



# Decay rates of arboreal and terrestrial nests of Eastern chimpanzees (*Pan troglodytes schweinfurthii*) in the Bugoma Central Forest Reserve, Uganda: Implications for population size estimates

Toni Romani<sup>1,2</sup>  | Roger Mundry<sup>3,4,5</sup> | Gerald Mayanja Shaban<sup>6</sup> |  
Marek Konarzewski<sup>1,7</sup> | Mary Namaganda<sup>8</sup> | Catherine Hobaiter<sup>6,9</sup>  |  
Thibaud Gruber<sup>6,10</sup> | Thurston Cleveland Hicks<sup>1</sup>

<sup>1</sup>The Faculty of 'Artes Liberales', University of Warsaw, Warsaw, Poland

<sup>2</sup>CyberTracker Italia, Osoppo, Italy

<sup>3</sup>Cognitive Ethology Laboratory, German Primate Center, Leibniz Institute for Primate Research, Göttingen, Germany

<sup>4</sup>Department for Primate Cognition, Georg-August-University, Göttingen, Germany

<sup>5</sup>Leibniz Science Campus Primate Cognition, Göttingen, Germany

<sup>6</sup>Bugoma Primate Conservation Project, Hoima, Uganda

<sup>7</sup>The Faculty of Biology, University of Białystok, Białystok, Poland

<sup>8</sup>Department of Plant Science, Microbiology and Biotechnology, School of Biosciences, College of Natural Sciences, Makerere University, Kampala, Uganda

<sup>9</sup>School of Psychology and Neuroscience, University of St Andrews, St Andrews, Scotland, UK

<sup>10</sup>Swiss Center for Affective Sciences and Faculty of Psychology and Educational Sciences, University of Geneva, Geneva, Switzerland

## Correspondence

Toni Romani, The Faculty of 'Artes Liberales',  
The University of Warsaw, Ul. Dobra 72,  
Warsaw 00-312, Poland.  
Email: [t.romani@uw.edu.pl](mailto:t.romani@uw.edu.pl)

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## Abstract

Chimpanzees were once thought to sleep primarily in the trees, but recent studies indicate that some populations also construct terrestrial night nests. This behavior has relevance not only to understanding the behavioral diversity of *Pan troglodytes*, but also to the conservation of the species, given that nest encounter rates are often used to estimate great ape population densities. A proper estimate of decay rates for ground nests is necessary for converting the encounter rate of nests to the density of weaned chimpanzees. Here we present the results of the first systematic comparative study between the decay rates of arboreal and terrestrial chimpanzee nests, from the Bugoma Central Forest Reserve in western Uganda. We followed the decay of 56 ground and 51 tree nests in eight nest groups between April 2020 and October 2021. For 15 of the ground and 19 of the tree nests, we collected detailed information on the condition of the nests every two weeks; we checked the remaining 73 nests only twice. On average, ground nests lasted 238 days versus 276

**Abbreviations:** BCFR, Bugoma Central Forest Reserve; BPCP, Bugoma Primate Conservation Project; FAs, field assistants; NS, nest site; P.t., *Pan troglodytes*.

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days for tree nests ( $p = 0.05$ ). Of the 107 total nests surveyed, 51% of tree and 64% of ground nests had disappeared after six months. Based on our results, we propose a modification of the formula used to convert nest density into chimpanzee density. Our results highlight the importance of taking into account potential differences in decay rates between ground versus tree nests, which will likely influence our understanding of the distribution of ground nesting behavior in chimpanzee across tropical Africa, as well as our estimations of the densities of ground nesting populations.

#### KEYWORDS

Eastern chimpanzees, ground nesting, nest decay, nest half-life

## 1 | INTRODUCTION

To better understand population dynamics and effectively conserve endangered species, it is essential to obtain accurate estimates of their population sizes (Hicks et al., 2014; McNeillage et al., 2006). Chimpanzees (*Pan troglodytes*) are, like all nonhuman great apes, elusive animals living at low densities, and thus are difficult to observe within their natural habitat. They do create, however, on a nightly basis sleeping structures called nests or beds, which can be used to estimate their occurrence and, provided that site-specific information on nest production and decay rates can be obtained or at least estimated, their density. Most species of nonhuman great apes build the majority of their night nests in trees, with the exception being the genus *Gorilla*, which also sleeps frequently in ground nests (Brugiere & Sakom, 2001; Mehlman & Doran, 2002; Sanz et al., 2007). Ground nesting is rare in orangutans (Ashbury et al., 2015) and bonobos (Serckx et al., 2016). Until recently, it was also thought to be so in chimpanzees, but we now know it to be common in some populations representing all four subspecies (*P. t. verus*: Koops et al., 2007; Pruetz et al., 2008. *P. t. troglodytes*: Tagg et al., 2013. *P. t. ellioti*: Last & Muh, 2013. *P. t. sweinfurthii*: Hobaiter et al., 2022). In fact, in some populations of chimpanzees, a sizable proportion of nests are terrestrial (e.g., in northern Democratic Republic of Congo: Hicks, 2010; Romani et al., 2023).

