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Performing monkeys of Bangladesh: characterizing their source and genetic variation

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Abstract

The acquisition and training of monkeys to perform is a century's old tradition in South Asia, resulting in a large number of rhesus macaques kept in captivity for this purpose. The performing monkeys are reportedly collected from free-ranging populations and may escape from their owners or be released into other populations. In order to determine whether this tradition, that involves the acquisition and movement of animals, has influenced the population structure of free-ranging rhesus macaques in Bangladesh we first characterized the source of these monkeys. Biological samples from 65 performing macaques, collected between January 2010 and August 2013 were analyzed for genetic variation using 716 base pairs of mitochondrial DNA. Performing monkey sequences were compared with those of free-ranging rhesus macaque populations in Bangladesh, India and Myanmar. Forty-five haplotypes with 116 (16%) polymorphic nucleotide sites were detected among the performing monkeys. As for the free-ranging rhesus population, most of the substitutions (89%) were transitions and no indels (insertion/deletion) were observed. The estimate of the mean number of pair-wise difference for the performing monkey population was 10.1264 ± 4.686 , compared to 14.076 ± 6.363 for the free-ranging population. Fifteen free-ranging rhesus macaque populations were identified as the source of performing monkeys in Bangladesh; several of these populations were from areas where active provisioning has resulted in a large number of macaques. Collection of performing monkeys from India was also evident.

Keywords

Performing monkey; rhesus macaque; performer; Bedey; Bangladesh

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Introduction

Bangladesh currently supports 10 species of non-human primates (NHP) including five macaques: Rhesus (*Macaca mulatta*), Assamese (*M. assamensis*), Pig-tailed (*M. leonina*), Long-tailed (*M. fascicularis*) and Stump-tailed (*M. arctoides*) (Khan 1982; Feeroz 2001; Feeroz et al. 2011, 2013; Hasan et al. 2013). Only Rhesus macaques are still found in considerable numbers throughout the country, inhabiting evergreen forests and tea gardens in the northeast and southeast, deciduous forest in the central part and mangrove forest in the southwest. They also inhabit numerous village sites throughout the country (Islam et al. 2000; Hasan et al. 2013) including shrines and temples where they may be provisioned. In addition to free-ranging and urbanized rhesus macaque populations there are an estimated 5000-10000 rhesus macaques involved in the performing monkey trade (Feeroz et al. 2013; Akhtar 2014).

The use of performing animals (bears, snakes, monkeys) is a centuries' old tradition in South Asia (Islam 2003). Semi-sedentary nomadic ethnic communities known variously as 'Bandarwala', 'Bedey' or 'Qalandar' (Engel et al. 2013; Feeroz et al. 2013; Akhtar 2014) obtain and train animals to perform for audiences. Ethnically, the Bedey are associated with the Mong-tong (*Mangta*) of Arakan, Myanmar who in 1638, accompanying the fugitive king of Arakan, spreading throughout Bengal and Assam (Islam 2003). Today, these small close-knit family groups maintain a nomadic lifestyle moving throughout South Asia with their monkeys (Maksud and Rasul 2006; Akhtar 2014). The Bedey of Bangladesh takes advantage of the ubiquity of the country's rhesus macaques and preferentially uses them for their performances (Akhtar 2014).

Every year, typically during the religious festival of Eid, the nomadic Bedey family groups gather in one of three villages to renew social bonds and to discuss community travel plans for the coming year. The largest of these villages, Kaliganj, is in the southwest of Bangladesh. The other villages, Joralganj and Abbasiapur, are located next to each in the southeastern part of Bangladesh. Kaliganj and Joralganj/Abbasiapur are located on opposite sides of the Jamuna River.

The Bedey monkey performers collect rhesus macaques from multiple sources including direct trapping from the free-ranging populations (Figure 1), as well as purchasing macaques from other ethnic groups who specialize in catching wild animals. Macaques are also traded among monkey performer groups. Intentional release of pet untrainable performing monkeys into the nearest monkey population is not uncommon (Feeroz et al. 2013; Engel et al. 2013; Hasan et al. 2014). The random release of monkeys may influence the gene pool of local monkey population, generating ambiguity in the natural biogeography of this species (Feeroz et al. 2013; Hasan et al. 2014) and may also increase the diversity of enzootic viruses in otherwise isolated populations (Engel et al. 2013).

