted toward patterns seen in wild mother-infant interactions, characterized by less maternal responsibility in maintaining proximity to her infant.

With described variations in physical contact and permissive behaviours existing among captive groups (Kaufman & Rosenblum, 1969; Maestripieri, 1994), and studies on Southern Pig-tailed Macaque and other macaque species showing an impact of setting on mother-infant interactions (Wolfheim et al., 1970; Berman, 1980; Nakamichi et al., 1990), it is important to observe wild Southern Pig-tailed Macaque mothers and infants to develop a more complete understanding of mother-infant interactions in Southern Pig-tailed Macagues. Additionally, no data yet exist regarding the patterns of maternal-infant interactions for the wild Southern Pig-tailed Macaque. We hypothesized that wild Southern Pig-tailed Macague mother and infant behaviours would change as infant age increased. To test the hypothesis, we made the following predictions:

Mother Perspective:

- 1. As infant age increased, the mother's amount of permissive behaviour would increase.
- 2. As infant age increased, the mother's amount of time spent in contact with the infant would decrease.
- 3. Maternal rank would be negatively associated with maternal permissive behaviours.
- 4. Parity would be positively associated with maternal permissive behaviours.

Infant Perspective:

- 5. As infant age increased, time spent in contact with the mother would decrease.
- 6. As infant age increased, the frequency of mother-directed vocalizations would decrease.
- 7. Maternal rank would be negatively associated with infant contact time.
- 8. Parity would be negatively associated with infant contact time.

Proximity:

- 9. Responsibility for maintaining proximity and contact within the mother-infant dyad would shift from mother to infant as infants aged.
- 10. As infant age increased, group-member proximity to mothers would increase.

METHODS

Study site

This study took place from 3 April to 10 September 2016 in the Segari Melintang Forest Reserve, Perak, Peninsular Malaysia. The forest reserve is approximately 2,720 ha consisting of coastal lowland, mixed dipterocarp forest and freshwater swamp forest zones. In 2016, the field site received an annual rainfall of 1,586.13 mm (average monthly rainfall of 102.4 mm during the study period) and average annual temperature of 28.3°C (monthly average temperature of 28.9°C during the study period; weather station Sitiawan; retrieved from https://www.weatheronline. co.uk). The forest is surrounded by oil palm *Elaeis guineensis* Jacq. plantations, rural settlements and secondary forest (Ruppert et al., 2018).

Study subjects

This study group of Southern Pig-tailed Macaques named group "Amy" has been followed since November 2012 (Ruppert et al., 2018). All the individuals can be identified and classified into their respective age-sex classes. During the study period, the study group comprised 17 adult females, ten adult males, nine juveniles and five to six infants. ED collected focal data on six mothers (Anna, Brienne, Emma, Goldie, Renate and Sandra) and their six infants (Anaconda, Brandy, Emanuel, Gollum, Reggie and Sausage). The home range for the study group is between 84 and 198 ha, depending on calculation method and year (Ruppert et al., 2018). We assigned a David's score (Gammell et al., 2003), a method used to calculate dominance rank within a group by tallying agonistic interactions and their outcomes, to each adult female within the study group. We assigned mothers to parity groups by counting the number of surviving offspring each had since November 2014. Each mother was classified to a parity category of 1 or 2 (1 or 2 successful offspring).

A total of 19 adult females were present throughout the entire study period and were observed for a total of 2,850 min. Due to staggered births within the sampling period, the numbers of infants and mothers changed. Mothers were observed for a total of 3,270 min (N=6 mothers). Infants (less than a year old at the beginning of the focal observation period) were observed for a total of 2,880 min (N=6 infants).

We used a chi-square goodness-of-fit test to test for total observation time (minutes) between adult females, which showed an even distribution in observation time across all adult females (χ^2 =3.84, df=18, N=19, p>0.05). We used a second chi-square goodness-of-fit test to test for total observation time (minutes) between group infants, which showed an uneven distribution in total observation time across infants (X²=210.08, df=5, N=6, p<0.0001), likely due to a late birth during the study period causing one infant to be observed for less time.

