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Brief communication

Size matters! The largest wild stump-tailed macaque *Macaca arctoides* troop ever reported, located in the Hollongapar Gibbon Sanctuary, northeastern India

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Very large and stable, socially coherent primate groups, not including fission-fusion societies, are usually rare in nature, owing to constraints imposed by various ecological and social factors. Moreover, unlike species in open habitats, those in forests tend to have smaller groups, and this becomes further accentuated in small and fragmented forest patches. We report here an unusually large troop of stump-tailed macaques *Macaca arctoides* from the Hollongapar Gibbon Sanctuary, a small and isolated lowland tropical rainforest patch in the Upper Brahmaputra Valley of northeastern India – this is possibly the largest wild group of the species recorded anywhere across its distribution range. We hypothesise the potential factors driving the formation of such a large social group of this vulnerable cercopithecine primate and discuss the conservation implications of this phenomenon.

Keywords. Lowland rainforest fragment; Predation risk; Upper Brahmaputra Valley; Assam

We dedicate this paper to the late Noren Bhuyan, our Noren da, who was one of our most able guides in the forest and an ever-trusted friend.

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1. Introduction

Stable, socially coherent groups vary in size among primate species from solitary individuals to over several hundred individuals, often with considerable variation in group size within the same species (Smuts *et al.* 1987; Beauchamp and Cabana 1990; Abernethy *et al.* 2002; Mitani *et al.* 2012; Nekaris 2014). Various ecological and social factors have been proposed to explain this variation in primate group size. Large groups, for example, have been traditionally believed to be better protected from predators due to dilution effects and increased vigilance (Hamilton 1971; Alexander 1974) although empirical evidence in its support for terrestrial primates remain inconclusive (Isbell 1994). On the other hand, a large group size could potentially decrease foraging efficiency and increase scramble or contest competition, thus imposing practical limits to the group size that is ecologically sustainable (Wrangham 1980; Chapman and Chapman 2000). We can thus hypothesise that large and stable primate groups are possible under situations where particular populations face high predation pressures, have a relatively large ecological niche breadth and the opportunity to forage over extensive areas in a habitat with abundant food resources. It is also important to note that, from a socio-behavioural perspective, such group sizes must continue to be socially coherent, obey individual cognitive constraints and thus be well located within the group's eco-cognitive niche (Dunbar 1996; Lehmann *et al.* 2007).

Primate groups living in fragmented habitats offer interesting insights into the evolution of group size as the responses of primates to habitat fragmentation is highly variable (Marsh and Chapman 2013). In forest fragments, primate group size, depending on the species, could either decrease (Donati *et al.* 2011), increase (Krishna *et al.* 2006) or remain stable (Zunino *et al.* 2007). Reduction in group size could serve to reduce scramble and context competition over food resources (Marsh *et al.* 2016) although such troops could be more vulnerable to predators. In general, certain fragment characteristics, such as the quality of resources available, appear to influence group size more (Rodriguez-Toledo *et al.* 2003) than do their size or degree of isolation though some species often cannot survive below a critical habitat size (Marsh *et al.* 2016).

It is thus always intriguing when certain primate populations or groups increase in size within habitat fragments that are clearly constrained in various aspects, because, in accordance with the ecological constraints model, increased group size will significantly enhance scramble and contest competition over the limited food resources available in such fragments (Chapman and Chapman 2000). There has been, for example, a significant increase in the size of a population of lion-tailed macaques *Macaca silenus*, if not in group size, within certain fragmented forests in southern India (Umapathy *et al.* 2011). Group size, however, did tend to increase, especially in the smaller fragments, and this was attributed to the higher reproductive rates, lower mortality, lack of dispersal and fission displayed by the species due to lack of space although the opportunistic and flexible feeding habits of the groups and the nature of available resources may have contributed to this rise as well (Krishna *et al.* 2006; Umapathy *et al.* 2011).