To estimate densities of nonhuman great apes (Kühl et al., 2008), conservation biologists typically use transects to conduct either standing crop (Tutin & Fernandez, 1984) or marked nest counts (Plumptre & Reynolds, 1996). Once researchers have obtained nest encounter rates, along with information on local nest decay and production rates, they can, using the DISTANCE formula (Buckland et al., 2001), convert such data into the density of weaned great apes:

$$\text{Density} = \frac{N}{2 \cdot L \cdot w \cdot p \cdot r \cdot t},$$

where  $N$  is the number of nests,  $L$  is the transect length,  $w$  is the effective strip width,  $p$  is the proportion of nest builders,  $r$  is the nest production rate, and  $t$  is the nest half-life (Heinicke et al., 2019; Kühl et al., 2008). The use of this method, despite its practicality, has some

disadvantages. Because rates of chimpanzee nest production decay vary significantly between populations and depend on a complex array of ecological and seasonal factors (Morgan et al., 2016), locally-acquired nest decay and production rates should be used whenever possible (Kühl et al., 2008; Laing et al., 2003; Wessling & Surbeck, 2022). These data are, however, often not available, in which case a range of values from other sites is typically used to provide an estimate (e.g., Hicks et al., 2014). Frequent ground nesting in some populations may complicate this approach, particularly if ground nests are ignored or missed by observers or if decay rates differ between terrestrial and arboreal nests. Morgan et al. (2016) reported that the terrestrial nests of Western lowland gorillas (*Gorilla gorilla gorilla*) decayed more rapidly than arboreal ones, which they argued was influenced by nest construction type, canopy cover, rainfall, and forest structure. To our knowledge, no study has compared decay rates between ground and tree nests in chimpanzees; thus between 2020 and 2021, we conducted such a study in the Bugoma Central Forest Reserve (BCFR), where the chimpanzees are known to regularly build nighttime ground nests (Hobaiter et al., 2022).

To establish the mean nest decay rate for BCFR, as well as to compare decay rates between tree and ground nests, between April 2020 and October 2021 we examined and then revisited 51 arboreal and 56 terrestrial nests constructed by eastern chimpanzees (*P. t. sweinfurthii*) at eight nesting sites. We hypothesized that the tree nests would last longer than the ground nests, as they were less likely to be exposed to standing water following rains or to be trampled by passing fauna. We also hypothesized that ground nests using a larger number of components in their construction would last longer, and that tree nests at an elevation above 15 m would decay more quickly than tree nests built lower in the canopy, given that they would more likely be exposed directly to rain and wind. For a subset of 34 nests that we were able to revisit nearly every two weeks, we describe in greater detail the manner in which both ground and tree nests decayed over a period of seven months.

The primary aim of this study was to compare the decay rates of ground and tree nests, which will allow us to refine evaluation methods for nest decay rates in areas where chimpanzees frequently build both. Doing so is not only important for acquiring accurate

population density estimates, which are crucial for the conservation of the species, but to better allow us to evaluate the occurrence of ground nesting as a potential cultural variant in chimpanzees. In addition, we aimed to provide a nest decay rate specific for the BCFR, which is home to a number of chimpanzee communities. The most recent chimpanzee census in BCFR was conducted by Plumptre et al. (2010), who used the average nest decay rate of 46 days (range: 14–161 days) from the Budongo Forest, which is located about 50 km to the northeast (Plumptre & Reynolds, 1996). The Budongo chimpanzee population, unlike that at BCFR, is not a ground nesting one (CH, unpublished data), which may affect both nest decay rates and the density estimations made at BCFR.

## 2 | MATERIALS AND METHODS

### 2.1 | Study site

The BCFR is an approximately 400 km<sup>2</sup> forest reserve adjacent to Lake Albert in the western rift valley of Uganda. It ranges in altitude between 1000 and 1100 m (Plumptre & Cox, 2005), and its habitat consists primarily of continuous medium altitude semi-deciduous forest interlaced by seasonally flooded rivers and swamps, as well as patches of woodland and grassland. During the wet seasons of 2020 and 2021, the average daily low and high temperatures were 23.2°C and 30.8°C; during the dry season they were 25.8°C and 32.3°C (for more details on the climate, see Supporting Information: 1). The forest is surrounded on all sides by cultivated fields, roads, and villages. Although it is a protected reserve, locals frequently enter it to gather firewood or to graze their cattle. In addition, timber-harvesting, charcoal-burning, hunting, and snaring are common within the BCFR. Since 2015, the Bugoma Primate Conservation Project (BPCP) has worked together with the Ugandan Wildlife Authority and the National Forestry Authority, as well as local communities, to protect the rich primate fauna and the delicate ecosystem of the BCFR. We carried out our research using nests made by the resident free-living population of eastern chimpanzees, one community of which is semi-habituated, in collaboration with the BPCP.