Study ethograms

Through the combination and modification of several published behavioural ethograms used on Southern Pig-tailed Macaques and other related macaque species (Bobbitt et al., 1964; Kaufman & Rosenblum, 1969; Maestripieri, 1994; Schino et al., 1995), we developed two ethograms: one mother-specific (Table 1) and one infant-specific (Table 2). These ethograms described all mother-infant interactions we saw in wild Southern Pig-tailed Macaque mother-infant dyads. The list of mother behaviours included permissive behaviours initiated by the mother and affiliative contact/non-contact behaviours. The infant ethogram had affiliative contact/non-contact behaviours and a vocalization that commonly occurs when infants are separated from their mothers. Each ethogram included the LEN face (Oettinger et al., 2007) and vocalizations that have been observed from both infants and mothers. We also recorded the proximities of other group members to the mother-infant dyad to test how mothers interact with other group members as the infant ages. We scored proximity into three categories: in contact, <1 m, and 1-5 m.

Sampling methods

We used focal animal sampling (Altmann, 1974) to record the mother-infant behaviours. ED collected

focal samples daily, between 07:00 h and 19:00 h, for a duration of 30 min per focal individual sample with a five-minute interval between samples to find the next focal individual. We randomized mothers and infants into a combined sequence, which we edited as the study progressed to account for new births. Subsequent sequences were generated upon completion of the previous sequence with a random sequence generator. ED observed all focal subjects before randomizing the sequence again. If a focal subject could not be found after five minutes, she moved to the next subject in the random sequence list. She then tried to find the missed focal animal for at least five minutes before continuing the sequence.

ED recorded the frequencies and durations of both mother and infant behaviours on an iPad mini in the field using Animal Behaviour Pro (University of Kent). The ethogram behaviours were programmed in the application to categorize behaviour frequencies and durations in focal samples.

Inter-observer reliability was assessed at the field site with a reliability value of at least 0.85 for animal identity (Martin & Bateson, 2007). ED's intra-observer reliability for ethogram behaviours was assessed using a prerecorded video focal of a mother Southern Pig-tailed Macaque scored at the beginning of the observation period and then each subsequent month (N=4). Intraobserver reliability with ethogram behaviours was at a mean of 87% (range 78-94%).

Analyses

We used R 3.3.2 (R Core Team, 2016) in R-Studio 1.0.136 (R Studio, 2016) to test relationships between the variables we measured: contact duration, permissive behaviour, mother-directed vocalizations, maternal rank, parity, self-directed behaviour, proximity and infant age. We used backwards selection in generalized linear mixed model (GLMM) analysis to eliminate non-significant variables and iteratively evaluated model improvement (Zuur et al., 2009). We set alpha at 0.05. All Spearman's rank correlation tests used individual data (multiple observations per individual) and not pooled individual data.

Mother perspective:

The null hypotheses for the correlation tests were 'no change in permissive behaviour as infants aged' and 'no change in contact duration as infants aged'. We used Spearman's rank correlation coefficient to test the predictions that mother permissive behaviour or mother-infant contact time were associated with infant age. A GLMM tested the prediction that mother
Table 1. Mother ethogram.

