Chimpanzees (Pan troglodytes) adapt their nesting behavior after large-scale forest clearance and community decline

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Abstract

Chimpanzees (Pan troglodytes) build nests at night for sleeping and occasionally during daytime for resting. Over the course of seven years, forest fragments in Bulindi, Uganda, were reduced in size by about 80% when landowners converted forest to agricultural land. However, unlike other studies on nesting behavior in response to habitat disturbance, chimpanzees at Bulindi had no opportunity to retreat into nearby undisturbed forest. To understand behavioral adaptations to forest clearance, we compared Bulindi chimpanzees' nesting characteristics before and after this period of major deforestation. After deforestation, chimpanzees built nests at lower heights in shorter trees, and reused a larger proportion of their nests. Additionally, average nest group size increased after deforestation, even though community size declined by approximately 20% over the same period. The substantial decrease in available forest habitat may have caused the chimpanzees to aggregate for nesting. However, more cohesive nesting may also have been influenced by dietary shifts (increased reliance on agricultural crops) and a need for enhanced safety with increased human encroachment. Conversely, the chimpanzees selected similar tree species for nesting after deforestation, apparently reflecting a strong preference for particular species, nested less often in exotic species, and built integrated nests (constructed using multiple trees) at a similar frequency as before fragment clearance. Chimpanzees living in unprotected habitat in Uganda, as at Bulindi, face mounting anthropogenic pressures that threaten their survival. Nevertheless, our study shows that chimpanzees can adjust their nesting behavior flexibly in response to rapid, extensive habitat change. While behavioral flexibility may enable them to cope with deforestation, at least to a certain point, the long-term survival of chimpanzees in fast-changing human-modified landscapes requires intensive conservation efforts.

KEYWORDS
behavioral flexibility, deforestation, integrated nests, Pan troglodytes, nest groups, nest reuse
1 | INTRODUCTION

Anthropogenic disturbances have resulted in a worldwide decline of nonhuman primate populations (Chapman & Peres, 2001; Estrada et al., 2019). Anthropogenic influences negatively impacting wild primate populations include large scale habitat loss and fragmentation resulting from logging, agriculture, and cattle-ranching, as well as other human threats such as bushmeat hunting and the primate pet trade (e.g., Chapman et al., 2006; Fa et al., 2002; Kühl et al., 2017; Nijman et al., 2011). Despite these threats, primates are commonly found in habitats severely impacted by humans (Galán-Acedo et al., 2019; Hockings et al., 2015; Riley & Fuentes, 2011). As a result, there is growing interest in the behavioral adaptations of primates to human‐disturbed environments (Hockings et al., 2015; Kalbinter & Chapman, 2018; McLennan, Spagnoletti, et al., 2017).

Among great apes, nesting behavior (e.g., the height at which nests are constructed and the size and species of trees selected) varies according to habitat and thus may be expected to change as a result of human habitat disturbance. All great apes construct nests (also known as “beds” or “sleeping platforms”) each night for sleeping, and occasionally for resting during the day (Fruth & Hohmann, 1996; Goodall, 1962). Chimpanzees (Pan troglodytes) specifically build new nests from living branches, twigs and foliage arboreally in trees, or, more rarely, on the ground (e.g., Goodall, 1962; Koops, McGrew, Matsuzawa, et al., 2012; Tagg et al., 2013; Zamma & Ihobe, 2015). They may also choose to reuse an existing nest, typically by adding fresh vegetation on top of an older nest (Fruth & Hohmann, 1996). It has been suggested that nest reuse is more common in drier habitats, where tree density is lower and fewer trees are available with fresh leaves for nesting (Fruth & Hohmann, 1996).

Preference for particular tree species for nesting varies among chimpanzee populations. Within habitats, preference is often independent of the availability of tree species (Carvalho et al., 2015; Furuichi & Hashimoto, 2004; Granier et al., 2014; Hakizimana et al., 2015; Samson & Hunt, 2014; Stanford & O’Malley, 2006). The preference for certain tree species could depend on the quality of the wood (e.g., strength and flexibility of branches) and leaves (e.g., size and density of foliage) (Fruth et al., 2017; Samson & Hunt, 2014). Other factors, such as socially learned or “cultural" preferences for particular species, may also exist (Baldwin et al., 1981; Goodall, 1962).