### 2.2 | Data collection

From April 2020 to October 2021, BPCP field assistants (FAs) encountered the nest sites investigated in this study while conducting a chimpanzee health monitoring study or while making assessments of human activities in the forest (Figure 1). The nests in the eight nest groups had all been constructed by chimpanzees the previous night. At six of these nest sites (NS), the FAs observed the chimpanzees leaving in the morning and at the other two they found fresh feces and urine. In 4 cases (NS191, NS699, NS709, and NS712), TR was present with the health monitoring team when they encountered the fresh nests (Supporting Information: 2). For the other four nest sites, TR accompanied the FAs to these sites while still fresh, and counted and marked all tree and ground nests (NS135 and NS710 were visited after one day and NS689 and

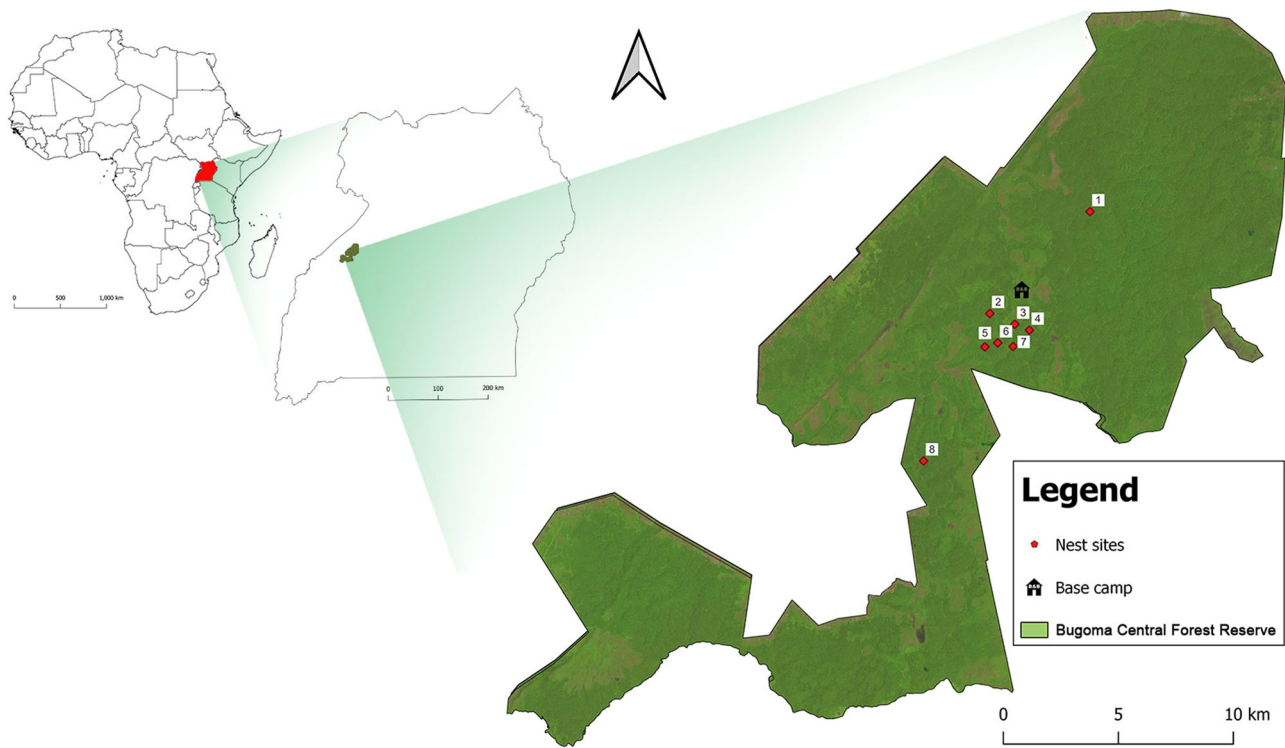
NS690 after seven days). TR also accompanied the team to the first nest site encountered (NS135).

Following Hicks (2010) and Romani et al. (2023), we defined a ground nest as a nest constructed at or below 50 cm above the ground. We considered nests to belong to the same nest site if we estimated that all nests had been made at the same time and were not separated by more than 20 m (Hicks et al., 2014; Romani et al., 2023). For each nest, we noted the GPS location, the estimated age (see Table 1 for definitions of nest ages), height above the ground, number of trees and other plants used (including tree diameter at breast height, for tree nests), plant type (herbaceous or woody), plant species, nest complexity (complex nest: "A structure made of branches, vines and/or herbs arranged into a structure, often in a circular bowl shape; frequently contains hair and/or associated with feces when the nest is fresh"; flimsy nest: "A nest made with minimal construction: a few leaves or branches brought together on the ground; little or no interweaving; usually flat; often without hair or dung when fresh", Romani et al., 2023), habitat type, forest structure, and whether the nest was covered or partially covered by the canopy. GM identified the plant species on-site, and these were later verified by MN at the Makerere University Herbarium (Supporting Information: 3). TR marked each of the 107 nests (56 ground and 51 tree nests at eight nest sites) with a yellow label bearing a unique ID and followed their decay on the return visits (Figure 2).