Behaviour	Definition
Ventral contact	Mother is seated with infant in ventral-ventral contact ⁴
Grooming	Inspecting or brushing aside hair using one or two hands ³
Foraging	Mother is searching for food while infant is physically separated ⁴
Ventral contact with cradle	Mother is seated with infant in ventral-ventral contact while also holding infant with hands and/or arms ⁴
Ventral contact with grooming	Mother is seated with infant in ventral-ventral contact with grooming ^{3,4}
Ventral contact with foraging	Mother is seated with infant in ventral-ventral contact while foraging
Mother approach	Mother initiates a decrease in the distance between mother and infant ^{3,4}
Mother leaves vertically	Mother initiates an increase in the distance between mother and infant in the vertical $plane^{2,4}$
Mother leaves horizontally	Mother initiates an increase in the distance between mother and infant in the horizontal $plane^{2,4}$
Within proximity	Mother is within proximity to infant (within arm's reach) but physically separated ²
Out of proximity	Mother is not within arm's reach of infant, mother and infant are separated ²
LEN	Mother makes LEN face, directed at infant ¹
Play	Playful actions with other group members ⁴
Restrain*	Mother prevents infant from moving away by holding its limb or tail ^{3,4}
Bite*	Mother bites infant in punitive fashion, not grooming ²
Rejection*	Mother denies physical contact with infant ^{3,4}
Nipple removal*	Mother removes nipple from infant's mouth while feeding ²
Weaning contact deterrence*	Mother does not allow infant to reach a nipple with its mouth i.e. blocking nipple ²
Scratching	Repeat movement of the hand/foot where the finger/toe-tips rub the $\ensuremath{hair^{\scriptscriptstyle 3}}$
Retrieval due to group movement*	Mother retrieves infant in order to move with the group ²
Retrieval due to danger*	Mother retrieves infant and places ventrally in reaction to a perceived social or physical danger to the infant by the mother ²
Cling carriage	Mother actively grasps and supports infant in the ventral-ventral position while in locomotion ²
Passive carriage	Mother is in locomotion with the infant in ventral-ventral position, but is not actively holding the infant ²
Groan vocalization	Mother is physically separated from infant and vocalizes a "Moo" sound directed at the infant ¹
Harsh bark	Mother vocalizes a short bark directed at the infant ¹
Out of Sight	Mother is not within observer's view
Other	Any behaviour that the mother presents but is not listed in the ethogram

*Indicates behaviours used for statistical analysis; ¹Bobbitt et al., 1964; ²Kaufman and Rosenblum 1969; ³Maestripieri 1994; ⁴Schino et al., 1995.

Table 2. Infant Ethogram.

Behaviour	Definition
Ventral contact with cling	Infant is in contact with the mother ventrally using all four limbs with the head close to her chest ²
Ventral contact with hold	Infant is in contact with the mother ventrally using two to four limbs, with head not in contact with the mother's chest ²
Grooming	Inspecting or brushing aside mother's hair using one or two hands ³
LEN	Infant makes LEN face, directed at mother ¹
Play	Affiliative (playful) actions with other group members, e.g. wrestle, chase, mock-bite $^{\!\!\!\!^{2,4}}$
Infant approach	Infant initiates a decrease in the distance between mother and infant ⁴
Infant leaves vertically	Infant initiates an increase in the distance between mother and infant in the vertical \ensuremath{plane}^2
Infant leaves horizontally	Infant initiates an increase in the distance between mother and infant in the horizontal $\ensuremath{plane^2}$
Scratching	Repeated movement of the hand or foot where the finger/toe-tips rub the hair and \ensuremath{skin}^{3}
Within proximity	Infant is within proximity to mother (within arm's reach), but physically separated 2
Out of proximity	Infant is not within arm's reach of mother, mother and infant are physically separated 2
Coo vocalization	Infant is physically separated from the mother and vocalizes a "Coo" sound directed at the mother $^{\rm 1}$
Out of sight	Infant is not within observer's view
Other	Any behaviour that the infant presents but is not listed in the ethogram

¹Bobbitt et al., 1964; ²Kaufman and Rosenblum 1969; ³Maestripieri, 1994; ⁴Schino et al., 1995.

permissive behaviour would increase as mother dominance rank decreased and mother permissive behaviour would increase as mother parity increased. We used the packages lme4 (Bates et al., 2015), Elo Rating (Neumann & Kulik, 2014), and ggplot2 (Wickham, 2009) to assess the variables of rank, parity, self-directed behaviour and infant age as predictors of the dependent variable, mother permissive behaviour.

Infant perspective:

The null hypotheses were 'no change in contact duration as infants aged' and 'no change in motherdirected vocalizations as infants aged'. We used Spearman's rank correlation coefficient to test the predictions that mother-infant contact time or motherdirected vocalizations were associated with infant age. A GLMM tested the prediction that mother-infant contact duration would increase with maternal dominance rank and decrease with parity. We used the packages Ime4 (Bates et al., 2015), Elo Rating (Neumann & Kulik, 2014), and ggplot2 (Wickham, 2009) to assess the variables of rank, parity, mother self-directed behaviour and infant age as predictors of the dependent variable, mother-infant contact duration.

