Watering holes: The use of arboreal sources of drinking water by Old World monkeys and apes

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Abstract

Water is one of the most important components of an animal's diet, as it is essential for life. Primates, as do most animals, procure water directly from standing or free-flowing sources such as pools, ponds and rivers, or indirectly by the ingestion of certain plant parts. The latter is frequently described as the main source of water for predominantly arboreal species. However, in addition to these, many species are known to drink water accumulated in tree-holes. This has been commonly observed in several arboreal New World primate species, but rarely reported systematically from Old World primates. Here, we report observations of this behaviour from eight great ape and Old World monkey species, namely chimpanzee, orangutan, siamang, western hoolock gibbon, northern pig-tailed macaque, bonnet macaque, rhesus macaque and the central Himalayan langur. We hypothesise three possible reasons why these primates drink water from tree-holes: (1) coping with seasonal or habitat-specific water shortages, (2) predator / human conflict avoidance, and (3) potential medicinal benefits. We also suggest some alternative hypotheses that should be tested in future studies. This behaviour is likely to be more prevalent than currently thought, and may have significant, previously unknown, influences on primate survival and health, warranting further detailed studies.

Keywords: Primate; tree-hole; dipping-and-licking; seasonal water; predator avoidance; self medication

1. Introduction

Water is essential for the sustenance of life and therefore, a vital component of an animal's diet. Primates, like most animals, procure liquid water either from natural ground sources such as pools, puddles, rivers, springs, and streams, from occasional anthropogenic sources (e.g., Willyer et al., 2015), or as pre-formed water (National Research Council, 2003), by consuming tender leaves, leaf petioles, fruits, flowers, stems, roots and bark (e.g., Poirier, 1970; Angus, 1971; Glander, 1978; Nishida, 1980; Chapman, 1988; Ciani et al., 2001). The consumption of water-containing plant parts has frequently been described as the main source of water for predominantly arboreal primate species or for those living in arid or semi-arid habitats, with little or no opportunity to directly access ground water. Preformed water in the foods of free-ranging nonhuman primates has been reported to vary from less than 5% of air-dried seeds in hot deserts to over 70% of the fresh weight of succulent plant parts in tropical rainforests (Baranga, 1982; Calvert, 1985; Rogers et al., 1990; Barton et al., 1993; Robbins, 1993; Edwards, 1995). Many of these species, thus, often lick dew and rainwater from leaves in the early morning or after rainfall, only rarely descending to the ground to drink (e.g., *Presbytis* [currently *Trachypithecus*] *johnii*, Poirier, 1970; *Macaca sinica*, Dittus, 1977; *Cebus albifrons*, Defler, 1979; *Procolobus badius temminckii*, Starin, 2002). Another source, more difficult to observe and thus, perhaps less frequently reported, is the drinking of rainwater accumulated in the holes of tree trunks (but see Dittus, 1977; Glander, 1978; Chapman, 1988; Starin, 2002).

In general, primates have two ways to obtain water from tree-holes. If the tree-hole is large, the animal can insert its head inside and directly drink the water with its mouth (Glander, 1978; Nowak 2008). If, however, the hole is narrow, the individual may insert its forearm inside, dip it in the water and then lick the adhering water from

it, a method known as ‘dipping-and-licking’ (Wrangham, 1981). In addition, some species also use innovative techniques to drink water from tree-holes. Chimpanzees *Pan troglodytes* and Sumatran orangutans *Pongo abelii*, at some sites, for example, have been observed to use their hands to scoop up water or employ leaves as a tool to sponge the water out from tree-holes (e.g., Reynolds and Reynolds, 1965; Sugiyama, 1995; Tonooka, 2001; van Schaik et al., 2003) while Zanzibar red colobus *Procolobus kirkii* individuals, in a mangrove forest refuge, would also tilt their heads up and scoop water into their open mouths with their hands (Nowak, 2008).