In this article, we report the discovery of the largest wild troop of stump-tailed macaque *Macaca arctoides* ever known. We also discuss the ecological and biological factors that may have given rise to such an unusual group size of the species within the Hollongapar Gibbon Sanctuary, a tropical lowland rainforest fragment of the Upper Brahmaputra Valley in north-eastern India.

2. Materials and methods

2.1 *Study area*

The Hollongapar Gibbon Sanctuary (figure 1) is a small (2098 ha) and isolated tropical lowland rainforest fragment, dominated by *Dipterocarpus-Mesua-Vatica* forest. The Sanctuary is known for its rich diversity of primates, including the rhesus macaque *Macaca mulatta,* northern pig-tailed macaque *Macaca leonina*, stump-tailed macaque *Macaca arctoides*, western hoolock gibbon *Hoolock hoolock*, capped langur *Trachypithecus pileatus* and the Bengal slow loris *Nycticebus bengalensis* (Sharma *et al.* 2012). The Sanctuary is, however, surrounded by a matrix of human settlements, agricultural fields and tea plantations. A major railway track also runs through the Sanctuary, which has no human settlements but nevertheless experiences a significant amount of non-timber forest product collection over the year (Sharma *et al.* 2020).

2.2 *Primate survey*

We conducted a ten-day primate census in the Hollongapar Gibbon Sanctuary between 12 and 22