As mitochondrial DNA (mtDNA) is solely maternally inherited (Hutchinson et al. 1974; Giles 1980) and its control region (CR) evolves more rapidly than nuclear DNA (Brown et al. 1979), it has been used as a molecular marker for identifying geographic origin of the species (Smith and McDonough 2005; Kyes et al. 2006; Smith et al. 2007; Hasan et al.

2014). We have previously demonstrated that free-ranging rhesus macaque mtDNA haplotypes collected from diverse geographic regions in Bangladesh are locality specific (Hasan et al. 2014). In a previous study, that focused on the role of anthropogenic factors in the emergence of infectious diseases (Feeroz et al. 2013), we included microsatellite data from a limited number of performing monkeys sampled throughout Bangladesh and compared those data with six free-ranging Rhesus macaque populations. Our preliminary data suggested that most of the performing monkeys originated in the Sundarbans (southwest).

In the present study we expanded our sampling and focused on the genetic variation in mtDNA of performing monkeys to determine the geographic source of these monkeys within and outside Bangladesh. Trained macaques typically represent the sole source of livelihood for the Bedey monkey performers. The animals are typically acquired when they are young and are always kept in their boxes or belted near the family tents. Breeding is actively discouraged among the performing monkeys because a pregnant monkey cannot be used for street shows. As the livelihood of monkey performers depend on the income from the street show, less than 1% of performers reported breeding between performing monkeys (Akhtar, 2014). Additionally, because the animals are kept in confinement close to the family encampments there is no opportunity for performing monkeys to breed with the wild rhesus populations.

We hypothesized that (i) monkey performers would exhibit no preference for a specific geographic source for monkeys and would randomly collect monkeys from free-ranging populations in Bangladesh as well as from the neighboring countries which they frequently visit and (ii) the performing monkey population currently in circulation with the Bedey would constitute a genetically more heterogeneous population than any of the other macaque populations in the country. We predicted that (i) random genetic heterogeneity would be evident in our genetic analysis and haplotype network.

Methods

We screened 65 performing rhesus monkeys. Between January 2010 and August 2013, 42 samples were collected in the southwestern village near Kaliganj and 23 from Joralganj in the southeast (Figure 2). Sampling was conducted in accordance with the University of Washington Institutional Animal Care and Use Committee (4233-01) and Bangladesh Ministry of Environment and Forest Permit. Biological samples were transported to the US under the permission of Convention on International Trade in Endangered Species (CITES). Detailed sampling techniques have been reported in Jones-Engel et al. (2006) and Feeroz et al. (2013). Briefly, performing monkey owners were located in our study villages and asked if they would allow us to collect biological samples from their animals. After obtaining consent, animals were either anesthetized to collect a blood sample or restrained by their owners for a fecal swab collection.

Fecal swab samples were collected from the surface of fresh feces. The swabs were then placed in lysis buffer (1M TrisHCl, 0.5M EDTA, 5M NaCl and SDS) and stored at room temperature prior to DNA extraction. The Wizard® SV Gel and PCR Clean-Up System was

used to extract DNA from the fecal swabs using the manufacturer's protocol. Blood samples were collected in EDTA as part of a larger project on host-pathogen diversity (Feeroz et al. 2013; Engel et al. 2013; Matsen et al. 2014) and stored at 4°C prior to centrifugation, aliquoting and storage at -80°C. The QIAGEN (QI Aamp DNA Blood Mini Kit) kit was used for blood DNA extraction. Extracted DNAs were quantified using the Qubit dsDNA HS Assay kit and diluted to 5 ng/μl for each PCR reaction. The non-coding D-loop region of mtDNA (nps15774-16541), including hypervariable region I (HVR I), a portion of cytochrome b gene and the tRNA genes for proline and threonine were amplified using primers 15167F (5'-3') ATGCAAGGCGCCACGATTT and 16050R (5'-3') CCGAGCGAATGCCACC. This primer pair was designed to replace a pair of previously-used primers that readily amplified a pseudogene (numtDNA) (Smith and McDonough 2005). This pseudogene (Collura and Stewart 1995; Bensasson et al. 2001) was easily identifiable by its extreme divergence from all Rhesus sequences amplified with the redesigned pair of primers, an abundance of transversions and indels, a paucity of polymorphic, but consistently heteroplasmic, sites and the failure of its HVS I to readily align with the reference *M. sylvanus* sequence. The redesigned primers yielded sequences with specific mutations that provide the haplogroup structure characteristic of true mtDNA sequences, with the majority of the variation in the HVR I region (Smith and McDonough 2005). This striking difference between the pseudogene and the mtDNA fragments amplified provided assurance that pseudogene sequences were not included in the sequences analyzed in this study. A 25 μl PCR reaction (nuclease free water, 10 μM dNTP, 10× PCR buffer, 50 μM MgCl₂, 10 μM forward and reverse primers and Platinum Taq DNA polymerase) containing 2 μl DNA template was used for sequencing, the detailed protocol for which is reported in Hasan et al. (2014).