The ‘dipping-and-licking’ method is well documented, particularly in New World primates (*Cebus capucinus*, Freese, 1978; *Alouatta palliata*, Glander, 1978; *Alouatta caraya*, Bicca-Marques, 1992; Giudice and Mudry, 2000; *Alouatta guariba clamitans*, Steinmetz, 2001; *Alouatta pigra*, Dias et al., 2014) but also in a few Old World species (*Erythrocebus patas*, Struhsaker and Gartlan, 1970; *Lemur catta*, Sussman, 1977; *Cercopithecus aethiops*, Wrangham, 1981; *Presbytis entellus*, Newton, 1992; *Macaca silenus*, Fitch-Snyder and Carter, 1993) and in certain great and small apes (*Hylobates lar*, Carpenter, 1964; *Pan troglodytes*, Reynolds and Reynolds, 1965; *Hylobates* spp., Chivers, 1977). In a very early notable study, hoolock gibbons *Hoolock hoolock* were observed to scoop up and drink water, using this technique, in captivity (Sanyal, 1892).

Here, we report on the contexts and diverse behaviours involved in the drinking of water accumulated in tree-holes by eight Old World primate species—chimpanzee *Pan troglodytes schweinfurthii*, Bornean orangutan *Pongo pygmaeus morio*, siamang *Symphalangus syndactylus*, western hoolock gibbon *Hoolock hoolock*, northern pig-tailed macaque *Macaca leonina*, bonnet macaque *Macaca radiata*, rhesus macaque

Macaca mulatta and central Himalayan langur *Semnopithecus schistaceus*—
inhabiting a wide range of habitats (Table 1).

We also propose three principal, non-exclusive hypotheses to argue why such
unusual drinking behaviour may be far more widespread than originally thought.
First, drinking of water from tree-holes may have evolved and been maintained in
response to habitat-specific or seasonal shortages in water from other, usually more
prevalent, sources. Second, this strategy of drinking from arboreal water sources
could be a possible anti-predator strategy or one to reduce competition with and/or
minimise aggression from conspecific individuals, or even avoid conflict with other
species such as humans. Finally, individual primates could be attracted to the water in
tree-holes as these could provide medicinal or other nutritional benefits due to the
presence of leachates in them, in addition to being possibly less contaminated in
comparison to other terrestrial water sources. The two main goals of this paper are,
therefore, to (1) present new information on the drinking habits of several Old World
primates from arboreal sources, and (2) propose potential ecologically relevant
functions of this behaviour.

Given that there are only limited published accounts of unusual drinking behaviour
displayed by Old World monkeys and apes, we wish to appeal to other field
primatologists to collect and collate related information in the future, particularly to
document the innovation capacities of nonhuman primate species facing
environmental challenges during foraging and to understand the selection pressures
driving such adaptive behaviours. Indeed, comparisons with species outside of the
Order Primates would provide an even wider perspective from which to consider the
possible ecologically relevant functions of this behavior.

2. Methods

Three of our study areas are located in India, and one each in Malaysia, Indonesia, and Tanzania (Fig. 1). All sites are different in terms of their climate, vegetation types and primate communities (Table 1). The species have been listed and discussed by region.

We used opportunistic sightings to record the drinking behaviours of the study species, during research designed for other purposes. Given this constraint, it is entirely possible that the frequencies of the reported behaviours have been underestimated.

3. Observations

N.S. observed dipping-and-licking behaviour in western hoolock gibbons and northern pig-tailed macaques in May 2009 during a field study on the primate communities of Hollongapar Gibbon Sanctuary (HGS), Assam state, northeastern India. On 3 May 2009, an adult male hoolock gibbon was observed in the mid-canopy, just above a tree-hole, to repeatedly dip his right hand inside the hole, filled with rainwater, and then lick the water from his fingers by positioning the hand over his mouth (Fig. 2A, Supplementary Material S1). Another record was made on 12 May 2009 in the same locality, when a northern pig-tailed macaque, on a different tree, was observed to drink water in a similar fashion. An adult macaque dipped its hand repeatedly inside a tree-hole and licked its palm covered with water (Fig. 2B, Supplementary Material S2).