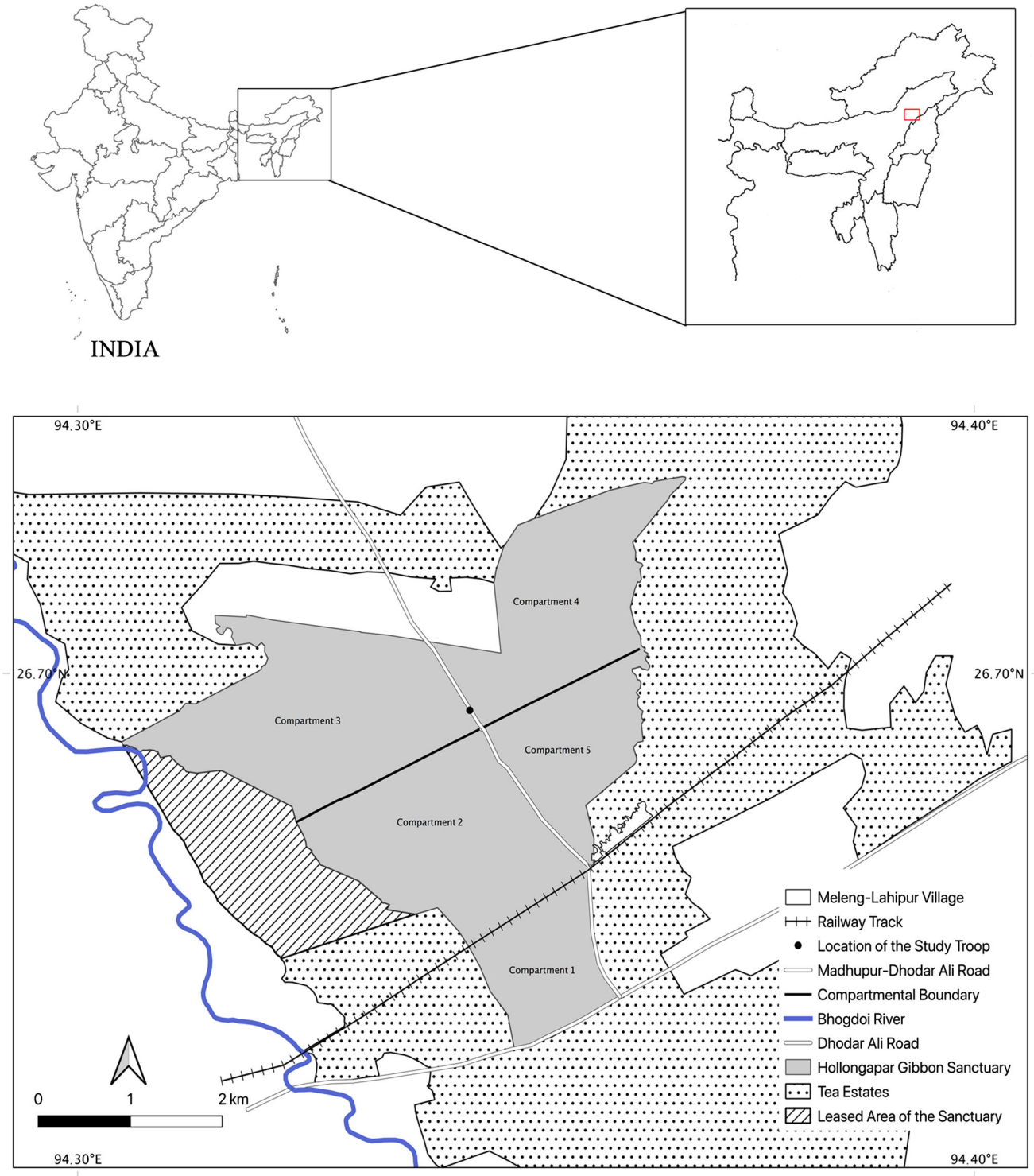

Figure 1. The Hollongapar Gibbon Sanctuary in Assam, northeastern India, showing the different forest compartments and the location of the study stump-tailed macaque troop.

December 2016. We adopted a complete-count method (Struhsaker 1981; Sharma *et al.* 2012) to estimate primate abundance, as it is ideally suited for small forest fragments. We used repeated, systematic trail-walks and also followed troops, whenever opportunistically sighted, over the entire day to ensure that all groups and individuals of the study species were enumerated. We have been studying identified

individual stump-tailed macaques in this Sanctuary since 2002 and were thus able to classify individuals into the following age-sex categories: Adult male: >5 years; adult female: >4 years; subadult male: 3–5 years; subadult female: 3–4 years; juvenile male and female: 1–3 years and infant male and female: <1 year.

3. Results

On 22 December 2016, at 08:54 h, we encountered a troop of stump-tailed macaques at the boundary of Compartments 3 and 4 of the Sanctuary (26.69612°N, 94.34373°E; figure 1). We counted the individuals but could not assign all of them to particular age-sex classes. We, however, recorded a video of the entire troop (Online Resource) and were then able to assign all individuals to the different age-sex categories with the help of this recording. We counted a total of 194 individuals, with their age-sex composition provided in table 1. The percentage of identified adult males, adult females as well as subadults, juveniles and infants of both sexes comprised approximately 24%, 23%, 12%, 24% and 13% of the troop respectively. The sex of 21 adult individuals, however, remained unidentified. The important demographic ratios for the troop included 0.9 adult female per adult male, 0.56 infant per adult female, 2.15 immature per adult female and 0.83 immature per adult individual.

4. Discussion

A survey of the literature reveals that our observed troop of 194 individuals is possibly the largest ever recorded for stump-tailed macaques anywhere (table 2), the Hollongapar Gibbon Sanctuary marking one of the westernmost points of the distribution range of this species. It is important to note that this troop was a stable group and not a mere congregation of small subgroups, as all the individuals always moved in a single unit and remained associated throughout the day, not even breaking out into foraging subgroups. What makes our finding even more remarkable is that our long-term studies on the primates of the lowland rainforest fragments of the Upper Brahmaputra Valley have revealed the increasing local extinction of stump-tailed macaques from many of the fragments, primarily driven by the small size of the fragments and the loss of food tree species in them, due to extensive felling (Sharma *et al.* 2014). Given the large home range (400–900 ha in the Hollongapar Gibbon Sanctuary, Sharma *et al.* 2012) required by the species, smaller fragments may not ultimately be able to support populations of this species, as has also been reported for other wide-ranging Neotropical primates (Schwarzkopf and Rylands 1989).