Most of the time, chimpanzees build their nests using one tree or plant species only (e.g., Fruth & Hohmann, 1996; Goodall, 1962). However, sometimes chimpanzees build an integrated (or "composite") nest, using multiple trees and/or plants of one or more species (Hernandez-Aguilar et al., 2013; McCarthy et al., 2017; McLennan, 2018). Often, one tree provides the main support, while one or more other trees provide additional support. Integrated nests are usually built in smaller trees with a smaller diameter at breast height (DBH) compared to nests in single trees (Hernandez-Aguilar et al., 2013). Small trees may not be capable of supporting a chimpanzee’s weight individually; however, a nest that integrates multiple small trees could provide adequate support. Chimpanzees typically build their nests at a height between 10 and 20 meters (Fruth & Hohmann, 1996). Nest height has been shown to be influenced by the sex of the nest‐builder, with males often constructing nests lower than females (Brownlow et al., 2001; Koops, McGrew, Matsuzawa, et al., 2012; Stewart & Pruett, 2020). Nest height can also be influenced by environmental factors such as predation pressure, humidity and, potentially, avoidance of insect vectors (Fruth et al., 2017; Koops, McGrew, de Vries, et al., 2012; Krief et al., 2012; Samson et al., 2013). When predation pressure is high, chimpanzees build their nests at greater heights and terrestrial nests are usually absent (Granier et al., 2014; Koops, McGrew, Matsuzawa, et al., 2012; Pruett et al., 2008; Tagg et al., 2013). Human disturbance may impact chimpanzee nesting behavior similarly to predation pressure, depending on habitat features (Hicks, 2010; Last & Muh, 2013). For example, in Lebialem-Mone Forest Landscape in Western Cameroon, terrestrial nests were absent in forests frequented by hunters, but were present in less disturbed forests (Last & Muh, 2013). Conversely, Tagg et al. (2013) found that chimpanzee ground nesting increased with higher human disturbance; however, most ground nests were built in swamps which were less frequented by hunters than other forest areas, but where suitable nesting trees were fewer. Overall, terrestrial nests are usually absent in areas with high human disturbance, especially hunting.

Several studies indicate that chimpanzee densities decline where forest is disturbed through logging, as measured from nest surveys (Balcomb et al., 2000; Morgan et al., 2018; Tutin & Fernandez, 1984). As chimpanzees prefer to nest in the vicinity of large trees bearing ripe fruits, the decline of such trees after logging may explain a reduction in chimpanzee nests (Balcomb et al., 2000; Basabose & Yamagiwa, 2002; Furuichi & Hashimoto, 2004). As a result of the loss of fruit trees, chimpanzees may retreat into nearby undisturbed forest where there is a higher density of fruit trees (White & Tutin, 2001). However, chimpanzees may avoid forest even when logging is light or when fruit availability was not reduced compared to intact forest, suggesting sensitivity to increased human disturbance that accompanies logging (Skorupa, 1986; White & Tutin, 2001). For example, logging may be accompanied by an increase in bushmeat hunting, including of chimpanzees (e.g., Hicks et al., 2009; Last & Muh, 2013), as logging opens up the forest for hunters. This would also explain the decrease of chimpanzees (and nests) in logged areas.

Between the Budongo and Bugoma Central Forest Reserves in western Uganda, chimpanzees inhabit a human‐modified landscape using small forest fragments among village homes, roads and agricultural land (McCarthy et al., 2015; McLennan & Asimwe, 2016; McLennan et al., 2021; McLennan, 2008). Deforestation in this landscape, which is known as the Budongo-Bugoma corridor,” has been extensive (i.e., most unprotected forest was logged and converted to other land uses since the 1990s; McLennan & Hill, 2015; Twongiyire et al., 2015). Hunting chimpanzees for their meat is taboo in this part of Uganda (McLennan, 2008), and can be excluded as an effect on nesting behavior (cf. Last & Muh, 2013; Tagg et al., 2013). Therefore, this region is ideal for examining the effect of deforestation and general human disturbance on chimpanzee nesting.
patterns. In previous studies of nesting in the Budongo–Bugoma corridor, forest degradation and clearance were suggested to be the cause of a high frequency of chimpanzee nests in exotic trees (especially Eucalyptus sp., McCarthy et al., 2017; McLennan et al., 2021), as well as a high frequency of integrated nests (McCarthy et al., 2017; McLennan, 2018).

The aim of our study is to examine the effect of forest clearance, and a community decline, on chimpanzee nesting behavior in the Bulindi chimpanzees, one of the chimpanzee communities inhabiting the Budongo–Bugoma corridor. This study differs from previous studies because it compares nesting behavior before and after major forest clearance in one community of chimpanzees living in fragmented forest surrounded by agricultural land, providing no opportunities to retreat into intact forest. Previous studies on the effects of forest disturbance (mainly logging) often involved surveys of nest densities, but not nest characteristics, in larger forests harboring multiple communities of chimpanzees (cf. Arnhem et al., 2008; Morgan et al., 2018; Plumptre & Reynolds, 1994; White & Tutin, 2001). Deforestation preceded by logging has been ongoing in Bulindi since at least the 1990s. However, forest disturbance peaked between 2007 and 2014, when about 80% of the riverine forest in the chimpanzees’ home range was converted entirely to agricultural land (McLennan et al., 2020). Over this same timeframe the chimpanzee community also decreased by approximately 20% (a conservative estimate because not all community members were identified at the start of the study; McCarthy et al., 2020). We compare chimpanzee nest characteristics before (2006–2007, “period 1”) and after (2014–2015, “period 2”) this period of major forest clearance. We make the following predictions about changes in the chimpanzees’ nesting behavior:

i) Because tree diversity is expected to decline following a large-scale reduction in forest area (where tree species composition is spatially heterogeneous, as at Bulindi; McLennan & Plumptre, 2012; McLennan, 2010), the diversity of tree species used for nesting will be lower in period 2 compared to period 1. This will also result in a different (more limited) choice of tree species for nesting in period 2.

ii) Due to the disappearance of many large trees during logging and forest clearance (McLennan & Plumptre, 2012), chimpanzees will build their nests in shorter trees with a smaller DBH in period 2 compared to period 1, and thus nest height will also be lower in period 2.

