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RESEARCH ARTICLE

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

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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 891 night nests, 189 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, such as high incidence of forest disturbance due to poaching and logging, which appear to make its use disadvantageous. While further study is required to establish whether this behavior meets the strict criteria for nonhuman animal culture, we support the argument that the wider use of population and group-specific behavioral 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
behavioral variation, chimpanzee, sleep, sleeping platform

1 | INTRODUCTION

All apes construct overnight arboreal nests by interweaving branches and other vegetation (Anderson et al., 2019; Fruth et al., 2018). Gorillas, although 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 (Brugiere & Sakom, 2001; Mfossa et al., 2022; Tutin et al., 1995). In contrast, orangutans, bonobos, and chimpanzees primarily build arboreal nests (van Casteren et al., 2012; Fruth & Hohmann, 1993; Fruth et al., 2018; Goodall, 1962; Hicks, 2010; Prasetyo et al., 2009), using multiple interwoven supporting branches, filling in with smaller softer material (Fruth et al., 2018; Furuichi & Hashimoto, 2000; Prasetyo et al., 2009; Samson & Hunt, 2012). There may be an effect of learning, with younger apes constructing more robust nests earlier if exposed to adults who build nests (orangutans: Lethmate, 1977; chimpanzees: McGrew, 2004; Videan, 2006), but further work with wild populations is needed to more carefully disentangle potential social learning from ecological and developmental influences. Each independent individual constructs their own nest, but individuals will typically nest in a party

Abbreviations: BPCP, Bugoma Primate Conservation Project; GPS, global positioning system; m, meters.

with others in the same or near-by trees (Fruth, 1995; Schaller, 1963; van Lawick-Goodall, 1968). Chimpanzees and bonobos typically construct nests at between 8 and 20 m in height, but they may be as low as 3–4 m where taller trees are limited (Fruth et al., 2018; Pruetz et al., 2008; Samson & Hunt, 2012). Full nests—night or day—are distinguished in their construction from other flimsier resting structures such as "day beds" and "cushions," which 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; Brownlow et al., 2001; Furuichi & Hashimoto, 2000; Koops et al., 2007). 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; Brownlow et al., 2001; Fruth & Hohmann, 1996; Fruth et al., 2018; McGrew, 2010; Plumptre & Reynolds, 1997), with bonobos also regularly constructing additional full nests during the day (Wessling & Surbeck, 2021).

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 (van Casteren et al., 2012; Samson & Hunt, 2014), 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 & 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 subspecies, 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%–10% of nests constructed in a given population; Koops et al., 2007; Matsuzawa & Yamakoshi, 1996), 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%–5% of night nests; Koops et al., 2007, 2012) and of Fongoli long term field site (~12% of night nests; Stewart, 2011a). Frequent ground nests have also been recently observed in Cameroon in Nigeria-Cameroon 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%–~9% of night nests; Guislain & Dupain, 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 Democratic Republic of Congo (~11% of nesting sites; Hicks et al., 2019).

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. In addition, while we consider the specific socio-ecological factors that would promote its use, we suggest that local factors such as extended anthropogenic disturbance would be likely to inhibit the building of ground nests, and highlight the possibility of a cultural explanation. Establishing a case for cultural behavior 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 group-differences in the behavioral 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.

2 | METHODS

2.1 | Site

The Bugoma Central Forest Reserve includes 400 km^2 of semi-deciduous tropical rain forest (located at 01°15′ N 30°58′ E and at 990–1300 m elevation). Located between the Central Forest Reserve of Budongo (425 km^2) and Kibale National Park (776 km^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 & 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 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, 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 community is ~10 km^2 (see Figure 1). During the study period, chimpanzees in the Mwera 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.