#### 2.2.1 | Revisits

TR, GM, and team revisited each of the nest sites at least twice (Supporting Information: 2), recording the presence or absence of each nest, as well as the state of decay of the nests still visible (see below). In addition, from April to October 2020, TR and team revisited a subset of 34 nests every two weeks (15 ground and 19 tree nests at sites NS135 and NS191). At each revisit, TR assigned the appropriate age category following Hicks (2010) and Romani et al. (2023), adapted from Tutin and Fernandez (1984) (see Table 1 for definitions). A nest was considered to have completely decayed (from here on, disappeared) when it was no longer possible for TR and team to recognize it as a nest (Buckland et al., 2001). To calculate the average nest half-life (the time after which half of the nests have disappeared), we used the retrospective method (Kamgang et al., 2019; Laing et al., 2003), which consists of marking each fresh nest and revisiting it only once, to check whether it had disappeared.

In addition to recording whether or not the marked nests were still visible, we photographed and filmed the nests during each visit, noted any presence of chimpanzee odor, and monitored the decay of chimpanzee dung based on its consistency, as well as the visibility of seeds or other digested material and any germinating shoots. For the nests themselves, we recorded the color and decay status (green and fresh, faded green to brown and dry, or darker brown and rotten) of their leaves and stems and placed them in the age categories listed in Table 1. For four ground nests



**FIGURE 1** Locations of the nest groups studied within the Bugoma Forest Central Reserve, Uganda. 1 = Nest site (NS) 699; 2 = NS710; 3 = NS191; 4 = NS135; 5 = NS709; 6 = NS690; 7 = NS689; 8 = NS710.

**TABLE 1** Definitions of nest age categories for ground and tree nests.

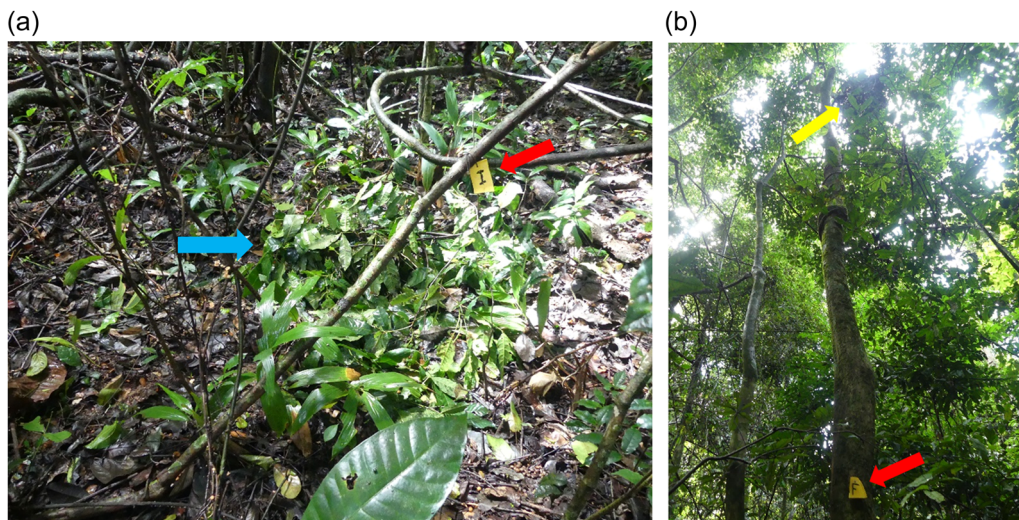
Category	Definition
Fresh (1)	Leaves are green and still appear to be alive. The nest appears springy or “fluffy.” Dung and hairs are more likely to be present, as well as the odor of chimpanzees and their dung and urine.
Recent (2)	Leaves of the ripped off/broken saplings are beginning to dry and change color, although bent-in saplings are still likely to be green. Dung is often still present, but in the dry season may have begun to mummify. Chimpanzee odor may still be present.
Old (3)	All remaining leaves are brown; some branches have lost their leaves or are wilted or rotten. The nest still maintains some of its original structure. Dung may still be visible in the form of germinated seeds. Chimpanzee odor is no longer detectable.
Rotten (4)	All remaining leaves are rotten. The nest structure is disintegrating. Any dung present before is no longer visible.
Skeleton (5)	Only the structure of the nest is visible, as a framework of branches or a “skeleton.”

(N135B, N135C, N135F, and N191J) and one tree nest (N135C) we set up camera traps to record their decay sequence over a period of seven months, recording a still image every hour from 9 a.m. to 4 p.m. (the time-lapse sequences of ground and tree nests are available at the following links: [https://www.youtube.com/playlist?list=PL\\_kRqRvBkPI57zqNXf22NuOWeOGzZo2d](https://www.youtube.com/playlist?list=PL_kRqRvBkPI57zqNXf22NuOWeOGzZo2d); DOI:10.17632/ncthx3yzs9.1).