Performing monkey mtDNA sequences were compared with those of 124 free-ranging mtDNA rhesus macaques from 28 populations throughout Bangladesh as reported in Hasan et al. (2014). Like all macaques, rhesus practice male dispersal and female philopatry (Sade 1972; Pusey and Packer 1987), however, geographic features and/or anthropogenic factors have for decades prevented the natural dispersal of animals between these 28 free-ranging populations. Moreover, each of the population showed locality specific mtDNA haplotype distribution (Hasan et al. 2014). Performing monkey sequences were also compared with those of Indian and western Myanmar Rhesus macaque sequences reported in Smith and McDonough (2005). Neighbor joining analyses and a maximum likelihood (MLK) analysis with the assumption of molecular clock using PHYLIP version 3.696 (Felsenstein 2005) were carried to estimate genetic distances among the D-loop regions of the performing monkey populations. Molecular clock constraints assume constant rates of nucleotide substitution. A median joining (MJ) haplotype network (Forster et al. 1996) was constructed using Network 4.612. The sequence closest to that of a performing monkey sample in both the MLK and NJ trees was considered to be the source locality of that performing monkey and was crosschecked with the immediate ancestral haplotype in the MJ haplotype network. The ARLEQUIN software package (version 3.5) (Excoffier and Lischer 2010) was used to estimate haplotype frequencies and molecular diversity indices.

Results

Overall genetic variation

Forty-five haplotypes [Genbank accession numbers for these sequences are xxxxxxxx (submission pending)] were detected in our performing monkey sample set; 27 from southwest (Kaliganj) and 18 from southeast (Joralganj) performing monkey villages. A total of 116 (16%) of the 716 nucleotide sites studied were polymorphic. Most of the substitutions (89%) were transitions and no indels (insertion/deletion) were observed providing a transition: transversion ratio of approximately 8:1. This value exceeds that of 3.6:1 for the general population (Hasan et al. 2014) and may reflect sampling error. A gene diversity of 0.967 ± 0.0146 and expected heterozygosity of 0.087 ± 0.014 were estimated for the total population. The mean number of pair-wise differences and average nucleotide diversity among the 716bp were 10.126 ± 4.686 and 0.014 ± 0.007 , respectively, compared to estimates of 14.076 ± 6.363 and 0.019 ± 0.009 , respectively in the general population. Maximum likelihood, with and without the assumption of molecular clock, and neighbor-joining gave similar topologies and bootstrap values for the D-loop haplotypes from the performing monkeys (Figure 3).

Sources of Monkeys

Our genetic data indicate that the monkey performers collect approximately one-quarter (26.15%) of their animals from free-ranging rhesus macaque populations in the southwest region of Bangladesh, and one-quarter (24.62%) from the central region. A smaller percentage of the animals were collected from the northeast and southeast (18.46% each). Approximately one-tenth (10.77%) of the animals appear to have been exchanged among monkey performers within and between southwest and southeast villages. The source of performing monkeys between southwest and southeast villages varied significantly ($\chi^2 = 25.44$, $df = 5$, $p > 0.001$). Figure 4 highlights that the monkey performers in the southeast collected monkeys from 9 local rhesus macaque populations throughout the country, they appear to focus on animals from the southeast region (47.83%). Similarly, performers in the southwest village collect monkeys from 10 local free-ranging populations, they exhibit a preference for animals from the southwest and central regions (30.95 % each).

