Habitual ground nesting in the Bugoma Forest chimpanzees (*Pan troglodytes schweinfurthii*), Uganda.

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Running Title: Ground nesting in Bugoma chimpanzees

Abstract

We report the presence of habitual ground nesting in a newly studied East African chimpanzee *(Pan troglodytes schweinfurthii)* population in the Bugoma Central Forest Reserve, Uganda. Across a 2-year period we encountered 989 night-nests, 205 of which were classified as ground nests, a rate of ~21%. We find no preliminary evidence of socio-ecological factors that would promote its use and highlight local factors that appear to make its use disadvantageous. While further study is required to establish this behaviour as meeting the strict criteria for non-human animal culture, we support the argument that the wider use of population and group-specific behavioural repertoires in flagship species, such as chimpanzees, offers a tool to promote the urgent conservation action needed to protect threatened ecosystems, including the Bugoma forest.

Keywords: Chimpanzee, Culture, Nesting, Uganda

Introduction

All apes construct overnight arboreal nests by interweaving branches and other vegetation (Fruth et al., 2018; Anderson et al., 2019). Gorillas, while able to climb while foraging, are the most terrestrial of the great apes and build overnight nests primarily on the ground using available herbaceous vegetation, although they increase the use of arboreal nesting seasonally, or when terrestrial vegetation is limited (Tutin et al., 1995; Brugiere & Sakom, 2000; Mfossa et al., 2022). In contrast, orangutans, bonobos, and chimpanzees primarily build arboreal nests (Goodall 1962; Fruth & Hohmann, 1993; Prasetyo et al., 2009; Hicks, 2010; van Casteren et al., 2012; Fruth et al., 2018), using multiple interwoven supporting branches, filling in with smaller softer material (Furuichi & Hashimoto, 2000; Prasetyo et al., 2009; Samson & Hunt, 2012; Fruth et al., 2018). There appears to be an effect of learning, with younger individuals constructing more robust nests earlier if exposed to adults who build nests (Lethmate, 1977; McGrew, 2004; Videan, 2006). Each independent individual constructs their own nest, but individuals will typically nest in a party with others in the same or near-by trees (Fruth, 1995; Schaller, 1963; Goodall, 1968). Nests are constructed each evening for overnight use, but they are also built during the day for a range of reasons from sleeping, to play, or sexual solicitation (Boesch, 1995; Plumptre and Reynolds, 1997; Fruth and Hohmann, 1996; Brownlow et al., 2001; McGrew, 2010; Fruth et al., 2018). with bonobos also regularly constructing additional full nests during the day (Wessling & Surbeck 2022). Chimpanzees and bonobos typically construct nests at between 8 to 20m in height, but they may be as low as 3-4m typically where taller trees are limited (Pruetz et al., 2008; Samson & Hunt, 2012; Fruth et al., 2018). Full nests – night or day – are distinguished in their construction from other flimsier resting structures such as ‘day beds’ and ‘cushions’, which typically involve only 1-2 bent branches, loosely interwoven, and may be as simple as

a single small sapling bent over or a clump of ferns (Boesch, 1995; Furuichi & Hashimoto, 2000; Brownlow et al., 2001; Koops et al., 2007).

Despite the use of arboreal night nesting in every chimpanzee community studied to date, our understanding of their function remains limited, with – potentially complementary – hypotheses currently including seasonal patterns (Samson & Hunt, 2014; van Casteren et al., 2012), thermoregulation (Koops et al., 2012; McGrew, 2004; Stewart et al., 2018), pathogen and parasite avoidance (Anderson, 1998; Lacroux et al., 2022), and predation avoidance (Koops et al., 2012; Kortlandt, 1992; Pruetz et al., 2008; Stewart & Pruetz, 2013). Some aspects of the local environment appear to impact the choice of nest location, for example a preference for slopes over flatter ground (Issa: Hernandez-Aguilar 2009; Mahale: Izawa and Itani, 1966; Suzuki, 1969; Assirik: Baldwin, 1979). However, in habitats where trees are limited this tends to lead to a concentration of nests in available trees (Hernandez-Aguilar 2009), rather than alternative strategies such as ground nesting.