### 2.3 | Statistical analysis

Researchers commonly use two methods to estimate nest decay rates, the Markov model and the logistic regression (Laing et al., 2003; Mathewson et al., 2008). We used our data set to evaluate these two different methods, and established which of them

provided the best fit for our data. The Markov model (Kemeny et al., 1956) is based on the transition between nest decay states, following the assumption that during the transition period between a fresh and a totally decayed nest, a matrix of probabilities exists between one state and another that is not influenced by the previous state. The transition through stages is unidirectional (the nest cannot return to a previous state) (Supporting Information: 4). The logistic regression model assumes that the data follow a binomial distribution and models the probability that a nest still exists after a given period of time. For the logistic regression model, we adapted the formula from Buckland et al. (2001) and Laing et al. (2003), taking into consideration whether the nest had disappeared at the time of revisit:



**FIGURE 2** (a) Ground nest (blue arrow) N191I and (b) tree nest (yellow arrow) N191F (B), with their respective labels (red arrows). Photos: TR.

$$P(x) = \frac{1}{1 + \exp[-(a + b \cdot x + c \cdot \text{location})]}$$

where the probability of a nest still existing by day  $x$  is  $P(x)$ , depending on the coefficients  $a$ ,  $b$ , and  $c$ , to be estimated, which represent the intercept, the slope (multiplied by the age of the nest at the revisit) and the effect of nest location (arboreal or terrestrial), respectively.

We fitted both the Markov and the logistic regression models to our data, including as independent variables the location (arboreal or terrestrial) and the number of days between the date of construction and our revisit. Given the limited number of nests used in our study, we decided not to include the effects of rainfall or temperature into the models. To achieve an even distribution of the nests within the maximum revisit interval (548 days), we were required to select 107 nests, so that roughly equal numbers fell into at least 6 intervals. To this end, we first divided the nest follow-times into 12 equally-sized intervals. We had revisited 15 of the ground nests and 19 of the tree nests multiple times (Figure 3, Supporting Information: 2 and 5), and thus had the choice to include them into one of multiple intervals (Supporting Information: 6). Furthermore, a nest could be included in any of the intervals in which it had not completely disappeared. Hence, we repeated the assignment of nests to particular intervals 100 times to assess the magnitude of uncertainty induced by the selection. In the Section 3, we report the average estimates across the 100 assignments and also their ranges.

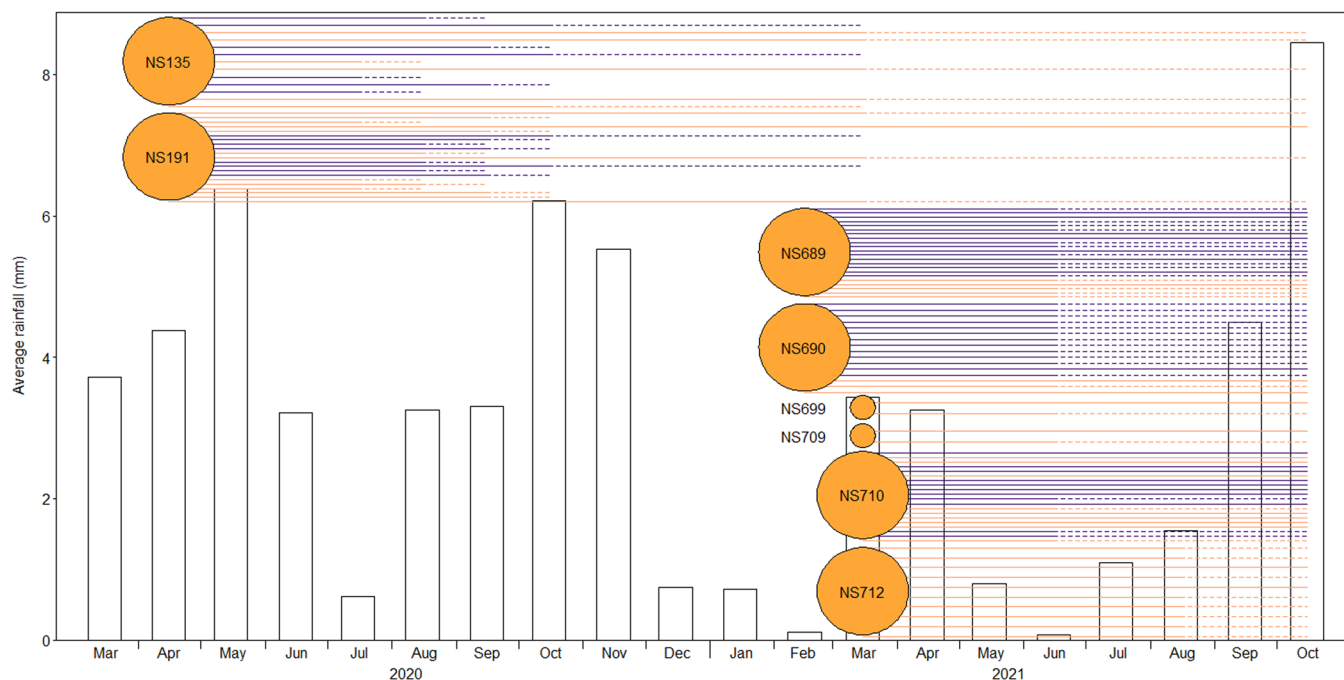
After five months, TR and GM revisited nest sites NS135 and NS191 with two experienced FAs who had not been present originally and were thus unaware of the location of the nests, to evaluate whether the “naïve” FAs were able to detect those nests. We conducted a reliability test on their each of the FAs' observations compared with those of TR, using a McNemar test (Siegel & Castellan, 1988).