The Hollongapar Gibbon Sanctuary is a rainforest fragment that has remained isolated from other forest patches for over a century now (Sharma, unpubl. data). We, however, reported an increase in the abundance of stump-tailed macaques in this Sanctuary between 1995 and 2008 (Sharma *et al.* 2012). The demographic profile of the recorded troop indicates an inter-birth interval of approximately two years, which is typical for the species. A percentage of 45% immature individuals in the group also reveals a high level of recruitment into this growing troop. What then could be the possible reasons for the existence of such a large group of this threatened species in this forest fragment?

We speculate that one of the most important factors behind such a large group size could be the omnivorous diet that typically characterises this macaque species. Its food ranges from fruits, shoots, tubers, flowers through leaves of various shrubs, trees, climbers, and the abundant bamboo (Sharma 2012) to fungi, insects, slugs and even frogs. This would then imply that the broad spectrum of items taken by stump-tailed macaques will far outstrip the relatively narrow diet regimes of the other, more diet-specialist, primates that are sympatric with the species in this forest, including the northern pig-tailed macaque, capped langur and the hoolock gibbon (Sharma 2012). The only exception would potentially be the rhesus macaque, which, however, occurs along the fringe areas of the Sanctuary, more often foraging in the neighbouring villages than in the forest interior (Sharma 2012). It is noteworthy that this observed lack of exclusivity in the food resources taken by the study troop from within the

Table 1. Size and age-sex composition of the study stump-tailed macaque troop in the Hollongapar Gibbon Sanctuary, Assam

Adult male	Adult female	Unidentified adult	Subadult	Juvenile	Infant	Total
44	41	21	21	44	23	194

Table 2. Summary of all published records of troop size in wild stump-tailed macaques across their distribution range

Site	Country	Troop size	References
South Burma	Myanmar	~4–5	Blanford 1888; Fooden 1990
Nagaland	India	~25–30, >40	Mills 1923; McCann 1933
West Thailand	Thailand	Solitary male (2), ~2–3, 5, ~10–15, ~20–30	Fooden 1967; Eudey 1981; Treesucon 1988
North-West Malaysia	Malaysia	<50	Medway 1969
Tripura	India	8, 10, 11, 13, 20	Mukherjee 1983
Yunnan	China	12–50 (number of troops unknown)	Fooden et al. 1985
Northwestern Thailand	Thailand	20	Treesucon 1988
Doi Inthanon NP	Thailand	20	Treesucon 1988
Huai Kha Khaeng WLS	Thailand	~20–30	Treesucon 1988
Thung Yai WLS	Thailand	20	Treesucon 1988
Ban Tha Salao	Thailand	20	Treesucon 1988
Kaeng Kra Chan NP	Thailand	15	Treesucon 1988
Khao Tao Mo	Thailand	22	Treesucon 1988
Huai Sat Yai	Thailand	~20–25	Treesucon 1988
Hup Jang	Thailand	~15–20	Treesucon 1988
Khlong Mala WLS	Thailand	20	Treesucon 1988
Khlong Nakha WLs	Thailand	~25–30	Treesucon 1988
Ban Kun Tu Lee	Thailand	~25–30	Treesucon 1988
Khlong Seang WLS	Thailand	30	Treesucon 1988
Ban Ply Num	Thailand	~20–25	Treesucon 1988
Khao Sok NP	Thailand	31	Treesucon 1988
Khao Phanom Bencha NP	Thailand	~25–30	Treesucon 1988
Khao Phra Bang Kram	Thailand	30	Treesucon 1988
Khao Nam Pry	Thailand	~20–30	Treesucon 1988
Khao Banthat	Thailand	~20–30	Treesucon 1988
Khao Pu NP	Thailand	~20–30	Treesucon 1988
Ton Nga Chang WLS	Thailand	60	Treesucon 1988
Thaleban NP	Thailand	~20–30	Treesucon 1988
Guangxi	China	30	Fooden 1990
Central Thailand	Thailand	30	Fooden 1990
Wat Tham Khao Daeng	Thailand	104	Malaivijitnond and Hamada 2005
Mizoram	India	18	Zothansiama and Solanki 2016
–	Thailand	45–120 (5 troops)	Aru Toyoda, 2019, pers. comm.
Kaeng Kra Chan NP	Thailand	~100 (3 troops)	Aru Toyoda, 2019, pers. comm.
Southern Thailand	Thailand	~100–120	Aru Toyoda, 2019, pers. comm.
Hollongapar Gibbon Sanctuary, Assam	India	110 and 132	Sharma 2012
Hollongapar Gibbon Sanctuary, Assam	India	194	Present study