The very occasional use of overnight ground nests is widely reported in all chimpanzee sub-species, including in Uganda (see below and c.f. Tagg et al., 2013). Excluding the minimally constructed day beds and cushions (Furuichi & Hashimoto, 2000; Koops et al., 2007), the use of fully constructed overnight nests on the ground is typically rare (5 to 10% of nests constructed in a given population; Matsuzawa & Yamakoshi, 1996; Koops et al. 2007), perhaps as a fall-back by sick or injured individuals (<1%; Furuichi & Hashimoto, 2000). Slightly more frequent use of overnight ground nests was reported by male West African chimpanzees (*Pan troglodytes verus*) of Seringbara in the Nimba Mountains in Guinea (~3% to 5% of night nests; Koops et al., 2007; 2012) and of Fongoli long term field site (~12% of night nests; Stewart 2011). Frequent ground nests have also been recently observed in

Cameroun in Nigeria-Cameroun chimpanzees (*Pan troglodytes ellioti*) of one (i.e., Andu) of the two field sites of the Lebialen-Mone Forest (~32% of night nests; Last & Muh, 2013) and in Central African chimpanzees (*Pan troglodytes troglodytes)* of La Belgique research field site in the Dja Biosphere Reserve (~3% to ~9% of night nests; Guislain & Duplain, 2005; Tagg et al., 2013). However, despite ~ 250 years of continuous observations across long-term research sites (Gombe, >60 years; Mahale, >60 years; Kibale-Kanyawara, >30 years; Kibale-Ngogo, >20 years; Kalinzu, >30 years; Budongo-Sonso, >30 years, Budongo-Waibira, >10 years); the customary use of overnight ground nests has only been reported in East African chimpanzee communities in the Northern DRC (~11% of nesting sites; Hicks et al., 2019), approximately 600km from the Bugoma Forest Reserve, and separated by a large body of water (i.e., Lake Albert).

Here we report on the presence of apparently habitual ground nesting in the newly studied East African chimpanzee *(Pan troglodytes schweinfurthii)* population in the Bugoma Central Forest Reserve, in Uganda. We find no preliminary evidence of specific socio-ecological factors that would promote its use and highlight local factors that appear to make its use disadvantageous. Establishing a case for cultural behaviour on the basis of either evidence of social transmission or the exclusion of alternative hypotheses, such as genetic or ecological variation may take decades in long-lived species. However, we argue that the use of apparently cultural group-differences in the behavioural repertoires in flagship species, including chimpanzees – irrespective of the socio-ecological or cognitive mechanism by which they are produced – offers an effective tool to promote the urgent conservation action needed to protect threatened ecosystems, such as the Bugoma forest.

Methods

Site

The Bugoma Central Forest Reserve includes 400km^2 of semi-deciduous tropical rain forest (located at 01°15′N 30°58′E and at 990-1300m elevation). Located between the Central Forest Reserve of Budongo (425km^2) and Kibale National Park (776km^2), Bugoma represents the largest contiguous forest habitat for chimpanzees in East Africa in which there has been no long-term research activity. In 2006, chimpanzee density was estimated at 1.9 chimpanzees per km^2 (giving an approximate population estimate of ~760 chimpanzees; Plumptre and Cox, 2006) but given widespread primate population declines (Estrada et al., 2017) a current population estimate of ~600 chimpanzees may be more appropriate. Following surveys in 2015, in 2016 the Bugoma Primate Conservation Project (BPCP, www.bugomaprimates.com) initiated daily habituation and monitoring activities across several chimpanzee communities. Our data are concentrated on the Mwera-South community, where regular contacts were initiated in 2016 and were typically occurring on most days by 2018. Chimpanzees in the Mwera-North community were also encountered, as their range overlaps with that of Mwera-South, but they are not intentionally followed and they still tend to flee when our presence is detected allowing us to distinguish between the groups. The current estimated range for the Mwera-South community is ~10km2 (see Figure 1). During the study period, chimpanzees in the Mwera-South community were followed on regular basis (several days a week for several hours per day) with an estimate of 60-80 individuals based on local East African chimpanzee community sizes (Wilson et al., 2014). However, as it was not possible to nest or denest them, direct observations of night nest building were not available.

Data collection

In addition to direct observations of chimpanzee behavioural and health data, project staff record the type and GPS location of signs of chimpanzee activity (prints, dung, feeding remains, discarded tools, and nests), and of illegal human activity (primarily hunting and logging) whenever they are encountered ad libitum.