Proximity:

The Hinde index is used to quantify the motherinfant relationship through the use of mother and infant approaches and leaves to assess responsibility for maintaining proximity within the dyad (Hinde & Simpson, 1975). We used Hinde's index (Hinde & Simpson, 1975) to measure the responsibility infants and mothers took for changes in proximity as the infant developed, with a null hypothesis of 'no change in the indices as infants aged'. The null hypothesis for group-member proximity was 'no significant change in group-member numbers within proximity as infant age increased'. We assessed group-member proximity relative to the mothers within one meter and more than one but less than five meters using Spearman's rank correlation coefficient to test the prediction that as infant age increases, group-member proximity to mothers would increase. Group-members

were separated into three classes: male, female and juvenile. We weighted each class to create an accurate proportion relative to group size.

RESULTS

Analyses conducted from each mother's perspective

Spearman's rank correlation coefficient tested the relationship between infant age and number of permissive behaviours from the infant's mother. We found a significant negative correlation for these two variables (r[5]=-0.735, p=≤0.05). We compiled a table of mothers, their infants and the categorical variables of maternal rank and parity for use in the GLMMs (Table 3).

We used GLMM to further explore what factors predicted a mother's permissive behaviour, focusing on mother dominance rank, parity (Table 4), self-directed scratching and infant age. Because our original data had many potential behaviours with a large number of zeros, we collapsed detailed behaviours into a binomial distribution of presence/absence of permissive behaviour regardless of specific behaviour type. Finally, we designated mothers (N=6) as a random effect to account for inter-individual differences in mothering style. The mother permissive behaviours decreased significantly with increasing age of their offspring (GLMM, -0.006±SE0.003, z=-1.978, p≤0.05; Table 4).

Analyses conducted from each infant's perspective

We found a significant negative correlation between infant age and the duration of mother-infant contact time from the infant's perspective (r[5]=-0.733, p=≤0.05). We did not find a relationship between infant age and frequency of infant vocalizations directed toward their mother (r[5]=-0.054, p=0.604). We used GLMM to test if mother dominance rank, mother parity, infant self-directed scratching and infant age predicted mother-infant relative contact time from each infant's perspective. We transformed the response variable 'mother-infant relative contact time' using a log+1

 Table 3. Adult females and associated infants, adult females' dominance rank in descending order, and parity categories.

Mother	Infant	Sex	Birth date	David Score Value	Parity Category
Anna	Anaconda	Male	August 2015	31	1
Goldie	Gollum	Female	July 2015	19	2
Emma	Emanuel	Male	February 2016	0	2
Sandra	Sausage	Female	April 2016	-4	2
Renate	Reggie	Female	July 2016	-4	1
Brienne	Brandy	Unknown	September 2015	-9	2

Table 4. GLMM	: infant-directed behaviours	s (as indicated in Table 1)	١.
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Predictor variable	Estimate	SE	z-value	p(> z)
Best Fit Model				
Intercept	0.241	0.781	0.309	0.757
Infant Age	-0.006	0.003	-1.978	0.048*

Table 5. GLMM: relative contact time.

Predictor variable	Estimate	SE	z-value	p(> z)
Best Fit Model				
Intercept	2.071	0.089	23.300	<2E-16***
SDB*	-0.081	0.056	-1.431	0.152
Infant Age	-0.005	0.001	-9.066	<2E-16***

*Self-directed behaviour; ***Highly significant.

transformation, and then we distributed the contact times into categories of 0.1 percent of time intervals (e.g. 0.01-0.1=1 etc.). We designated the infants (N=6) as a random effect to account for differences among individuals. The relative mother-infant contact duration per focal sample decreased significantly with

increasing age of the offspring (GLMM, -0.005 \pm SE0.001, z=- 9.066, p \leq 0.05; Table 5).

Proximity

The Hinde index in four of the six observed mothers showed the infant as responsible for a greater proportion of contacts broken (Fig. 1).



Fig. 1. Proximity graph of combined mothers' Hinde graphs (N=6).



Fig. 2. Scatterplot of adult male, adult female, juvenile proximity frequency at 1-5 m plotted against infant's age.