iii) Due to an absence of nonhuman predators and hunting by humans in Bulindi, ground nesting by chimpanzees is expected in both periods. However, increased human activities around forest patches after forest clearance might lead to an increase in local people entering the forest at unpredictable times. Therefore, ground nests should be less common in period 2 because chimpanzees are expected to avoid building nests on the ground in diminished areas of forest frequented by villagers.

iv) Due to the large-scale reduction in forest area available for nesting, there will be fewer suitable or preferred nesting trees leading to a greater proportion of reused nests in period 2.

v) Due to the disappearance of many large trees during logging and forest clearance (McLennan & Plumptre, 2012), integrated nests, built using more than one tree, will be more common in period 2, since smaller trees may not be sturdy enough to support a chimpanzee’s weight by themselves.

vi) Since most forest was converted into agricultural land after period 1, chimpanzees will build a larger proportion of their nests in exotic tree species in period 2.

vii) Nest group size and the number of nests constructed in one tree will decrease in period 2 as a result of a decline in community size between periods and the disappearance of many large trees capable of supporting multiple nesting chimpanzees. Alternatively, nest group size and the number of nests in one tree might increase in period 2, if chimpanzees nest more cohesively due to the smaller available habitat, including fewer suitable nesting trees, and/or a need for enhanced safety because of increased human encroachment.

2 | METHODS

2.1 | Ethics statement

This study involving wild chimpanzees was noninvasive and approved by the Uganda National Council for Science and Technology and the Uganda Wildlife Authority. Research adhered strictly to ethics guidelines detailed by the Association for the Study of Animal Behaviour (UK) and the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates.

2.2 | Study site

Data were collected in Bulindi (1°29′N, 31°28′E) in Hoima District, western Uganda, situated midway between the Budongo and Bugoma Forests. Outside these two forest reserves, the land is densely populated with >150 persons per km², but not all forest occurs along rivers and Cyperus papyrus swamps. Since the 1990s, forest throughout the “Budongo–Bugoma corridor” was logged for timber and converted to farmland (McLennan & Hill, 2015; Twongyirwe et al., 2015), leaving only small patches of forest. Nevertheless, chimpanzees survive in this human-dominated landscape, which covers about 1000 km², using remnant forest fragments and agroforestry plantations amidst farmland and villages (McCarthy et al., 2017; McLennan et al., 2021; McLennan, 2008). A genetic census estimated a regional population of 260–320 chimpanzees in the Budongo–Bugoma corridor, in nine or more communities (McCarthy et al., 2015). The Bulindi chimpanzees are one of these communities.

Common trees in riverine fragments at Bulindi include Phoenix reclinata palms, Trilepisium madagascariensis, Antiaris toxicaria, Pseudospondias microcarpa, and Funtumia africana (McLennan & Plumptre, 2012). However, tree species composition changes
along a gradient from swampy valley centers to better drained soils at forest edges (McLennan, 2010). Forest clearance in Bulindi peaked between 2007 and 2014, when about 80% of the forest within the chimpanzees’ home-range was converted to farmland (McLennan et al., 2020). Due to conservation incentives, and because most remaining forest was swampy and unsuitable for farming, forest clearance slowed considerably by 2014 (McLennan et al., 2020). However, by that time, the combined area of forest patches in Bulindi had shrunk to <0.5 km² (see McLennan et al., 2020). During this period of rapid deforestation, avoidance of human disturbance was not possible since there was no undisturbed forest available for the chimpanzees to retreat into (cf. White & Tutin, 2001). Although the limits of their home range was similar in both periods (ca. 20 km²; McLennan, 2010; and unpublished data), their core area of activity had shrunk considerably by period 2 (unpublished data) and their nest building was confined to smaller forest areas in period 2 compared to period 1 (Figure 1). Nevertheless, the Bulindi chimpanzees have adjusted to this changing landscape, most notably by foraging increasingly on cultivated foods (McLennan et al., 2020). As a result of the encroachment and changes in the chimpanzees’ foraging behavior, competitive interactions between the chimpanzees and local people have increased (McLennan et al., 2019).

2.3 Study population

Chimpanzees at Bulindi were first studied during 2006–2007. During that time, community size was unknown since the apes were unhabituated and some individuals were not identified (McLennan & Hill, 2010). However, there were minimally 25 individuals in the community, including six adult males, at least seven adult females, each with 1–2 dependent offspring, and 2–3 subadults (McLennan & Hill, 2010; McLennan, 2010). All individuals were identifiable from 2012, when community size had declined to 19. The chimpanzees were habituated by 2014–2015 when community size varied from 18 to 21 individuals including 2–3 adult males, 5–6 adult females, and 2–3 subadults (ranges due to demographic changes over the 2-year period), plus juveniles and infants (McCarthy et al., 2020; McLennan et al., 2019).