S.G. observed the dipping-and-licking behaviour in six individual bonnet macaques in Bandipur National Park (BNP), Karnataka state, southern India, on three occasions. On 15 April 2013, a juvenile male was observed to dip his hands inside a hole on the

trunk of a *Ficus benghalensis* tree. He then brought out his palm, soaked in rainwater that had accumulated in the hole, and licked the dripping water off it, repeating this behaviour multiple times. On 21 April 2014, three juvenile females and an adult female (mother of one of the juveniles), belonging to the same troop as the former juvenile male, were observed to perform dipping-and-licking in the same *F. benghalensis* tree, but at a different tree-hole than that observed earlier (Fig. 2C, Supplementary Material S3). The next day, on 22 April 2014, another juvenile male of this troop was observed to drink from the same tree-hole using the dipping-and-licking method.

In her study on central Himalayan langurs in Kedarnath Wildlife Sanctuary (KWS), Uttarakhand state, northern India, H.N. observed one particular semi-rural troop of this species to have six principal feeding sites, all of which had mountain-fed streams or other stable sources of drinking water in their vicinity; these sources were regularly used by the langurs. At one oak forest site, however, the closest perennial water source was located adjacent to a human settlement and between January and September 2015, H.N. observed 11 bouts of drinking by both central Himalayan langurs and rhesus macaques at a particular tree-hole on an oak *Quercus leucotrichophora* tree. Individuals of both species were able to insert their heads inside the hole to drink directly with their mouths but occasionally used the dipping-and-licking technique with their hands (Fig. 2D, Supplementary Material S4). On 11 September 2015, H.N. observed one adult female, two adult males and one juvenile langur using both techniques to drink water from the hole (Supplementary Material S4) while two adult females, three juveniles and two subadult males were again seen drinking there on 13 September 2015. On one of these occasions, the white chin hairs of a langur became stained with a yellow colouration after it had drunk directly from

the tree-hole. On another occasion, a rhesus macaque individual was, in fact, subsequently observed to remove and discard material resembling decomposed plant tissues from the same hole, prior to drinking water from it. On 12 September 2015, two rhesus macaques (a subadult and an adult male) were observed to supplant langurs from the same hole and use it to drink, employing the same technique as the langurs.

R.M. recorded 33 events of water-drinking behaviour by wild Bornean orangutans in Danum Valley Conservation Area (DVCA), Sabah, Malaysia between May to July and September to December 2013 and between February to December 2014. Of these 33 events, 22 acts were performed by adult females carrying offspring ($n = 6$ individuals), four by adolescents ($n = 3$) and seven by immature individuals ($n = 4$). In 31 of these 33 events, individuals accessed water from inside tree-holes by dipping their hands in the water. There were, however, two different ways that the water was then consumed. One consisted of cupping the fingers to collect the water, bringing the hands to the mouth and then either drinking from the cupped hands or pouring the water into the mouth (Supplementary Material S7). The other way consisted of dipping the fingers into the water and transferring water to the mouth, without cupping the fingers, but in a rapid grabbing-like movement (Fig. 2G, Supplementary Material S8).

The differences in the two methods by which orangutans obtained water from the tree-holes may have been due to differences in the size and depth of the tree-holes, or possibly, even a matter of individual preference. Less frequently, when the opening was large enough, they were observed to drink from tree-holes directly with their mouths. In the two other drinking events observed, an adult female carrying her infant was observed climbing down through the liana and drinking from the stream,

immersing her mouth directly in the water (Supplementary Material S9). Adult female orangutans in DVCA were rarely observed on the ground and this was the only context in which they were seen, other than short-distance travel from one tree to another. The immatures followed their mothers' behaviour and were often observed to drink water at tree-holes after their mothers finished drinking, with the exception of a seven-year-old juvenile, which drank before his mother. Adult male orangutans were never seen to drink water from tree-holes during the study period although there were casual observations of them obtaining water from both tree-holes and streams in the area at other times.