We used Spearman's rank correlation coefficient to test the relationship between infant age and number of group-members within 1 m proximity and 1-5 m proximity. We found no correlations within 1 m (male r[5]=0.101, p=0.331, female r[5]=-0.155, p=0.133 and juvenile r[5]=-0.156, p=0.132). The results showed significant correlations in the 1-5 m proximity category for adult females and juveniles (adult females: r[5]=0.278, $p=\le0.05$; juveniles r[5]=0.274, $p=\le0.05$; Fig. 2). The correlation for adult males was not significant: (r[5]=0.197, p=0.055; Fig. 2).

DISCUSSION Mother perspective

The mother's perspective is by far the more common of the two perspectives reported in mother-infant studies, therefore we explored the mother-infant relationship from the perspective of each social partner to gain deeper insight into how the mother-infant relationship changes through time. Our prediction (#1) that 'as an infant ages, the frequency of her or his mother's permissive behaviours would increase was not supported by our results. In captive Pig-tailed Macaque mothers, permissive behaviours increased after the infant reached three weeks of age, regardless of whether the mother was responsible for maintaining or preventing proximity (Rosenblum & Kaufman, 1968). In this study, we instead found a negative relationship between mother permissive behaviour and infant age. It is noteworthy that just before our data collection began (March 2016; we did not observe the exact timeline of takeover events as no observers were in the field), the alpha and beta males left the study group and new alpha and beta males moved in, causing a male hierarchy shift. This sharp turnover in the male hierarchy may have influenced maternal behaviours. At the time of the male dominance shift, a mother-infant dyad within the study group went missing, which may be an extreme response to the dominance shift. Adult females trying to develop relationships with the new dominant males may explain the decline in mother permissive behaviour as infants aged.

We found support for the prediction (#2) that as infant age increases, the duration of mother-infant contact time decreases. Maestripieri (1994) found that captive pig-tailed macaque mother-infant pairs gradually decreased their time spent in contact, a finding that corresponds to the results in this study. Here, the relationship between contact duration and infant age is stronger than the relationship between mother permissive behaviour and infant age. As the infants in the study group aged, they spent less time in contact with their mothers. Captive Southern Pig-tailed Macaque mothers were found to initiate the LEN face when there was an increase in distance from the infant (Maestripieri, 1996). This species-specific behaviour was rarely seen throughout our observation period and was thus not analysed. The small decrease in mother permissive frequency might be explained by the small sample size and difficulties in collecting data on the same developmental periods of all the infants, which were born at different times across the duration of the study.

We predicted (#3) that lower ranked mothers would be more protective of their infants due to greater threats (see also Thierry, 2004). This prediction was not supported by our data. Infant age was the only significant variable that predicted mother permissive behaviour. In captivity, primiparous pig-tailed macaque mothers often neglect their firstborn (Maestripieri et al., 1997), so we expected parity to predict (#4) mother permissive behaviour. Since most of the previous mother-infant Southern Pig-tailed Macaque studies are captive subjects, parity could have been more noticeable in captive populations instead of wild populations. In our GLMM model, there was not a strong correlation between a mother's dominance rank and her degree of permissive behaviour. We used selfdirected behaviour (scratching) as a predictor variable to assess maternal anxiety when the infant was separated from the mother. This common behaviour in past captive studies (Maestripieri, 1994) was also commonly observed in our wild study group.

Infant perspective

We collected behavioural observations from the infant's perspective to obtain a complete record of mother-infant contacts. When the same correlations were run from both mother and infant perspectives, we found significant negative relationships between mother-infant contact time and age (#5). Even though infants can show variability, infants in our data set all followed a similar pattern with respect to their ages and contact time with mothers. Maestripieri (1994) also found a gradual decrease in contact time between mother and infant in the captive dyads he studied.

We found no linear relationship between motherdirected vocalizations, infant vocalizations, and infant age (#6). If the infants had moved from the mothers by choice, we expected a general decrease in this behaviour as the infants grew more independent. Gouzoules & Gouzoules (1989) also found that Southern Pig-tailed Macaque agonistic screams/ vocalizations became more fine-tuned with age, indicating that infants would learn which calls were most effective and only use those calls if they needed their mother's help. However, our study group was generally quiet and followed the Southern Pig-tailed Macaque stereotype of rarely vocalizing (Oi, 1990).