2.4 Data collection

The data collected for this study were divided into two “periods”: between October 2006 and December 2007 (corresponding to “Period 1,” before major forest clearance) and between January 2014 and December 2015 (“Period 2,” after major forest clearance). A similar proportion of nests were recorded in wet months (>100 mm rainfall in most years) in period 1 (64%) and period 2 (72%), with remaining nests recorded in dry or transitional months; for information on climate at Bulindi, see McLennan, Hasegawa, et al. (2017). In both periods, nest data were collected in morning hours. Nests were located based on where chimpanzees were heard vocalizing, or were found opportunistically while searching for chimpanzees, nests and fecal samples in forest patches (McLennan, 2010, 2018). Only fresh nests were considered in this study. Fresh nests were <2 days old, characterised by having only green and healthy leaves, typically with urine or dung below. Recent (with wilted, green to brown leaves, between 2 days and 2 weeks old) and old nests (only brown, dried leaves) were excluded for this analysis. After locating a fresh nest, we searched the area to locate all nests judged to have been constructed at the same time. In both periods, a “nest group” was defined as the number of same-aged nests found within 30 m of the nearest nest (Furuichi et al., 2001; Mulavwa et al., 2010). Nest group size was not determined if a thorough search was not possible (e.g., due to extremely dense vegetation or if nests were built above water), if there was reason to suspect a collection of nests was built over two consecutive nights, or if there was uncertainty regarding reuse of older nests. We recorded the locations of nests with a handheld GPS (Figure 1).

Although chimpanzees were habituated by period 2 and were more likely to be located near or at a nest site compared to period 1,
nests were searched for and recorded after chimpanzees departed the site; therefore the identity of the builder of a nest was rarely known and we made no inferences about nest group size in period 2 from the number of individuals observed in morning parties. A recent study of day-nest building at Bulindi found that the chimpanzees also build day nests for resting on most days, and these are sometimes indistinguishable from night nests (Cibot et al., in prep.). Therefore, day and night nests were not explicitly differentiated in either period. Whether forest clearance influenced day nesting behavior in the chimpanzees is unknown; however, we assume that the majority of nests recorded in both periods were night nests, as indicated by the presence of dung and urine below.

The following nest characteristics were recorded using identical methods in both periods:

(i) Tree/plant species used;
(ii) Tree height, measured with a clinometer and rangefinder (as described in McLennan & Plumptre, 2012); tree height was not recorded in rare instances when nests were built in climbers;
(iii) Nest height (measured to the basal aspect of the nest with a clinometer and rangefinder; height of very low nests was sometimes estimated). Tree and nest height data were not recorded for a subset of nests in period 2 because of equipment malfunction (see Table S1);
(iv) Nest tree DBH, measured at 1.3 m or above buttresses; tree DBH was not recorded for nests in strangling figs or nests lacking a measurable supporting stem (such as nests built in clusters of immature palms or climbers; McLennan, 2018);
(v) Whether or not an older nest was reused;
(vi) Whether or not a nest was integrated (i.e., constructed from ≥2 trees/plants, excluding nests with minor integration of climbing plants). For integrated nests using >1 species, we identified the “main” tree species as the species providing the dominant support and/or structure for the nest;
(vii) The number of same-age fresh nests in the tree (i.e., assumed to have been built at the same time).

The sample size of nests in each period for which each measured variable was recorded is given in Table S1. Some aspects of nest structure, including integrated nests, were published previously by McLennan (2018) for the period 2012–2015. The present study uses a subset of that data (from 2014 to 2015, to compare with data from 2006 to 2007), because deforestation was still occurring during 2012–2013 (McLennan et al., 2020).

2.5 | Diversity of nesting trees

We used the Shannon diversity index and the Morisita-Horn (MH) index to assess potential changes in the diversity and composition of trees used for nesting in period 1 and 2 (Magurran, 2004). The Shannon diversity index (H’) was calculated for each period using the following equation:

\[ H' = \sum_{i=1}^{a} \frac{a_i}{N} \ln \frac{a_i}{N} \]

Here, \( p_i \) is the proportion of nests constructed in species \( i \). The Shannon diversity index takes into account both species richness (number of species used) and species abundance (number of nests per species). A higher value of \( H' \) in either period indicates a greater diversity of tree species used for nesting. To assess compositional similarity among tree species used for nesting between periods, the MH index was calculated using the following equation:

\[ MH = 2 \sum \frac{(a_i \cdot b_i)}{(d_a + d_b) \cdot (N_a \cdot N_b)} \]

where \( N_a \) is the total number of nests in period 1; \( N_b \) is the total number of nests in period 2; \( a_i \) is the number of nests in species \( i \) in period 1; \( b_i \) is the number of nests in species \( i \) in period 2; and \( d_a \) and \( d_b \) are calculated as:

\[ da = \sum \frac{a_i^2}{N_a^2} \]

The index returns a value between 0 and 1, where 0 indicates no similarity (i.e., chimpanzees used completely different species for nesting in periods 1 and 2) and 1 indicates total similarity (i.e., chimpanzees used the same species for nesting and at similar frequencies in both periods).

Results of the Shannon diversity index and MH index provide a comparative measure of selection of nesting tree species between periods, where chimpanzees may choose to nest in the same individual tree more than once. Thus, the results do not compare actual species diversity between periods, although a higher diversity index for nests might be expected to reflect higher forest diversity.

2.6 | Statistical analysis

To test for overall differences in nest height, and height and size (DBH) of nesting trees between period 1 and 2, three Mann-Whitney U tests were performed (one for each variable). We also tested for differences between periods in nest height, and height and DBH of nesting trees within tree species using Paired Wilcoxon tests. Only tree species with a minimum of five recorded nests in both periods were included in this analysis (Table S2).