After grouping the nests into the intervals described above, we created four different datasets: in data sets A ( $n = 68$  nests) and C ( $n = 70$ ), we randomly sampled a maximum of 10 nests per interval (Supporting Information: 6a,c). In data sets B ( $n = 104$ ) and D ( $n = 106$ ), we randomly sampled a maximum of 16 nests per interval (Supporting Information: 6b,d). We fitted each of the two models (the Markov and logistic regression) with these four different data sets. From each of the models, we obtained separate estimates for the mean half-lives of the tree and ground nests, the time at which half of the nests had completely decayed. For the logistic regression model, we derived confidence intervals of model estimates and fitted values using 1000 nonparametric bootstraps (10 bootstraps per assignment of nests to intervals). We evaluated the range of the confidence intervals in data sets A–D and established that data set B best represented the data (we report the results of datasets A, C, and D for both models in Supporting Information: 7–9). For each bootstrap of the logistic regression, we determined the difference between the half-lives of the ground and tree nests. To extract the one-tailed  $p$  value, we then considered how many of these differences were greater than zero.

We implemented the models using the statistical program R (version 4.1.0 or higher; R Core Team, 2022). For the model we present here (subset B), we randomly excluded three nests to achieve an even distribution of nests within the intervals. The final data set was comprised of 104 nests (55 ground and 49 tree nests) in eight nest sites.

### 3 | RESULTS

A total of 67 of the nests we studied (26 ground and 41 tree nests) were built during the wet season and 40 (30 ground and 10 tree nests) during the dry season. We were able to follow the decay of



**FIGURE 3** Visualization across time of the nest sites (NS) which we monitored from the day of their discovery, represented by the orange circles. Average daily rainfall appears across the x-axis. Red lines: ground nests; blue lines: tree nests (see Supporting Information: 2 and 5 for more details). Solid lines indicate the duration of time that a nest was visible to observers. Dashed lines indicate the time at which a nest had disappeared between revisits.

**TABLE 2** Estimated nest half-lives (means and ranges) and their confidence limits (CI) for ground and tree nests (GNs, TNs), data set B (55 ground and 49 tree nests; results of logistic regression analysis).

	Days (range)	CI lower	CI upper
GNs	238 (214–363)	215	271
TNs	276 (241–330)	246	309

71% (76/107) of the nests until they disappeared (Figure 3 and Supporting Information: 5). Lumping ground and tree nests together, the mean decay time was 200 days ( $n = 107$ ). If we only consider the nests that we actually observed to have disappeared, the mean decay time was 285 days ( $n = 76$ ).

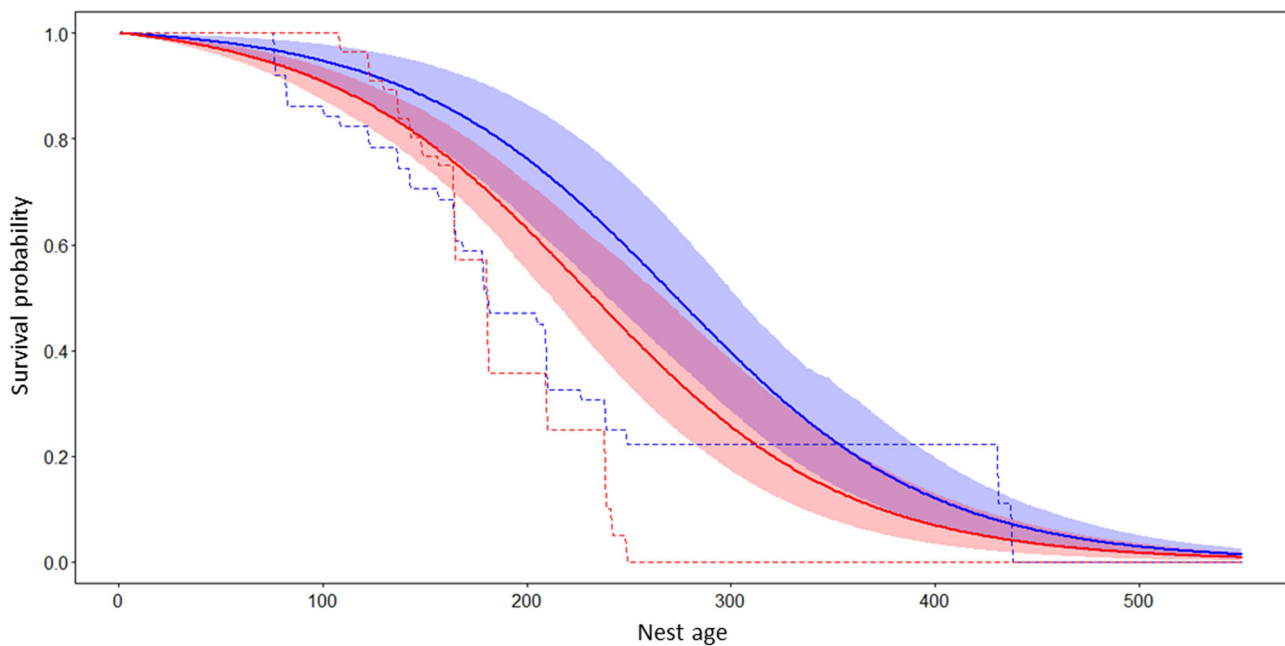
### 3.1 | Estimation of the half-lives of ground and tree nests