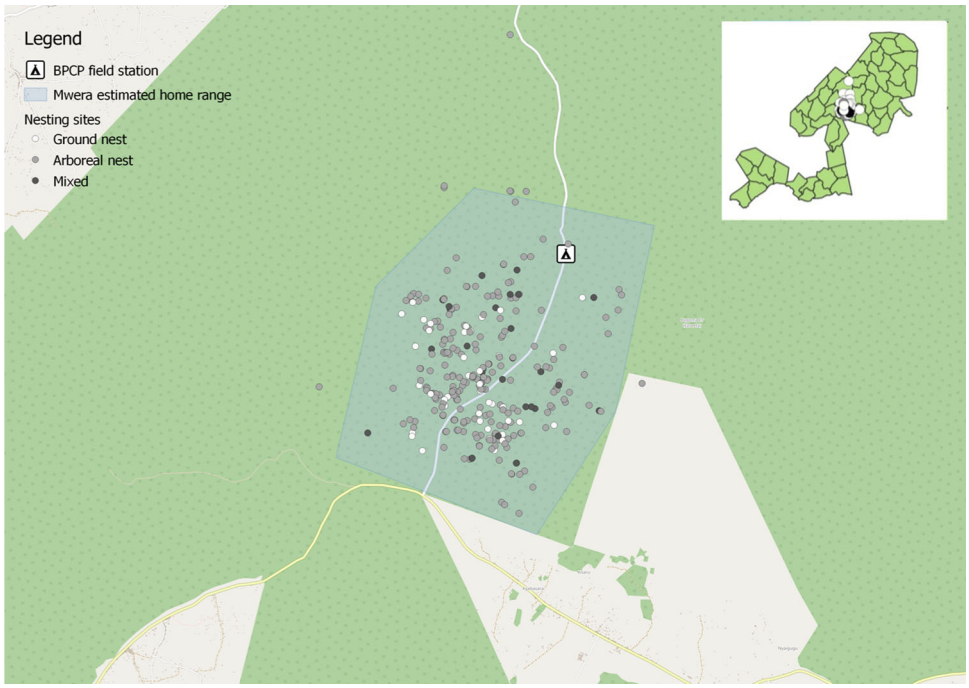

FIGURE 1 Location of nesting sites within the current estimated range of the Mwera chimpanzee community in Bugoma Central Forest Reserve. White: ground nest only site; gray: tree nest only site; black: ground and tree nests in same site. Inset shows full boundaries of the Forest Reserve.

2.2 | Data collection

In addition to direct observations of chimpanzee behavioral 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 30 m 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 COVID-19 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. Nest decay rates vary substantially between populations and are shaped by local ecological and seasonal factors (Morgan et al., 2016; Wessling & Surbeck, 2021). We followed Romani et al. (2023); who recently described nest stages and decay rates for the Bugoma Central Forest Reserve. Other nesting data, including: density of surrounding forest (Open, Medium, Dense), forest type (primary, 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 (hereafter: terrestrial herbs) in ground nest construction, are only available for the pre-COVID-19 outbreak, that is from August 2019 to February 2020.

3 | RESULTS

3.1 | Presence of ground and tree nests

Between August 2019 and July 2022, we recorded 891 night nests within 310 nesting sites, number of nests per site ranged from 1 to 21 (Figure 1). We recorded 692 tree nests and 189 ground nests (21%). Ground nests occurred in 78 of the 310 sites (25% of nest sites) and co-occurred with tree nests in 31 of these sites (10% all nest sites; 40% of sites with a ground nest; up to 15 ground nests within a site). Ground nests were observed year-round (50% in drier season months December–February, June–August; 50% in wetter season months March–May, September–November).

Between August 2019 and February 2020, we recorded additional information on nest construction and local habitat for 138 nesting sites containing 323 night nests (282 tree nests, 41 ground nests). Tree nests varied in height from 1 to 45 m; and $n = 11$ (4%) were at 2 m 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 (see Figure 2). A small number ($n = 2$) incorporated terrestrial herbs 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

FIGURE 2 Three ground nests. Pictures of three ground nests at three separate nest sites. Note the inclusion of multiple bent and interwoven branches together with substantial quantities of smaller leafy material, distinguishing them from flimsier resting structures such as "day beds" and "cushions."

($n = 4$); similarly, the majority of nest sites were located in mixed-secondary forest ($n = 121$) rather than disturbed ($n = 8$) or savannah ($n = 1$; unknown $n = 8$).