To test if frequencies of nest re-use, integrated nests, and use of exotic tree species for nesting differed between period 1 and 2, \( \chi^2 \) contingency tests were performed using observed frequencies in each period.

To test if nest group sizes differed between period 1 and 2, a Mann Whitney U test was performed. A second Mann Whitney U test was performed to test for a difference between periods in the number of fresh nests that were constructed in a single tree. Chimpanzee community size was larger in period 1, including more
subadult and adult individuals (≥15–16 in period 1; 10–11 in period 2). Although the number of juvenile nest builders was not established in period 1, larger nest group sizes were theoretically possible in period 1. Therefore, larger nest groups in period 2 would indicate an increased tendency of chimpanzees to aggregate together for nesting. Similarly, a greater average number of nests per tree in period 2 would further indicate increased “cohesiveness” during nesting.

Statistical analyses were performed using R version 3.5.1. Statistical tests were two-tailed and a value of \( p < .05 \) was considered significant. All \( N \) values are provided in Section 3 (see also Supporting Information).

3 | RESULTS

3.1 | Nesting tree species diversity and use

A total of 499 and 529 fresh nests were recorded in period 1 and period 2, respectively (\( n = 1028 \) nests in both periods). Similar to other sites, the selection of tree species for nesting by chimpanzees in Bulindi was independent of overall availability in period 1 (Supporting Information; data on tree species availability were unavailable for period 2).

The Shannon diversity index indicated that there was slightly greater diversity in tree species selected for nesting in period 1 (\( H' = 2.89 \)) compared to period 2 (\( H' = 2.60 \)). The MH index gave a value of 0.90, indicating high compositional similarity of species used for nesting in both periods.

The top three selected species differed only slightly between period 1 and 2 (helping to explain the high similarity in tree species used; Table 1). In both periods, \( P. \) microcarpa was the most important nesting tree (29.1% and 33.8% of all nests, respectively), followed by \( Macaranga \) schweinfurthii (11.2% and 13.6%, respectively). In period 1, exotic cacao \( Theobroma cacao \) (cocoa) was the third most important species (5.4% of nests compared to 0% of nests in period 2). In period 2, the palm \( P. \) reclinata was the third most important species (7.6% of nests, compared to 4.4% of nests in period 1).

A total of 56 different tree species were used for nesting over both periods. Twenty-nine species were used in both periods, whereas 15 species were used only in period 1 and 12 species were used only in period 2. Most species used in one period only represented <1.0% of nesting trees in that period, but there were a few notable exceptions. In period 1 exotic \( T. \) cacao was the third most important nesting tree, but was never used in period 2. Similarly, \( Khaya \) sp. was the fourth most important nesting tree in period 2, but no nests were recorded in this species in period 1 (Table 1).

| # | Species \(^1\) | Percentage nests in species | Species | Percentage nests in species |
|---|---|---|---|---|
| 1 | \( Pseudospondias microcarpa \) \(^2\) | 29.1 | \( Pseudospondias microcarpa \) | 33.8 |
| 2 | \( Macaranga schweinfurthii \) \(^2\) | 11.2 | \( Macaranga schweinfurthii \) | 13.6 |
| 3 | \( Theobroma cacao \) | 5.4 | \( Phoenix reclinata \) | 7.6 |
| 4 | \( Glennia africana \) | 5.0 | \( Khaya \) sp. | 5.5 |
| 5 | \( Parkia filicoides \) \(^2\) | 4.6 | \( Funtumia africana \) | 4.9 |
| 6 | \( Phoenix reclinata \) \(^3\) | 4.4 | \( Trilepisium madagascariensis \) | 3.8 |
| 7 | \( Trichilia dregeana \) \(^2\) | 3.6 | \( Lovoa trichilioides \) | 3.6 |
| 8 | \( Antiaris toxicaria \) \(^3\) | 3.0 | \( Glennia africana \) | 3.0 |
| 9 | \( Lovoa trichilioides \) | 2.8 | \( Neoboutonia melleri \) | 2.5 |
| 10 | \( Albizia zygia \) \(^2\) | 2.8 | \( Antiaris toxicaria \) | 1.9 |

Note: The tree species in bold font are those present in the top 10 in both periods.

\(^1\)For integrated nests constructed using >1 tree species, we identified the nesting tree species as the one providing the dominant support for the nest.

\(^2\)Indicates a “preferred species” during period 1 (i.e., used for nesting significantly more than expected based on species abundance; McLennan & Plumptre, 2012; species abundance data were not available for period 2, see Supporting Information).

\(^3\)Indicates a “less preferred species” during period 1 (i.e., used for nesting significantly less than expected based on species abundance; McLennan & Plumptre, 2012; see Supporting Information).
3.2 | Nest height, and height and DBH of nesting trees

Average nest height, and height and DBH of nesting trees decreased between period 1 and 2 (Table 2). However, only the decrease in nest and tree height were statistically significant (Mann-Whitney U test, nest height: $U = 58,877$, $p = .008$, $n_{\text{period1}} = 498$, $n_{\text{period2}} = 210$; nest tree height: $U = 62,391$, $p < .001$, $n_{\text{period1}} = 496$, $n_{\text{period2}} = 210$; nest tree DBH: $U = 107,000$, $p = .349$, $n_{\text{period1}} = 476$, $n_{\text{period2}} = 434$). On average, nest height decreased by 1.95 m, the height of nest trees decreased by 3.56 m, and the DBH of nest trees decreased by 4.53 cm (Table 2). Nest height ranged from 0 to 42 m in period 1 (with a single ground nest recorded), and 1.8–29.4 m in period 2 (no ground nests recorded); height of nest trees ranged from 1.8 to 47.0 m in period 1, and 2.0–35.8 m in period 2. Finally, nest tree DBH ranged from 5.0 to 186.2 cm in period 1 and 6.5–190 m in period 2.