Between October 2007 and April 2009, L.M. observed 541 drinking events among 11 groups of wild siamangs in the Way Cangk locality of the Bukit Barisan Selatan National Park (BBSNP) in Sumatra, Indonesia. Adult males ($n = 20$), adult females ($n = 11$), large juveniles ($n = 8$) and small juveniles ($n = 5$) were observed drinking water with the use of their hands 233, 141, 115 and 52 times respectively during the study period. In 12 other instances, siamangs collected water directly using their mouths. Individual siamangs collected rainwater from holes in tree trunks by a typical sequence of hand motions and postural modifications that allowed them to efficiently extract the liquid with cupped fingers and bring it to their mouths (Fig. 2F, Supplementary Material S5). Evidence that this was an important activity for the population came from the alternative observation that there were at least four occasions at the peak of the dry season when the siamangs, which typically remained in the high layers of the canopy and virtually never descended to the ground, climbed down along lianas and drank directly from a nearby river (Supplementary Material S6). Access to a water source in tree-holes, thus, appeared to be of importance to the siamangs. This hypothesis was further supported by observation of social tensions

that were generated in the groups when they accessed these holes, with adult females initially monopolising the water source. They were typically followed by adult males and then by subadults, while juveniles were generally tolerated during drinking episodes.

At Mahale Mountains National Park (MMNP) in Kigoma state, Tanzania, on 13 December 1991, M.A.H. observed three chimpanzees (two immature males and a mature male) approach a *Monates elegans* tree. The tree had a small natural opening about 1.5 m above the ground (Fig. 2E). The cavity extended down into the central part of the trunk to a depth of approximately 30 cm. A thickened layer of bark formed a small over-hanging lip and created a small recess above and around the natural opening. There was, in this recess, a dark, resinous material-covered nest of a flying insect, tentatively identified to be a species of the sweat bee *Megalopta*. Dark stains from the nest streaked down into the hole, suggesting that a rainwater-leached substance from the nest may have been deposited in the hole. The chimpanzees lined up, in accordance to their relative age, with the younger individuals behind, patiently waiting for a chance to access the tree-hole. Each individual then climbed up to the hole, in turn, inserted their hands inside, withdrew liquid-dripping fingers and licked them, this process being repeated several times by each individual. When the group left, M.A.H. smelled and tasted a few drops of the same liquid. It was salty and had a strong smell of human sweat. This behaviour was observed only once at this location. During the same season, however, at another site, M.A.H. periodically observed chimpanzees using similar techniques to drink water from a tree of another species *Parinari curatellifolia* (dates not recorded). In this case, the chimpanzees used a sponge made of softened woody material scraped from the interior of the tree-hole by hand. A later visual inspection of the hole revealed the water inside to be brownish in

colour but with no evidence of any insect nest in the hole, as in the previous case. Chimpanzees have occasionally been observed to drink water from holes in trees in MMNP but the frequency has never been too high, possibly due to their having ample year-round access to streams throughout their home ranges.

4. Discussion

We have documented and systematically collated the ‘dipping-and-licking’ method of drinking of water (Wrangham, 1981) in several wild populations of Old World primate species, including the Bornean orangutan, siamang, western hoolock gibbon, northern pig-tailed macaque, bonnet macaque and the central Himalayan langur, and provided further evidence for its presence among chimpanzees. It is noteworthy, in this context, that there are species or their particular populations, which have never been reported to use this method to drink water in spite of prolonged observations (e.g., *Trachypithecus johnii*, Poirier, 1970). Whether this reflects a species-typical failure or simply a lack of opportunity or need for some populations of an otherwise capable species to simply employ this method during their foraging for water, however, remains to be discovered.

It may be expected that arboreal primates would be, in general, more likely to drink water from tree-holes than would largely terrestrial species. The arboreal species that we studied, indeed, did display relatively higher frequencies of drinking from tree-holes than did the terrestrial monkeys and apes. It is, nevertheless, important to understand why largely terrestrial primates occasionally also do drink water from tree-holes.

First, in response to our hypothesis that seasonal water shortages could play a role in primates switching to alternative water sources, we expected that drinking from

285 tree-holes would be more prevalent during dry seasons, provided, of course, these
286 holes did have adequate water in them. However, contrary to our expectations, this
287 behavioural strategy was observed particularly during the wet season in not only the
288 arboreal hoolock gibbon but also in the relatively terrestrial species like the pig-tailed
289 macaque, rhesus macaque and the central Himalayan langur, and in habitats that had
290 abundant fruits or tender leaves at the time and when water was available from
291 multiple free-flowing sources. In the Bandipur National Park in southern India,
292 however, there were three instances of bonnet macaques using tree-holes in a
293 relatively dry period, but when afternoon showers had filled up the holes with water.