A ‘nesting site’ was defined as one or more nests of the same age in which no two nests were more than 30m apart (Furuichi & Hashimoto, 2000). Following increasing encounters with overnight ground nests, in 2019, BPCP staff started to collect detailed information on overnight nests. However, data collection was impacted by the Covid19 outbreak with 1) a stop of data collection from February 2020 to July 2020 and 2) a change of data collection protocol after this period. Therefore, here, we provide the following nesting data: GPS location, approximate age (1 day, 2 days, under a week, over a week), the nest type (ground, tree) and the number of ground and tree nests in the nesting site from August 2019 to June 2022. Other nesting data, including: density of surrounding forest (Open, Medium, Dense), forest type (climax, secondary-mixed, disturbed, water-swamp, grassland), the height from the ground of all tree nests (m), the primary tree species used, the width and length of ground nests (cm), and the use of bent or detached branches and the inclusion of Terrestrial Herbaceous Vegetation (THV) in ground nest construction, are only available for the pre-Covid19 outbreak, i.e. from August 2019 to February 2020.

Data availability

All data used for the analyses and figures in this manuscript are available in a publicly accessible GitHub repository: https://github.com/Wild-Minds/GroundNesting_Bugoma

Ethical statement

This study was observational and did not involve any interventions, apart from daily visits to the chimpanzee communities' territories. BPCP staff follow strict hygiene and observation distance rules to prevent disease transmission. Following the Covid19 outbreak, from March 2020 data collection moved from chimpanzee follows to biomonitoring only. Permissions to collect data were provided by the National Forest Authority of Uganda, the Uganda Wildlife Authority, and the Ugandan National Council of Science and Technology, and all data collection adhered to national and international guidelines, including the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates, and the Code of Best Practices for Field Primatology.

Results

Presence of ground and tree nests

Between August 2019 and July 2022, we recorded 989 night-nests within 336 nesting sites, number of nests per site ranged from 1 to 20 (Figure 1). We recorded 784 tree nests and 205 ground nests (21%). Ground nests occurred in 82 of the 336 sites (24%) and co-occurred with tree nests in 29 of these sites (6% all nest sites; 35% of sites with a ground nest; up to 15 ground nests within a site). Ground nests were observed year-round (57% in the dry season; 43% in wet season).

Between August 2019 and February 2020 we recorded additional information on nest construction and local habitat for 138 nesting sites containing 310 night-nests(269 tree nests, 41 ground nests). Tree nests varied in height from 1-40m; and n=11 (4%) were at 2m or less from the ground. All ground nests that could be measured (n=39) contained detached interwoven branches, and most (n=34, 87%) incorporated bent branches as well. A small number (n=2) incorporated THV into the construction. The majority of nest sites were located in medium-density forest (n=117) as opposed to open (n=17) or high-density (n=4);

similarly, the majority of nest sites were located in mixed-secondary forest (n=121) rather than disturbed (n=8) or savannah (n=1; Unknown n=8).

Discussion

Bugoma chimpanzees regularly construct ground nests overnight and, in addition, construct tree nests at a height that would be vulnerable to human threat (<2m). In addition to their observed frequency, we find ground nests most often appeared as clusters suggesting that they were not built by a single individual or a single family. As these chimpanzees are not fully habituated, direct observations of overnight ground nest building were not possible. The estimated number of independent individuals in the community (~40) is similar to the total number of ground nests encountered, so it remains possible that each ground nest observed was built by a separate individual on only one occasion; however, we would suggest that this is less likely than the repeated building of ground nests by at least some individuals. If so, ground nesting in the Mwera-South community of chimpanzees meets the criteria for a 'habitual' behaviour (Whiten et al., 1999).