Within tree species, there was no significant difference in average nest height, tree height and tree DBH between period 1 and 2 (Paired Wilcoxon test, nest height: $U = 35$, $p = .492$, $n = 10$ species; nest tree height: $U = 40$, $p = .232$, $n = 10$ species; nest tree DBH: $U = 55$, $p = .233$, $n = 12$ species). Of 10 tree species in the sample with tree and nest height data available from both periods, average nest height decreased in six species and increased in four species between period 1 and 2 (Figure 2a). Of those same ten species, average nest tree height decreased in seven species and increased in three (Figure 2b). Finally, of the twelve species in which DBH of nest trees was measured in both periods, eight decreased in average DBH and four increased in average DBH (Figure 2c).

3.3 | Reused, integrated nests and nests in exotic trees

The frequency of reused nests increased from 4.2% of nests in period 1% to 7.6% of nests in period 2 ($\chi^2$ contingency test, $\chi^2 = 4.59$, $p = .032$; Figure 3). There was no significant difference in the frequency of integrated nests between period 1 (19.8% of nests) and 2 (17.0% of nests) ($\chi^2$ contingency test, $\chi^2 = 1.19$, $p = .28$; Figure 3). The use of exotic species for nesting decreased from 5.6% of nests in period 1 to only 1.3% of nests in period 2 ($\chi^2$ contingency test,

### Table 2

|                     | Period 1 | Period 2 | Period 1 and 2 combined |
|---------------------|----------|----------|-------------------------|
| Nest height (m)     | 12.09 (±8.05) | 10.14 (±6.23) | 11.50 (±7.60)          |
| Nest tree height (m)| 18.47 (±9.91) | 14.91 (±8.01) | 17.30 (±9.50)          |
| Nest tree DBH (cm)  | 48.14 (±37.75) | 43.61 (±31.92) | 46.00 (±35.14)         |

**FIGURE 2** Comparison of average nest height (a, $n = 10$ species), nest tree height (b, $n = 10$ species), and nest tree DBH (c, $n = 12$ species) in individual tree species used for nesting in periods 1 and 2 (results of Mann-Whitney U test). Only species with at least five recorded nests in both periods were included in the analysis (see Table S2). Green lines indicate species in which nest height, tree height, or tree DBH decreased between periods 1 and 2 (as expected), whereas black lines indicate species in which nest/tree height or DBH increased between periods (against expectation). DBH, diameter at breast height.
χ² = 13.08, p < .001; Figure 3). In period 1, the exotic species used were cocoa (27 of 28 nests in exotic trees) and mango *Mangifera indica* (one nest). In period 2, six of seven nests in exotic trees were in mango trees, while one was in a jackfruit *Artocarpus heterophyllus* tree.

3.4 | Nest group size

Nest group sizes increased significantly between period 1 and 2 (Mann Whitney *U* test, *U* = 5076.5, *p* < .001, *n*₁ = 130, *n*₂ = 107, Figure 4a). In period 1, average nest group size was 3.24 (±2.76 SD; median = 2; range: 1–16). In period 2, average nest group size was 4.76 (±3.46 SD, median = 4; range: 1–14).

3.5 | Number of nests in one tree

In period 1, the average number of nests per tree was 1.38 (±1.01 SD; median = 1, range = 1–11). This increased slightly, but significantly, to 1.47 in period 2 (±0.94 SD; median = 1, range = 1–6; Mann-Whitney *U* test, *U* = 60,170, *p* = .027, *n*₁ = 361, *n*₂ = 356, Figure 4b).

4 | DISCUSSION

To our knowledge, this study is the first to compare nesting characteristics in one community of chimpanzees before and after major forest clearance (80% reduction in forest area over 7–8 years; McLennan et al., 2020), when the chimpanzees had no opportunity to retreat into other undisturbed forests. Following this major habitat disturbance, chimpanzees in Bulindi showed some adjustments to their nesting behavior by building nests at lower heights in shorter trees, and by reusing nests more often. Furthermore, cohesiveness of nesting parties—as indicated by the size of nest groups and the number of nests built in one tree—increased after forest clearance, in spite of a decline in community size over the same period (McCarthy et al., 2020). Conversely, the chimpanzees continued to select most of the same tree species for nesting (especially the two most preferred species), constructed integrated nests at a similar frequency, and actually nested less frequently in exotic tree species following forest clearance.