4 | DISCUSSION

Bugoma chimpanzees regularly construct ground nests overnight and, in addition, construct tree nests at a height that would be vulnerable to human threat (<2 m). 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 were not fully habituated at the time of data acquisition, direct observations of overnight ground nest building were not possible. The estimated number of independent individuals in the community (~40) is a fraction of the total number of ground nests encountered, so it is impossible that each ground nest observed was built by a separate individual on only one occasion. Similarly, up to 15 ground nests were found in a single nest site, thus, it cannot be the case that these are the work of a single extremely prolific individual. We would suggest that the most likely explanation is the repeated building of ground nests by at least some individuals. If so, ground nesting in the Mwera community of chimpanzees meets the criteria for a "habitual" behavior (Whiten et al., 1999).

The transition to regularly sleeping on the ground has been suggested as an important driver of hominin behavioral-cognitive changes in our divergence from other apes (Coolidge & Wynn, 2006) and, thus, the factors that drive more regular occurrence of ground-sleeping in apes are of interest across diverse fields. It is possible that local ecological factors promote the use of ground nesting in the Bugoma communities. While systematic research is needed to confirm this, we believe that limitations in the number of suitable trees for tree nesting (c.f., McCarthy et al., 2017) is unlikely to be driving ground nesting, 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 neighboring 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., 2008; Tagg et al., 2013), but Bugoma chimpanzees seem to nest on the ground year-round (see also Koops et al., 2012). Nesting on the ground may provide important differences in thermoregulation (Stewart, 2011b) or in pathogen avoidance (Lacroux et al., 2022; Stewart, 2011b; Videan, 2006), which are of substantial interest for future investigation in Bugoma; however, the frequent co-occurrence of ground and tree nests in the same nest site suggests that any effect here varies by individual characteristics. One possibility is that there are sex-specific differences: for example, ground nesting may be more prevalent in male chimpanzees, who already typically nest at lower heights (e.g., Brownlow et al., 2001). Chimpanzees also appear to select nesting tree species for "comfort," taking into account features such as high leaf density (Lacroux et al., 2023), an aspect that could also vary by individual or sex.

Another ecological explanation 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 neighboring 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.

Ground nesting has sometimes been explained by scholars as resulting from an absence of predators or human activity

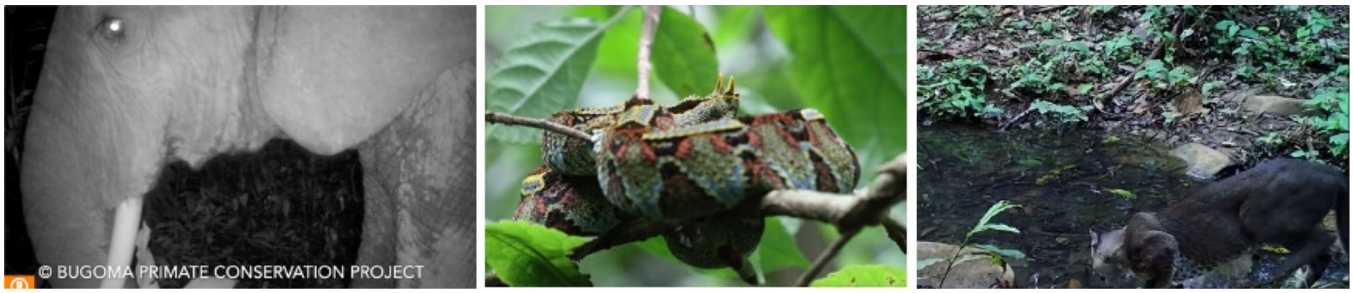

FIGURE 3 Large primarily terrestrial mammals and reptiles present in the Bugoma Central Forest Reserve that represent a potential threat to chimpanzees. Pictures captured directly or by camera trap within the home range of the Mwera community. From Left to right: African elephant (*Loxodonta cyclotis)*; rhinoceros viper (*Bitis nasicornis)*; golden cat (*Caracal aurata)*.