The different sources of the performing monkeys in Kaliganj and Joralganj are also represented in the haplotype network in Figure 5 that exhibits several shared haplotypes between performing monkeys and those in different regions of Bangladesh and elsewhere. Performing monkeys in Joralganj share one haplotype (BR18) with monkeys in the northeast region and one (BR40) with monkeys in the Southeast. In addition, consistent with the results shown in Table 2, approximately half of the haplotypes represented in Joralganj form an exclusive cluster with half of the Southeastern haplotypes to the exclusion of all other haplotypes. Performing monkeys in Joralganj and Kaliganj also share a haplotype (KJR27) and four different pairs of other haplotypes, one from each village, (KJR21 and CTR05, KJR10 and CTR14, KJR27 and BR23 and CTR14 and BR23) are only one mutational step removed from each other, suggesting that monkeys are exchanged between the two villages. Performing monkeys in Kaliganj share haplotypes with monkeys in all four regions (e.g., Central: BR23, Northeast: In2 25, Southeast: BR23 and Southwest: BR12 and BR24).

Our data suggests that some of the performing monkeys of Kaliganj were collected from India (Table 1). As illustrated in Figure 5, performing monkeys in Kaliganj share haplotypes Ind 22, Ind2 24, Ind2 25, BR17 and KRJ25 with rhesus macaques of Indian origin. In addition, haplotype KJR06 from Kaliganj appears in a well-defined cluster that includes four Indian and one Nepalese rhesus macaque haplotypes. Also, performing monkey haplotypes CTR01 and CTR04 from Joralganj occur in another remote cluster with haplotype Ind2 26 from India. Among the 15 local populations of performing monkey collected in Bangladesh, approximately 65% come from 9 populations where monkeys are habituated with provisioning by the local people, visitors or government authorities (Table 1).

Discussion

The use of macaques in the performing monkey tradition is centuries old in South Asia. How the acquisition and movement of animals throughout the region may have impacted population structure is only now being investigated. Among our sample of performing monkeys, the number of haplotypes identified is high relative to the sample size (45 haplotypes out of 65 samples) in comparison to those of the free-ranging rhesus macaque populations of the country (Hasan et al. 2014). The weaker bootstrap values in the MLK analysis suggest lack of geographic differentiation among the performing monkeys and the genetic substructure reflected in the MLK tree reflects the effects of alleged admixing among performing animals from different geographic populations.

Given that performing monkeys are collected from diverse monkey populations throughout the country, it is reasonable to have identified a high incidence of haplotypes relative to sample size. In the present study, the southwestern region of Bangladesh was identified as the primary source of performing monkeys, consistent with our previous findings based on short tandem repeat (STRs) loci (Feeroz et al. 2013). Regional preference for monkey collection between two of the performing villages was also evident. The southeast village of Joralganj is adjacent to the forests of the Chittagong Hill Tracts (Hasan et al. 2013) that support a diverse gene pool of rhesus macaques (Hasan et al. 2014). While this observation is consistent with the higher nucleotide diversity observed among the performing monkeys in Joralganj ($\pi = 0.017 \pm 0.009$) than among those in Kaliganj ($\pi = 0.011 \pm 0.006$), these two estimates are within the range of one standard deviation of each other and, therefore, not statistically significantly different. Our genetic data indicate that monkey performers prefer to collect monkeys from monkey populations that are close to their village, although performing monkeys appear to be exchanged amongst the performers as well as obtained from India.

It is possible that the provisioning by local people has both increased population sizes of village monkeys and encouraged their commensal co-habitation with humans and this may have facilitated the collection of performing monkeys from these areas. Macaque populations have increased dramatically in regularly provisioned areas like Charmuguria in the southwest, Chashnipeer shrine in the northeast and Rajban Bihar pagoda in the southeast of Bangladesh (Hasan et al. 2013) in the last decade, providing the opportunity for monkey traders to collect animals from these areas. Human-monkey conflicts have been increasing in these provisioning areas (Hasan et al. 2013), which in turn may be generating local support

for the illegal trapping of these “nuisance” macaques. It is not surprising that our data reflect that a large proportion of the performing monkeys originated from these provisioned sites, where we also observed numerous locally made monkey traps during the study period.

Though the performing monkey owners are often evasive regarding the source of monkey collection as capturing and keeping monkeys is prohibited under the Wildlife (conservation and security) Act, 2012, ethnographic interview data compiled by Akhtar (2014) on the location of monkeys collected for the performing trade identified sites in the southwest (Sundarbans, Naria, Nandanshar, Kartikpur, Kolargaon), central (Madhupur, Narayanganj) and northeast (Chashnipeer shrine) of Bangladesh. Our mtDNA and haplotype data confirm these ethnographic data.