294 It must also be recognised that certain trees in some habitats may be particularly
295 suitable for the accumulation of water in their tree-holes and thus facilitate drinking
296 behaviour more often than from other sources in the same habitat. In the Bandipur
297 National Park, for example, other troops of bonnet macaques did not display such
298 drinking behaviour, even after rains. They had instead been observed to lick rainwater
299 from leaves or acquire drinking water from other sources by lapping up water from
300 the ground, kitchen-pipes, buckets, bottles or other opportunistic anthropogenic
301 sources. Although the individuals in the study troop, in which dipping-and-licking
302 behaviour was observed, had also utilised other water sources, the presence of a
303 particular tree with a hole that accumulated rainwater may have afforded a convenient
304 opportunity for the display of the observed behaviour by this troop. In this context, it
305 is noteworthy that the water-hole was used mostly by juvenile individuals of this
306 troop, a possible outcome of the curiosity-driven behaviour of immature individuals.
307 Alternatively, it is possible that the acquisition of water from sources other than those
308 used by the adults of the group is a juvenile strategy to avoid confrontation with or
309 aggression from the adults of the group.

Our results and arguments thus suggest that certain habitats and suitable trees may facilitate the drinking of water from tree-holes by individual primates. Wet seasons are also likely to be the most suitable times when tree-holes contain water, which can be profitably exploited by primates, although this begs the question of why these species do not invariably drink from free-flowing water sources, which are also easily available during these seasons.

A possible response to this question could be represented by our second hypothesis that arboreal primates may take recourse to drinking water from tree-holes at certain times and in specific localities in order to avoid terrestrial predators (e.g., Starin, 2002). Gibbons, siamangs and orangutans are strongly adapted to arboreal life and are, thus, usually not motivated to descend to the ground in search of water, except perhaps under exceptional circumstances. This reluctance to be terrestrial could perhaps be ascribed to increasing risks of predation when on the ground. This possibility appeared to be supported during our studies when we observed siamangs in Sumatra and Bornean orangutans in Sabah, both extremely arboreal species, to descend to the ground rather rarely, and that too only in search of water. Moreover, the importance of tree-holes as sources of water for the siamangs was clearly evidenced when we observed intra-group inter-sexual scramble competition for these sources of water.

A noteworthy variation of such decision-making was encountered during H.N.'s studies on the central Himalayan langur in northern India. The semi-rural troop of this species, which extracted water exclusively from a tree-hole, when ranging in this particular area (but drank from ground water sources in other areas), possibly did so in order to avoid the risk of encountering humans, which appeared inevitable had they used the only perennial water source available. Additionally, it is perhaps illuminating

that the largely terrestrial rhesus macaques at this site also employed this particular tree-hole to extract water and were even observed to compete with the langurs for this resource. Our predation-avoidance hypothesis could also potentially explain the unusual cases of bonnet macaques in the Bandipur National Park, which employed particular tree-holes as sources of rainwater even though the observed troop was largely terrestrial and usually obtained water from perennial ground sources across its home range.

Our third hypothesis was that, regardless of an arboreal or largely terrestrial habit, certain primate populations may obtain potentially medicinal or other nutritional benefits from substances that may leach into the rainwater, which accumulates in holes, from the tree or from other materials deposited on the tree. During the period of observation at Mahale in Tanzania, for example, many of the chimpanzees, which were followed, exhibited signs of gastrointestinal disorder (diarrhoea), parasitosis (oesophagostomiasis) and simultaneously exhibited one or both of two self-medicative behaviours—leaf-swallowing, which is known to physically expel adult *Oesophagostomum stephanostomum* worms, or ingest the pharmacologically active, bitter pith of *Vernonia amygdalina*, which is known to reduce symptoms of *O. stephanostomum* infection (Huffman et al., 1996, 1997; Huffman and Caton, 2001).