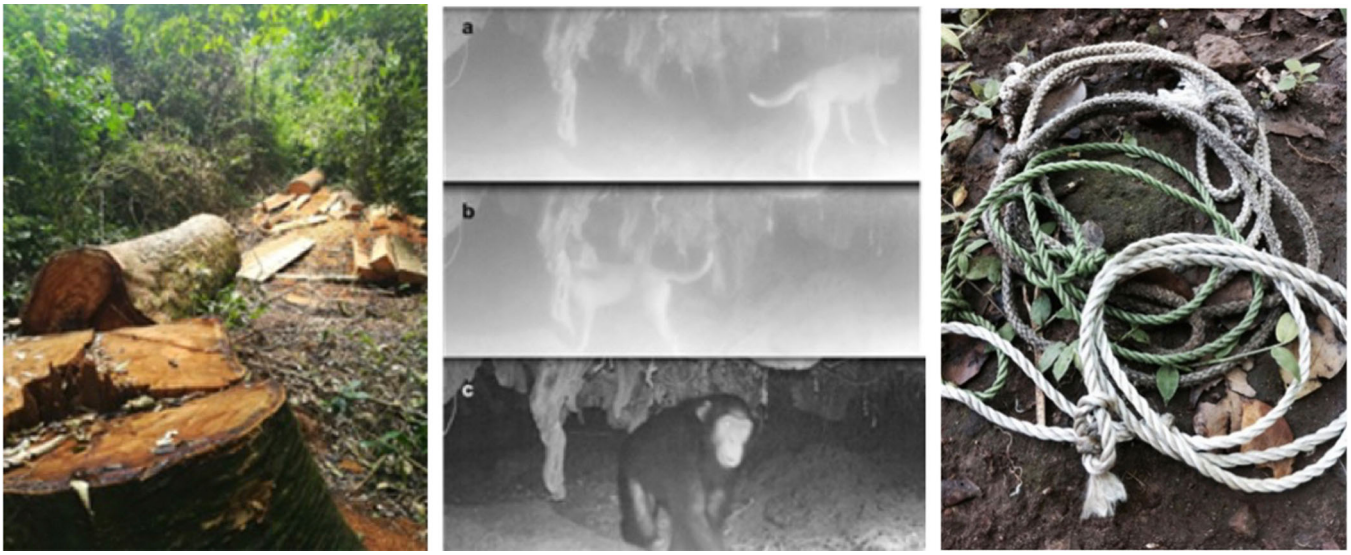

FIGURE 4 Human activities in the Bugoma Central Forest Reserve. Pictures captured directly or by camera trap in the home range of the Mwera community. Left to right: illegal timber felling; overlapping presence of hunting dogs in key resource locations for chimpanzees; use of wire and nylon snares for trapping small game.

(Hicks, 2010; Pruetz et al., 2008; McCarthy et al., 2017; Last & Muh, 2013). In Bugoma 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 3). 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 4). 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 et al. (2013) also found that chimpanzee ground nesting appeared to increase with human pressure.

While substantial further research is needed, we do not, as yet, have clear evidence for any ecological or physical drivers of ground nesting in Bugoma. Given the significant risk to life by, at least, human hunters, it is possible that there is a cultural component to the Bugoma chimpanzee ground nesting. If true, this would highlight that, as in other species (Franz & Matthews, 2010; Laland & Williams, 1998), some socially acquired chimpanzee behavioral variants may not have a positive effect on individual fitness. Behavioral 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 behavior 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 behavior. 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 behavioral variation from a conservation perspective has started to receive significant attention (Brakes et al., 2019, 2021). The loss of a specific community involves the irreversible loss of a unique genetic heritage, as well as the information and individual knowledge that any local culture is founded on. 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). Nonhuman behavioral variation is 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 organizations, as well as planned sustainable resource generation from eco-tourism projects may benefit from a clear and strong case for the unique behavioral repertoire of the chimpanzees in this area.

AUTHOR CONTRIBUTIONS

Catherine Hobaiter: Conceptualization (lead); data curation (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); resources (equal); visualization (lead); writing—original draft (equal). **Harmonie Klein**: Data curation (equal); formal analysis (equal); investigation (equal); writing—review and editing (equal). **Thibaud Gruber**: Funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); resources (equal); writing—original draft (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

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

ETHICS 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. Regular follows were resumed in 2022. 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 Nonhuman Primates, and the Code of Best Practices for Field Primatology.

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