The extensive conversion of forest habitat to cultivated lands throughout the Subcontinent has effectively eliminated the ability for free-ranging primates to naturally disperse. Natural migration of primates requires contiguous forest or riverine patches and unfortunately, such ecological conditions are now only found in a few areas in the eastern boundaries of Bangladesh and India and in a very small area in northeastern Bangladesh.

One of the performing monkey haplotypes (KJ23) detected in an animal sampled from the southwest performing monkey village (Kaliganj) was identical to a haplotype from India (AY64022) reported by Smith and McDonough (2005), indicating collection of performing monkeys from India. Moreover, the Indian haplotype that we present in this dataset (Ind 22 in Fig. 4) belongs to the haplogroup Ind1 which is found only west of Calcutta and originated in northwestern India (Smith and McDonough 2005), for decades it has been physically impossible for macaques to disperse from this region of India.

As monkey performers typically visit India and Myanmar (Akhtar 2014), as part of their annual “tours”, detection of performing monkeys in Bangladesh that originated from India is not surprising. However, no indication of performing monkeys originally collected from Myanmar was evident in our sample.

An estimated 5,000 rhesus macaques are currently part of the performing monkey tradition in Bangladesh. Although keeping monkeys in captivity is a punishable offence under the Wildlife (conservation and security) Act 2012, more than a half-million people are directly involved in the performing monkey profession for their livelihood (Akhtar 2014). It will be important for all of the stakeholders (Bedey, Bangladesh Forest Department, villages that are impacted by the presence of rhesus macaques) to work together to develop an integrated management plan that recognizes the cultural and economic significance of this century's old tradition as well as the conservation needs of these macaques in their natural habitat. Our study, which employs robust genetic tools to identify monkey collection sites, is an example of how field and laboratory studies can inform conservation strategies.

The close proximity of a performing monkey haplotype to that from a local population sampled in Bangladesh indicates the particular population from which that performing monkey was collected. Moreover, Monkey performers always keep their monkeys in close condition (in a box or tie with a chain). They do not allow the monkeys to breed as they cannot use a pregnant monkey for street shows. As the livelihood of monkey performers

depend on the income from the street show, less than 1% of performers allow their monkeys for breeding, usually when they engage in other occupation for a long time (Akhtar 2014). Thus, there is no chance of admixture of performing monkeys with the wild population.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

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Fig. 1. A permanent monkey trap set by local people

Fig. 2.

Location of performing monkey village in Bangladesh. Green area (except northwest) indicates distribution of rhesus macaques in forests. Yellow dots and corresponding numbers indicate populations of rhesus macaques with those performing monkeys were compared. 1.Sadhana, 2.Dhamrai, 3.Narayanganj, 4.Bormi, 5.Madhupur, 6.Satchari, 7.Kalenga, 8.Fenchuganj, 9.Chashnipeer, 10.Syed Jahan, 11.Malnichara, 12.Khadimnagar, 13.Haripur, 14.Jaintapur, 15.Chandpur, 16.Chunati, 17.Fashiakhali, 18.Dulahazara, 19.Charmuguria, 20.Kolargaon, 21.Naria, 22.Nandanshar, 23.Kartikpur, 24.Wajirpur, 25.Karamjal, Sundarbans, 26. Gojni, 27. Hazarikhil and 28.Rajban Bihar.

Fig. 3. Maximum likelihood (MLK) tree (phylogram) of haplotypes from the different performing monkey populations. The MLK percentages of the 1000 bootstrap replicates supporting a particular clade within the MLK tree are indicated at each branch.

Fig. 4. Sources of performing monkeys in Joralganj and Kaliganj performing monkey villages

Fig. 5. Median-joining haplotype network of performing monkey haplotypes and rhesus macaque haplotypes from Bangladesh, India and Myanmar

Sources of performing rhesus macaques in Bangladesh based on mtDNA haplotype data

Note:

¹ Sites in each of the regions of Bangladesh where free-ranging monkeys were sampled.

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Performing monkeys that were likely exchanged within and between performing monkey villages based on haplotype data;
2
3 Performing monkeys that were likely collected from India based on haplotype data