We predicted (#7 and #8) that mother-infant contact time would be lower with lower maternal rank and lower parity. Neither of our predictions were supported by our data, and infant age was the only significant variable that predicted contact time duration. Maestripieri (1994) found that captive pig-tailed macaque motherinfant pairs showed a gradual decrease over weeks in percentage of time infants spent in contact with mothers. Contact patterns can greatly influence the mother-infant dyad and ultimately, infant development (Rosenblum & Kaufman, 1968). In Rhesus and captive Long-tailed Macaques, mother-infant pairs gradually spent less time in contact with their mothers as they aged (Berman, 1980; Nakamichi et al., 1990). In Vervet Monkeys Chlorocebus pygerythrus (F. Cuvier), Fairbanks (1989) found mothering styles to vary significantly between mothers, with each showing different contact patterns with their infants. An infant leaving the mother could also mean the infant is taking opportunities to play and explore social independence from the mother (de Jonge et al., 1981). In this study, we found a gradual decrease in contact duration between mother and infant, but we also found similar contact patterns across the six mothers and their infants relative to infant age.

Proximity

Proximity is a distinct affiliative behaviour that indicates mutual preference between animals (Troisi et al., 1989). Infants spend most of their early development after birth either in direct contact or proximity to their mothers. In wild and captive macaques, mothers are responsible for maintaining proximity and infant contact in these early life stages (Berman, 1980; Nakamichi et al., 1990). Berman (1980) showed that infants play a more dominant role in proximity maintenance within the dyad at a certain point. Two mothers in the present study never had a negative Hinde index value, which indicated that their infants were responsible for a greater proportion of contacts made with their mothers than contacts broken (sensu Brown, 2001). These were the mothers of the oldest infant (born July 2015) and the youngest infant (born July 2016) in our dataset. It was not possible to distinguish a trend between mother dominance rank and the proximity indices calculated because the dyads were not observed at the same stages of infant development. Infants had a greater proportion of broken contacts between 100 and 350 days of age, but infants resumed a greater proportion of contacts made after 350 days of infant age (#9). This period showed the most variation in mother-infant contact and proximity behaviours and points to the start of infant independence within this study group. Pig-tailed Macaque weaning age is 12 months (Sponsel et al., 2002), so the shift in maintaining proximity from mother to infant and again to mother may correspond to infant weaning.

Rosenblum & Kaufman (1968) found that captive Southern Pig-tailed Macaque mothers were reluctant to socially engage with others after giving birth. All age classes in our study showed an increased frequency of proximity to the mothers at the 1-5 m range, but only adult females and juveniles showed significant correlations with infant age. Aggression in the group can play a significant role in shaping mothering styles (Maestripieri, 1998). At our field site, there was some male-male and male-female aggression at the beginning of the observation period, which could have had an effect on mothers' protectiveness and guarding behaviours. Maestripieri (1998) found that pig-tailed mothers affiliated more with their infants if they experienced hostility from other group members. During times of aggression, mothers kept their infants close and away from other group members. While it is surprising that the study group mothers did not appear as careful given the change in male dominance rank at the 1 m to 5 m distance, they did not let many males enter within the 1 m range of proximity, which indicated a few selected males were allowed in close proximity.

We found that Southern Pig-tailed Macaque mothers and infants living in a wild population showed changes in mother-infant interactions over time. Mother permissive and contact behaviours both decreased with increasing infant age. Mothers' ranks and parities did not predict their permissive behaviour. As infant age increased, the duration of mother-infant contact time decreased (from the infant's perspective). We found no correlation between infant age and motherdirected vocalizations, and infant contact time with the Southern Pig-tailed Macaque mothers could not be predicted by maternal dominance rank or parity trends. Responsibility for maintaining proximity and contact changed between mothers and infants as infants aged. Group-member proximity to mothers increased significantly in female and juvenile classes at distances of 1-5 m.