Contrary to our first prediction, the diversity of trees used for nesting was only slightly lower in period 2, and there was a high compositional similarity in the overall choice of tree species for nesting between period 1 and 2. This pattern is similar to the changes in the Bulindi chimpanzees’ diet during the same two periods, which were also relatively minor considering the extent of forest loss (McLennan et al., 2020). Nesting tree selection was overall independent of tree species abundance in period 1 (Supporting Information). We predicted that the diversity of species used for nesting would be lower in period 2 because species composition at Bulindi varied spatially before fragment clearance (McLennan & Plumptre, 2012; McLennan, 2010). The loss of such a large proportion of forest—including most forest on well-drained soils, which was more species-rich than swamp forest (McLennan, 2010)—was therefore expected to result in reduced tree diversity. However, since
a survey of tree species composition was not carried out in period 2, we can only speculate what caused the similarities and differences between the two periods. The high similarity in tree species used in both periods may reflect a strong preference for certain species. Thus, if a preferred species was represented by fewer specimens after forest clearance, chimpanzees might nest in those remaining trees repeatedly. While we did not explicitly study the chimpanzees’ use of individual trees over time, qualitative observations suggested they indeed nested in many of the same individual trees repeatedly throughout period 2, such as several large specimens of *P. microcarpa* (McLennan, personal observations; see also below).

Nevertheless, the selection of some tree species changed drastically between periods. For example, in period 1 exotic *T. cacao* trees were the dominant understorey species in abandoned forest plantations (McLennan & Plumptre, 2012). Cocoa was the third most commonly used species for nesting in period 1 (Figure 5a), but was not used at all in period 2. This is easily explained by the fact that almost all cocoa trees were removed during forest clearance before

FIGURE 5 Use of exotic tree species for nesting by chimpanzees at Bulindi. (a) Nest in a cocoa tree *Theobroma cacao* in an abandoned forest plantation in period 1; (b) Adult male chimpanzee at Bulindi resting in a planted *Eucalyptus* sp. tree. Since the present study in 2014–2015, the chimpanzees occasionally nest in *Eucalyptus* trees as local landowners have increasingly established exotic timber plantations (Photos: M. McLennan)

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Human disturbance has been shown to influence ground nesting in other populations of chimpanzees, where terrestrial nesting may be altogether absent (like at Bulindi) or occurs predominantly in dense or swampy areas difficult to access for people (Hicks, 2010; Last & Muh, 2013; Tagg et al., 2013). Elsewhere in the Budongo–Bugoma corridor ground night nests accounted for 1.2% of nests (McCarthy et al., 2017). Why the frequency of ground nesting should differ between Bulindi and nearby communities is unclear; however, social or "cultural" factors, in addition to habitat and anthropogenic factors, may influence ground nesting behavior in chimpanzees (Hicks, 2010; Koops, McGrew, Matsuzawa, et al., 2012; Tagg et al., 2013).

As expected, the chimpanzees reused nests more often after largescale forest clearance (prediction 4). The frequency of nest reuse at Bulindi in period 1 (4.2% of nests) was similar to that reported elsewhere in the Budongo–Bugoma corridor (4.0%, McCarthy et al., 2017), but had increased to 7.6% of nests by period 2 (Figure 6). An 80% decrease in forest area from periods 1 to 2 clearly led to a large reduction in available trees (McLennan et al., 2020). When fewer (suitable) trees and thus fewer fresh leaves are available, chimpanzees are more likely to reuse nests (Fruth & Hohmann, 1996; McCarthy et al., 2017). Additionally, as noted above, qualitative observations suggested the chimpanzees nested repeatedly in certain individual trees in period 2, which may be expected to promote nest reuse. Chimpanzees of the Sonso community in Budongo Forest, a large forest reserve 25 km north of Bulindi, also reused a large proportion of their nests. However, this seems to have been related to the relatively large number of chimpanzees with limb injuries from snares, who may experience difficulty building new nests (Plumptre & Reynolds, 1997). In contrast, none of the chimpanzees in Bulindi were handicapped by snare or trap injuries in period 2.

Nest integration was also relatively high in Bulindi compared to elsewhere in the Budongo–Bugoma corridor (6.7% of nests; McCarthy et al., 2017), even though the frequency of reintegrated nests declined slightly from period 1 (19.8% of nests) to period 2 (17.0%), contrary to prediction 5 (Figure 6). A somewhat lower frequency of integrated nests (14.8%) was reported for the 4-year period 2012–2015 (McLennan, 2018). The overall high proportion of integrated nests at Bulindi is probably influenced by two species that were commonly used for nesting (M. schweinfurthii and T. cacao in period 1, and M. schweinfurthii in period 2). These species tend to form clumps of individual stems with small diameter sizes; a chimpanzee frequently incorporates multiple stems when building a nest in these species. Therefore, the lower proportion of integrated nests in period 2 may be related to the clearance of forest containing T. cacao (cocoa) trees after period 1. In most forested habitats integrated nests account for ≤10% of chimpanzee nests (Fruth & Hohmann, 1996). The high percentage of integrated nests at Bulindi is similar to that recorded in Fongoli, Senegal (19%) and Issa Valley, Tanzania (18%–20%), where chimpanzees inhabit dry savanna habitat (Stewart, 2011)—although a lower proportion of integrated nests was subsequently reported at Issa Valley (5%; Hernandez-Aguilar et al., 2013). Frequent construction of integrated nests at Bulindi and in savanna habitats could reflect a relative paucity of large trees in these study areas compared to most chimpanzee habitats. Whether construction of elaborate integrated nests (Figure 6a) also involves a social or "cultural" element, as was suggested for ground nesting, requires further investigation (McLennan, 2018).