We have excluded the results obtained using the Markov model because this model predicted very long nest half-lives and showed a poor overall fit to the data (i.e., by the time that our empirical data showed that most of the nests had disappeared, the Markov analysis showed that approximately 30% of those nests were still present; we present the result of one simulation for the data set B in Supporting Information: 9). Based on the results of the logistic regression model, we found that the average half-life for the 55 ground nests was 238 days; for the 49 tree nests it was 276 days for (Table 2, Supporting

Information: 10 and Figure 4). This represents a difference of slightly over 1 month, which was significant ( $p = 0.05$ ).

#### 3.1.1 | Empirical evaluation of decay rates for ground and tree nests

The majority of the ground nests in this study were complex (86%) and 95% were covered by canopy. Most of the nests ( $n = 97$ ) were observed in mixed forest, except for 10 (9%) that were found in monodominant *Cynometra alexandri* and *Lasiodiscus mildbraedii* (a mix of both species) forest (NS712); out of 107 nests, we observed 8% in vine tangles and 6% on hillsides. The majority of the tree nests (77% [39/51]) were built between 2.1 and 10 m in height; with 14% (7/51) between 10.1 and 25 m in height, and 8% (4/51) between 0.51 and 2 m (Supporting Information: 12). Of the 107 nests which we monitored, 20% (11/56, Supporting Information: 5) of ground nests and 28% (14/51, Supporting Information: 5) of tree nests had disappeared within 200 days. We were only able to follow the decay



**FIGURE 4** Actual (dashed lines) and estimated (solid lines and polygons) survival probability of a nest (representing the time at which it had not yet disappeared) as a function of nest age, along with the logistic regression, depicted separately for tree nests (blue) and ground nests (red). The model depicted represents the average of the logistic models fitted to 100 assignments of nests by intervals (data set B). The colored polygons represent the 95% confidence limits of the fitted model.

of 34 nests (19 arboreal and 15 terrestrial) for more than 12 months; 24% (8/34) of these were still present after 1 year (all of which were tree nests). None of the 34 nests survived more than 18 months (Figure 3, Supporting Information: 5). The six tree nests built higher than 15 m lasted on average 158 days (range: 76–181 days), more than 4 months less than the estimated average half-life for all of the tree nests (the small sample did not allow us to test for significance).

The chimpanzees used a mix of woody plants and herbs to construct the 56 ground (Supporting Information: 3 and 11 provide a list of the plant species used). As can be seen in Supporting Information: 14, for ground nests, the most-frequently-used woody species were *Argomuellera macrophylla* (23%, 13/56), *Acalypha neptunica* (14%, 8/56), *Ocotea kenyensis* (14%, 8/56), and *Maerua* sp. (13%, 7/56). None of the nests found were predominately composed of herbs. As highlighted in Supporting Information: 13, the main species used to construct tree nests were *Maerua* sp. (25%, 13/51) and *Lasiodiscus mildbraedii* (22%, 11/51). After 300 days, 86% (6/7) of the tree nests constructed in *Maerua* sp. were still present, whereas of the 44 tree nests constructed using other species, all had disappeared, except for one tree nest built using *Trichillia martineau* (Supporting Information: 13). After 250 days, 40% (2/5) of ground nests primarily composed of *Acalypha neptunica* and 9% (1/11) of those primarily composed of *Argomuellera macrophylla* survived, whereas all of the 40 ground nests constructed using other species had disappeared by that time (Supporting Information: 14). We predicted that ground nests using more components in their construction would have survived longer. After 200 days, 58% (11/19) of ground nests using a maximum of nine sapling species survived

whereas only 26% (5/19) survived which had used between 10 and 19 components (Supporting Information: 14) (sample size was too small to conduct statistical analysis).