NP, National Park; WLS, Wildlife Sanctuary

forest itself could have prevented it from foraging in nearby croplands, plantations or settlements, unlike the above-mentioned lion-tailed macaques of southern India, which have managed to survive by changing their food habits, incorporating the consumption of unpredictable and exotic items, such as coffee and tea berries as well as many more foods of human origin, in their now-regular diet (Singh *et al.* 2002; Dhawale *et al.* 2020).

Another important factor that could sustain the formation and maintenance of such a large primate group is the predation pressure faced by the species. The potential predators of stump-tailed macaques in the Sanctuary were the common leopard *Panthera pardus,* clouded leopard *Neofelis nebulosa*, domestic dogs and raptors, especially *Accipiter* sp. (Chetry *et al.* 2003). The density of common leopards had also arisen in recent years due to the release of most leopards, rescued from the neighbouring human habitations, in this forested patch by the Forest Department. Although common leopards prefer barking deer *Muntiacus muntjak* and, to a lesser extent, the wild pig *Sus scrofa,* they are also known to prey on primate species, including macaques (Sinha *et al.* 2005; Hayward *et al.*

2006) and, thus, potentially stump-tailed macaques as well (Chetry *et al.* 2003). Leopards especially prey on monkeys on the ground during the day (Zuberbühler and Jenny 2002), which could make stump-tailed macaques particularly vulnerable to predation in this Sanctuary.

There are three principal reasons for us to believe that the large group size of the study troop could have indeed been sustained in response to predation pressures. First, diurnal and group-living primates often reduce their predation risks by preferring to roost in tall trees with large crowns and trunks with many horizontal branches (Fichtel 2012), a practice regularly adopted by the stump-tailed macaques in the Sanctuary (Sharma 2012) and at other sites as well (Siama and Solanki 2016). Second, male primates are known to be more vigilant than are females, as they are better at detecting potential predators (van Schaik and Hörstermann 1994), a pattern that was observed in another troop of stump-tailed macaques in Hollongapar (Bhashyam 2016). Third, the adult male: adult female ratio of 1:0.9 appeared to support the hypothesis that primate groups, which experience high predation risks, tend to have relatively more males (van Schaik and van Noordwijk 1989).

Terrestrial primate groups are usually more populous than are those of arboreal primates and typically occur in relatively open habitats (Clutton-Brock and Harvey 1977). The stump-tailed macaque troop of Hollongapar, however, is unique as it was entirely a forest group that never exploited human-origin food resources in the surrounding agricultural matrix—a factor that may have also contributed to its lowered mortality rate—although the species is known to cause considerable damage to crops elsewhere (McCann 1933).

A final point regarding the study macaque troop concerns the species-typical socioecological mechanisms, possibly derived from both phylogenetic origins as well as phenotypically flexible responses to local ecological conditions, which may have allowed for the unusual social coherence displayed by the group (Henzi and Barrett 2005; Sinha 2005). The cognitive capacities of the species, perhaps expressed to an unusual extent in the study troop, which has made it possible for this particular group to thus function efficiently within its eco-cognitive niche (Lehmann *et al.* 2007; Bhashyam 2016; Sinha 2017) definitely need to be elucidated in the years to come.

We conclude this note by highlighting the vital importance of conducting long-term studies on the structure and dynamics of this last remnant stump-tailed macaque population, including the monitoring of the study troop, in the future, as the species has now virtually disappeared from all the forest fragments of the Upper Brahmaputra Valley (Sharma *et al.* 2012, 2014). Hollongapar is possibly one of the last strongholds of the species, not only in northeast India, but possibly in southern Asia as well.

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