One of the biggest differences between this study

group of wild Southern Pig-tailed Macague and other macaque species was the lack of influence that maternal dominance rank and parity seemed to have on mother-infant interactions. As a Grade Two (Thierry, 2004) species, this study group did not seem to behave in accordance with what we expected for their position on that scale. The study group members did show the gradual mother-infant contact decrease that has been characterized in mother-infant relationships of many macaque species. As the first study to investigate the wild perspective of Southern Pig-tailed Macague mother-infant interactions, there are both similarities with what has been reported in the literature for captive individuals of this species, and differences, suggesting that ecological and sociological environments may play a vital role in mother-infant interactions.

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ANNOUNCEMENT

The IUCN SSC Primate Specialist Group Section on Human-Primate Interactions

Siân Waters & Susan Cheyne (Vice Chairs)

Non-human primates are geographically widespread, and many primate species are at risk of extinction due to anthropogenic activities including the pet trade, and persecution of primates by people for crop foraging behaviour (commonly referred to as human-primate conflict). Human-primate interactions are complex, vary widely, occur in many different contexts and are often poorly understood. Human-primate interactions depend on social and cultural as well as economic factors and can vary from a primate being worshipped as a deity in one place to the same species being persecuted and killed in another. Currently most of the literature about the human-primate interactions on human-primate conflict in agroecosystems, but other interactions occur between people and primates and their study will benefit from a coordinated interdisciplinary approach.

An interdisciplinary approach is essential to understanding the human dimension of human-primate interactions, be they positive or negative. The group is composed of specialists with expertise in human-primate relations in various contexts, coming from a wide range of disciplines across natural and social sciences and the humanities.

We are currently seeking members only from habitat countries with experience of human-primate interactions at the academic or practical level in these topics:

- a) Primate tourism
- b) Primate hunting (subsistence and sport)
- c) Primates in agroecosystems
- d) Primate trade
- e) The changing role of primates in human culture (religion, history, media etc.)

Our activities as a group will include:

- Coordinating a reference library of human-primate interactions (HPIs). This would be wider-ranging than the existing primate resource page of the IUCN SSC Human-Wildlife Taskforce group, which focuses on human-primate conflict in agroecosystems. Members of each sub-group would be responsible for developing and updating the HPI reference library (which will eventually be available on our website).
- 2) Provide interdisciplinary advice and expertise on problematic human-primate interactions.
- 3) **Build capacity** where needed, particularly in the study of the human dimension of human-primate interactions, by providing training workshops in the application of social science methods and ethics in primate range countries.
- Add to existing IUCN SSC Primate Specialist Group technical guidance materials, resources and tools as and when appropriate.

Please contact Siân at psg.hpi@gmail.com and Susan at section.small.apes@gmail.com if you would like more information about the section. We also have a Facebook group for those interested in following the activities of this group https://www.facebook.com/groups/187157948858667

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Instructions to Contributors

Scope

This journal aims to provide information relating to conservation of the primates of Asia. We welcome manuscripts on any relevant subject, including taxonomy and genetics, biogeography and distribution, ecology and behaviour, active threats and primate-human interactions. Submissions may include full articles, short articles and book reviews.

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Scientific nomenclature should be used at first mention of any species or subspecies. Nomenclature should include taxonomic authority (at first mention) as currently recognised by IUCN (or more recent/authoritative sources), e.g. Northern Pigtailed Macaque *Macaca leonina* (Blyth) (see www.iucnredlist.org). Authors are referred to The Plant List (www.theplantlist.org) for up-to-date plant nomenclature.

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Measurements should always be metric, or where this is inappropriate, the metric equivalents given in parentheses. Time should be designated in the 24-hour system (as e.g. 17:30 h) and date in the European system (e.g. 7 December 2011). Summary statistics should include measures of both central tendency and dispersion where appropriate, e.g. means and standard deviations (SD). Reports of all statistical tests should include the name of the statistical test, the name and value of the test statistic, the degrees of freedom, the probability value used to determine significance and the authors' interpretation. Probabilities should be reported as exact values if not significant, otherwise rounded off to either p<0.05, 0.01 or 0.001.

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Acknowledgements

Remember to thank those who have contributed substantially to your paper, not forgetting (in the final submission) the reviewers.

References

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Asian Primates Journal

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