It is possible that local ecological factors promote the use of ground nesting in the Bugoma communities. For example: a limited number of suitable trees for tree nesting (McCarthy et al. 2016). While systematic research is needed to confirm this, we believe that this is highly unlikely both because of the regular co-occurrence of tree and ground nests in the same nesting party; and because the secondary mixed-forest habitat in which the majority of nest sites are located is similar in structure to that of the neighbouring Budongo Forest Reserve, in which no overnight ground nests have been reported in over 40-years of cumulative observation across two communities. Another explanation could be seasonality (Pruetz et al. 2018; Tagg et al., 2013), but Bugoma chimpanzees seem to nest on the ground

year round (see also Koops et al. 2012). An alternative might be that large numbers of individuals are unable to construct tree nests due to injury or illness. Again, we believe that this is unlikely. Our long-term data collection includes health monitoring of the chimpanzees and while there are outbreaks of respiratory infection in some individuals, these appear similar to those reported in other Uganda forest populations (Scully et al., 2018). A more likely pressure would be the impact of snare wires which regularly maim chimpanzees who trap their hands and feet in them – these injuries can include wasted and amputated limbs. However, once again, the neighbouring Budongo communities also have high numbers of snare-injured chimpanzees (Reynolds, 2005; Stokes & Byrne, 2006; Waller & Reynolds, 2001), including individuals missing hands and feet (including individuals where more than one limb is amputated), and do not report any use of ground nesting. In contrast, ground nesting has sometimes been explained by scholars as resulting from an absence of predators or human activity (Pruetz et al. 2008; Hicks, 2010; McCarthy et al., 2012; Last & Muh, 2013). However, it's unlikely the case at Bugoma as a number of features of the forest make ground nesting potentially risky. While there are no recent confirmed sightings of chimpanzees' main nonhuman predator (leopard, *Panthera pardus*) in Bugoma, other large animals that could present potential risk were regularly directly or indirectly (through camera-traps) observed over the study period, including elephant (*Loxodonta cyclotis*), golden cat (*Caracal aurata*), python (*Python sebae*), and rhinoceros viper (*Bitis nasicornis*; Figure 2a). Elephant presence has been previously described as impacting ground nesting at Lope (Tutin et al., 1995) and they are also present other sites where ground nesting has been observed (i.e., La Belgique, Tagg et al., 2013; Bili-Uele, Hicks 2010). Perhaps the most significant risk to chimpanzees in Bugoma is human activity. Hunting is prominent; as well as the use of snare wires designed to target duiker and pig species, hunters in Bugoma are regularly encountered with large packs of dogs in the chimpanzees' range (Figure 2b). The

butchered remains of chimpanzees, apparently following human hunting, have been discovered by the project on two occasions, with additional unconfirmed reports (Bugoma Primate Conservation Project, unpublished data). Interestingly, while it remains counter-intuitive, Tagg and colleagues (2013) also found that chimpanzee ground nesting appeared to increase with human pressure. Given the lack of obvious ecological or physical drivers, together with the combination of significant risk to life by, at least, human hunters, we suggest that there is likely a cultural component to the Bugoma chimpanzee ground nesting. Importantly, this highlights that, as in other species (Laland & Williams, 1998; Franz & Matthews, 2010), some socially acquired chimpanzee behavioural variants may not have a positive effect on individual fitness. Behavioural variants linked to improving vital rates, such as survival, were suggested as being of particular conservation importance (Brakes et al., 2021), but establishing these connections is challenging (Carvalho et al., 2022) and association with individual fitness may vary with fluctuating local pressures, for example human hunting.

Chimpanzee cultures have been shown to be inflexible, with resistance to the modification or acquisition of new behaviour even where it could be advantageous (Boesch & Boesch-Achermann, 2000; Gruber et al., 2011; but see Hobaiter et al., 2014), suggesting that they may be similarly resistant to its loss where it appears to be disadvantageous. With increasing human pressure on the forest, it is unclear how the Bugoma chimpanzees will react with respect to their nest building behaviour. Closely monitoring ground nest building in Bugoma forest may provide a direct assessment of the impact of anthropogenic activities on wild semi-habituated chimpanzees.