In the case of the semi-rural troop of central Himalayan langurs, the observed yellow staining of the chin hairs of an individual after it had drunk water from a tree-hole suggested that the water could have contained materials leached into it, most likely from the wood itself or possibly from the oak leaves that had accumulated inside the water-filled hole. Oak leaves are characteristically high in condensed tannins, a group of compounds known for their significant anti-parasitic activity (e.g., Hoste et al., 2009; Williams et al., 2014). It is tempting to speculate that the langurs

could have sought out the water from this particular tree-hole for its particular anti-parasitic properties but this hypothesis remains to be tested.

In the case of the chimpanzees of Mahale too, it is unlikely that they used the tree-hole simply for water, as there were many free flowing streams in the area. One must, therefore, consider the possibility that there was some added appeal from the extracts of wood and the sweat bee nest, which attracted the individuals to this water. Elsewhere, in the habitat, chimpanzees have also been observed to lick the material that had accumulated below sweat bee nests on rocks.

Additionally, there are a few possibilities, currently beyond the scope of our observations, which could constitute productive avenues of future research. Commonly explored relationships in folivorous-frugivorous New World primates, for example, are those between the degree of folivory and the frequency and timing of drinking behaviour in certain species populations or the possible influence of relative humidity and diet composition on the time of drinking of water (Norconk et al., 1996; National Research Council, 2003; and references therein); our knowledge of Old World monkeys and apes would clearly benefit from such explorations.

Finally, although we do not have any information yet regarding the origins and spread of this unusual behaviour in the study species and populations, it is possible that certain individuals may have independently acquired such behavioural strategies by accident or trial-and-error learning and that these strategies may have then spread in the groups, to which these individuals belong, by social learning (reviewed in Avital and Jablonka 2000). More detailed observations need to be conducted on these and other neighbouring groups within each population to discern whether such behaviours of cultural origin display rapid-spread, parent-offspring or group-specific patterns (Cavalli-Sforza and Feldman, 1981; reviewed in Huffman and Sinha, 2011).

It may also be pertinent to note here that, amongst our study species, cultural traditions in food acquisition and handling as well as other foraging-related strategies have been well documented in chimpanzees (Tomasello, 1990; McGrew, 1992; Whiten et al., 1999; Matsusaka et al., 2006; Huffman and Sinha, 2011), orangutans (van Schaik et al., 2003) and in bonnet macaques (Sinha, 2005; Huffman and Sinha, 2011).

In conclusion, our observations, we believe, are useful in furthering a more comprehensive understanding of how primates procure water, an essential component of their diet. We have suggested a number of possible reasons why certain unusual forms of water acquisition strategies may be prevalent in certain primate species and populations, and the benefits that may accrue to the practitioners of these behaviours. We believe that the drinking water from holes in trees might be more prevalent than previously thought, given the wide range of species and habitats represented in this preliminary investigation. While such behavioural strategies may be of relatively rare occurrence in most primate populations, more systematic observations are required to accurately ascertain the frequency and significance of these strategies for particular populations or individuals (see, for example, Dittus, 1977). We hope that this report will stimulate similar research in other primate species and further discussions on the possible functions of these unusual behaviours for the health and general survival of primate populations and their individual members.

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589 **Table 1.** Characteristics of the study areas.

No	Study site	Area (km ²)	Latitude	Longitude	Elevation (m asl)	Annual rainfall (mm)	Maximum/ minimum temperature (°C)	Forest type	Primate community, including the study species	Reference
1	Hollongapar Gibbon Sanctuary (HGS), Assam, India	20.98	26.691°N	94.338°E	110 – 120	2,000	28/19	Dipterocarpus-Mesua-Vatica	Bengal slow loris <i>Nycticebus bengalensis</i> , capped langur <i>Trachypithecus pileatus</i> , western hoolock gibbon <i>Hoolock hoolock</i> , northern pig-tailed macaque <i>Macaca leonina</i> , rhesus macaque <i>Macaca mulatta</i> , stump-tailed macaque <i>Macaca arctoides</i>	Sharma et al., 2012
2	Bandipur National Park, (BNP) Karnataka, India	874	11.662°N	76.627°E	680 – 1454	141.4	33/11	Dry deciduous, moist deciduous and dry scrub	Bonnet macaque <i>Macaca radiata</i> , southern plains gray langur <i>Semnopithecus dussumieri</i>	Chatterjee, 2012
3	Kedarnath Wildlife Sanctuary, (KWS) Uttarakhand, India	975	20.484°N	79.280°E	1558 – 2000	2,044	16/6	Pine and oak, temperate oak-fir and maple, sub-alpine oak-fir and maple, Rhododendron, sub-alpine fir, alpine meadows and rocks	Central Himalayan langur <i>Semnopithecus schistaceus</i> , rhesus macaque <i>Macaca mulatta</i>	Kala and Gaur, 1982; Gairola, 2010