Chimpanzees at Bulindi formed larger nest groups after forest clearance, despite a moderate decline in community size (prediction 7). The average nest group size (NGS) in period 2 was larger than reported in other studies of chimpanzee communities with more adult and subadult members (Bulindi period 2: NGS = 4.76 ± 3.46 SD, 10–11 (sub)adults, this study; Kahuzi-Biega, D.R. Congo: NGS = 4.3 ± 3.0 SD, 14 (sub)adults, Basabose & Yamagiwa, 2002; Budongo, Uganda: 4.5, 24 adults (excluding subadults), Brownlow et al., 2001; Nimba, Guinea: 2.2 ± 1.6 SD, number of (sub)adults unknown, Granier et al., 2014). However, chimpanzees were not undergoing rapid habitat loss in these other studies. Chimpanzees at Bulindi may have nested more cohesively in period 2 (including building nests more frequently in the same tree as others in the nesting party; Figure 6) as a consequence of the large decrease in suitable habitat, that is, forest. While nests were distributed more widely across the chimpanzees’ range in period 1 (Figure 1), the extensive forest clearance reduced opportunities for chimpanzees to range in small parties and nest in different forest fragments within the home range in period 2. A second reason may relate to changes in the chimpanzee diet.

**FIGURE 6** Examples of chimpanzee nests at Bulindi. (a) Integrated nest: low nest constructed in multiple young trees (Neoboutonia melleri, Funtumia africana, and Pseudospondias microcarpa); (b) Nest reuse: fresh nest in Macaranga schweinfurthii built on top of a very old, disintegrating nest; M. schweinfurthii was the second most important tree species for nesting in both periods; (c) Three nests constructed near one another in a P. microcarpa tree; P. microcarpa was the most commonly selected species for nesting at Bulindi in both periods (Photos: M. McLennan)
Following fragment clearance and the loss of many food trees, agricultural fruits assumed greater importance in the chimpanzee diet (McLennan et al., 2020). Agricultural foods offer certain nutritional advantages over some wild foods, being higher in carbohydrate energy and lower in hard-to-digest fibre (McLennan & Ganzhorn, 2017; Riley et al., 2013). Thus, the chimpanzees’ increased intake of cultivated foods could have reduced feeding competition and travel costs associated with searching for dispersed food sources, allowing for larger foraging (Chapman et al., 1999) and also nesting parties. In support of this, Kalinzu chimpanzees in southwest Uganda nested in larger groups when food availability was high (Furuichi et al., 2001).

Finally, the reduced community size at Bulindi—including fewer mature males (McLennan et al., 2020)—may have acted in concert with the ecological changes to increase nesting cohesion. When community size declined substantially in Tai National Park, Côte d’Ivoire, the chimpanzees formed larger, more cohesive parties (Lehmann & Boesch, 2004). Larger parties could increase group safety (Lehmann & Boesch, 2004), because small communities with fewer mature males for defence are at greater risk from predators or rival groups (van Schaik & Hörstermann, 1994). Although chimpanzees at Bulindi do not encounter natural predators or rival chimpanzee communities, their interactions with local people are frequently agonistic (McLennan & Hill, 2010, 2013). We hypothesize that human disturbance may have had a similar effect on promoting cohesion at Bulindi following a decline in community size and number of mature males, which is potentially reflected in the greater cohesiveness of nest groups in period 2. However, additional data—for example on the size, duration and composition of daytime parties—are needed to establish if chimpanzees at Bulindi show high sociality generally (cf. Lehmann & Boesch, 2004).

Despite experiencing major habitat change (conversion of riverine forest to farmland), chimpanzees in Bulindi continue to survive in an extensively human-impacted environment. Chimpanzees in Bulindi have already been shown to adjust their feeding behavior flexibly in response to major forest loss (McLennan et al., 2020). Our current study shows that these chimpanzees, unable to retreat into undisturbed forest, are also flexible in aspects of their nesting behavior, potentially enabling them to adapt to the changing conditions. Subsequent to this study, most landowners in Bulindi refrained from further forest clearance owing to conservation incentives. Continuing deforestation would presumably result in increased use of exotic trees for nesting by the chimpanzees, as observed elsewhere in the Budongo–Bugoma corridor (McCarthy et al., 2017; McLennan et al., 2021). While behavioral flexibility may help these adaptable great apes cope with rapid habitat change, at least in the short-term, chimpanzees living in unprotected habitat in Uganda, including at Bulindi, face mounting anthropogenic pressures that threaten their survival. Besides habitat loss from agriculture, infrastructural development and urbanization, direct threats to chimpanzees include mortality from crop protection measures (traps and snares), retaliatory killings, and vehicle collisions (Cibot et al., 2019; McLennan & Asiimwe, 2016; McLennan et al., 2012, 2021; Reynolds et al., 2003), and potentially a heightened risk of anthropogenic disease transmission (e.g., Scully et al., 2018). Conserving chimpanzees and other wild primates in unprotected human-modified landscapes requires long-term integrated approaches that reduce threats to primate survival, and combine habitat conservation and restoration with locally appropriate conservation incentives and livelihood support for local residents.

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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