The importance of community and population specific cultural behaviour from a conservation perspective has started to receive significant attention (Brakes et al., 2019;

Brakes et al., 2021). The loss of a specific community involves the irreversible loss of a unique culture and the information or individual knowledge that it is founded on. The importance of these cultural markers in chimpanzee conservation was recently recognised by the United Nations Convention on the Conservation of Migratory Species, who dedicated a Concerted Action to the conservation of West African chimpanzee (*Pan troglodytes verus*) nut cracking, the first time a non-human animal behaviour was recognised in this way. The wider Bugoma forest habitat is under considerable pressure, not only from illegal activities such as hunting and logging, but also from clear-felling for crop production, from local energy resource extraction, and from increased infrastructure and anthropogenic activities (McLennan et al., 2020; Plumptre et al., 2020). Non-human cultures are sensitive to the impact of human anthropogenic activity on the transformation, fragmentation, and degradation of habitats (Gruber et al., 2019; Kalan et al., 2020). Widespread urgent calls to action throughout 2019 to 2022 for its protection by Ugandan and international organisations, as well as planned sustainable resource generation from eco-tourism projects may benefit from a clear and strong case for the unique behavioural repertoire of the chimpanzees in this area.

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Figure 1: Location of nesting sites within the current area of research in the Bugoma Central Forest Reserve. White = tree nests only; Grey = tree and ground nests together; Black = Ground nests only. Inset shows full boundaries of Forest Reserve.

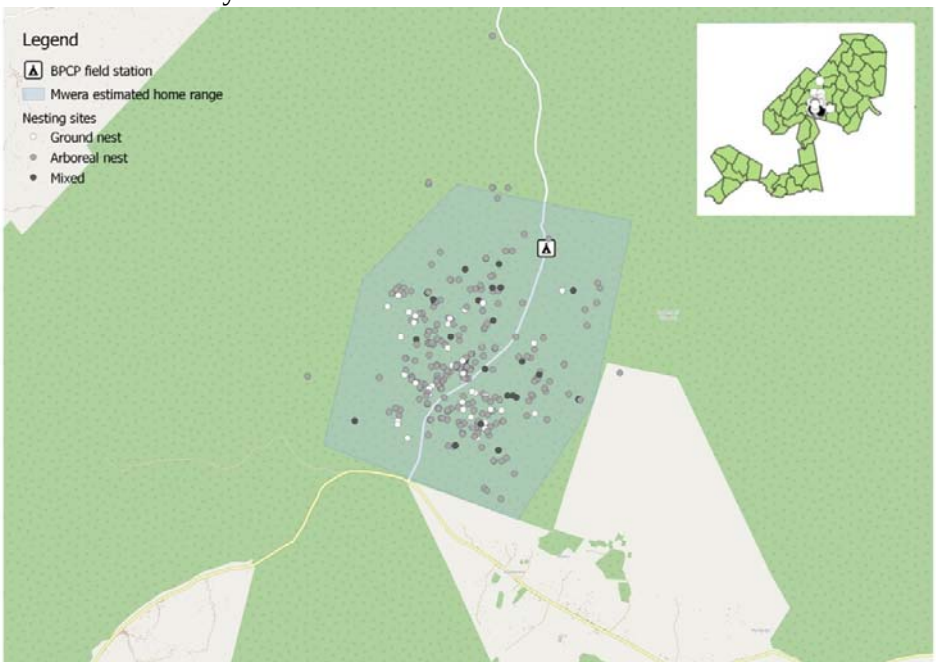
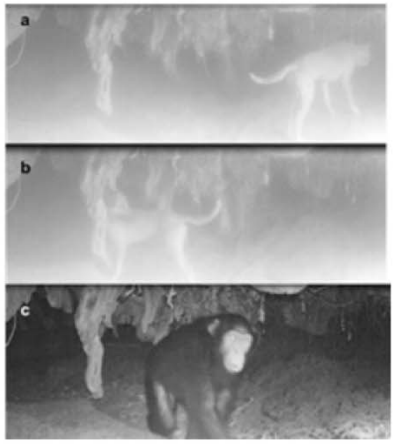


Figure 2: Large primarily terrestrial mammals and reptiles present in the Bugoma Central Forest Reserve that represent a potential threat to chimpanzees. Pictures captured directly or by camera trap within the home range of the Mwera community. From Left to right: African elephant (*Loxodonta cyclotis)*; Rhinoceros viper (*Bitis nasicornis)*; Golden cat (*Caracal aurata)*.

Figure 3: Human activities in the Bugoma Central Forest Reserve. Pictures captured directly or by camera trap in the home range of the Mwera community. Left to right: illegal timber felling; overlapping presence of hunting dogs in key resource locations for chimpanzees; use of wire and nylon snares for trapping small game.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