No	Study site	Area (km ²)	Latitude	Longitude	Elevation (m asl)	Annual rainfall (mm)	Maximum/ minimum temperature (°C)	Forest type	Primate community, including the study species	Reference
4	Danum Valley Conservation Area, (DVCA), Sabah, Malaysia	438	4.965	117.690	231 – 384	2,881	22/32	Lowland Dipterocarpus	Horsfield's tarsier <i>Cephalopachus bancanus</i> , Bornean slow loris <i>Nycticebus menagensis</i> , long-tailed macaque <i>Macaca fascicularis</i> , pig-tailed macaque <i>Macaca nemestrina</i> , red leaf monkey <i>Presbytis rubicunda</i> , silvered leaf monkey <i>Trachypithecus cristatus</i> , Hose's leaf-monkey <i>Presbytis hosei</i> , proboscis monkey <i>Nasalis larvatus</i> , Bornean gibbon <i>Hylobates muelleri</i> , Bornean orangutan <i>Pongo pygmaeus</i>	Kanamori et al., 2010
5	Way Canguk field station, Bukit Barisan Selatan National Park, (BBSNP) Sumatra, Indonesia	9	5.650°S	104.160°E	30	3,000 – 4,000	35/27	Dipterocarpus	Siamang <i>Symphalangus syndactylus</i> , agile gibbon <i>Hylobates agilis</i> , Sumatran surili <i>Presbytis melalophos</i> , silvered leaf monkey <i>Trachypithecus cristatus</i> , long-tailed macaque <i>Macaca fascicularis</i> , southern pig-tailed macaque <i>Macaca nemestrina</i> , Sunda slow loris <i>Nycticebus coucang</i> , western tarsier <i>Cephalopachus bancanus</i>	O'Brien et al., 2003

No	Study site	Area (km ²)	Latitude	Longitude	Elevation (m asl)	Annual rainfall (mm)	Maximum/ minimum temperature (°C)	Forest type	Primate community, including the study species	Reference
6	Mahale Mountains National Park (MMNP), Kigoma, Tanzania	1,600	6.250°S	29.917°E	773 – 2462	1,750	27/12	Highland montane savanna, evergreen montane forest, gallery forest, Miombo Brachystegia woodland, Combretum woodland	Chimpanzee <i>Pan troglodytes</i> , yellow baboon <i>Papio cynocephalus</i> , blue monkey <i>Cercopithecus mitis</i> , red-tailed monkey <i>Cercopithecus ascanius</i> , red colobus <i>Colobus badius</i> , vervet monkey <i>Cercopithecus aethiops</i> , Angolan black-and-white colobus <i>Colobus angolensis</i> , thick-tailed greater galago <i>Otolemur crassicaudatus</i> , lesser galago <i>Galago senegalensis</i>	Nishida, 1990; Itoh, 2015; Nakamura and Itoh, 2015

Legends to the figures

Fig. 1. Location of study areas for the six species displaying arboreal drinking behaviours during this study. The species have been listed by region.

Fig. 2. The six species displaying arboreal drinking behaviours, described in this study. (A) Western hoolock gibbon, (B) Northern pig-tailed macaque, (C) Bonnet macaque, (D) Central Himalayan langur, (E) Chimpanzee, (F) Siamang, and (G) Bornean orangutan.

599 **Figure 1.**

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Figure 2.