Taking into consideration the 34 nests from the two nest sites that we were able to revisit multiple times (NS135 and NS191; Supporting Information 15 and 16), three ground nests (20%,  $n = 15$ ) and six tree nests (32%,  $n = 19$ ) had moved from the category “rotten” to “disappeared” by the final visit, whereas all of the remaining nests still visible (12 ground and 13 tree nests) had disappeared after being categorized as “skeleton.” Two ground nests and one tree nest had disappeared after only 4 months due to a tree-fall. We determined that seven of the ground nests had changed to the age category “old” one month earlier than their accompanying tree nests. Likewise, on average ground nests changed from “rotten” to “skeleton” one month earlier than tree nests at the same sites (Table 3; the visual progression of the decay of 15 ground and 19 tree nests can be seen in photos taken at each revisit, at the following DOI:10.17632/ftkktcpmjy.1).

In only one case out of the 15 ground nests surveyed did the component leaves remain primarily green for more than two weeks (26 days). The leaves of 13 tree nests, on the other hand, remained green for up to one month. Although the leaves of ground nests sometimes began to turn brown earlier than two weeks, on the whole leaves of ground nests had transitioned to the “mostly brown” state after three months (Table 4a), while tree nest leaves had done so only after four months, having started to turn brown after one month (Table 4b). In two cases we observed that ground nests had lost all their leaves after three months, versus 10 cases for tree nests. The

**TABLE 3** The number of ground and tree nests (GN, TN) from nest sites NS135 ( $n = 13$ ) and NS191 ( $n = 21$ ) per age category and separated according to time passed since construction.

Days from construction	Age category												Total nests still present
	Fresh		Recent		Old		Rotten		Skeleton		Disappeared		
	GN	TN	GN	TN	GN	TN	GN	TN	GN	TN	GN	TN	
Up to 4 days	15	19									0	0	34
1–2 weeks			15	19							0	0	34
1 month					7	11	8	8			0	0	34
2 months							15	19			0	0	34
3 months							14	15	1	1	0	3	31
4 months							5	12	5	0	5	4	22
5 months									4	9	6	3	13
11 months									0	8	4	1	8
18 months									0	0	0	8	0

Note: See Table 1 for a definition of age categories and Supporting Information: 15 and 16 for details on each nest site.

**TABLE 4** Number of days taken to transition from green to brown leaves and then to a rotten state of the leaves in (a) ground nests (GNs,  $n = 15$ ) and (b) tree nests (TNs,  $n = 19$ ).

(a)	No. GNs	Average no. days			Min no. days			Max no. days
Mostly green	15	12			2			26
Mostly brown	15	90			14			170
Mostly rotten	12 <sup>a</sup>	121			40			326
(b)	No. TNs	Nest as viewed from bottom			Nest rim			
		Average no. days	Min no. days	Max no. days	Average no. days	Min no. days	Max no. days	
Mostly green	18	27	7	81	30	2	81	
Mostly brown	19 <sup>b</sup>	132	40	548	158	40	548	
Mostly rotten	9 <sup>c</sup>	272	90	548	269	90	548	
No leaves	11	123	49	319	123	49	319	

Note: For the tree nests we considered the view from the bottom and the rim only, as for the higher nests we judged it unsafe to climb into the canopy to evaluate the top part.

<sup>a</sup>In two cases due to a tree-fall the nests had disappeared before the leaves had decayed into the rotten brown state. In one case they had all disappeared following a period of being brown and dry ("rotten").

<sup>b</sup>In four cases the nests had lost all of their leaves when they were still brown and dry ("rotten").

<sup>c</sup>In six cases the nests had disappeared before the leaves became rotten.

leaves of tree nests survived in the "rotten" state five months longer than those of ground nests (Table 4). At the first visit, we were able to perceive chimpanzee odor in all of the ground nests except one, whereas for seven tree nests, we could not detect odor (it should be mentioned that it was more difficult to detect odor emanating from the canopy). The odor had disappeared from all of the ground nests after less than one month. Dung was present in the majority of ground nests but we found it beneath only 10 of the tree nests. In the majority of nests, most of the dung had vanished completely after 3 months. Only in one case was the dung from a tree nest still visible

after one year (due to the germinating seeds) but not recognizable after one and half years (Table 5).

### 3.2 | Reliability of naïve observers in detecting older nests

For two nest sites (NS135 and NS191), we compared the detectability of older nests (i.e., those more than 3 months old) between observers who knew the location of the nests from previous visits



**TABLE 5** State of dung in ground (GNs,  $n = 19$ ) and tree nests (TNs,  $n = 15$ ).

No. GNs	No. TNs	
2	9	None
9	8	Dung disappeared in less than 3 months
3	1	Dung disappeared in less than 5 months
1	0	Dung disappeared between 6 months and 1 year
0	1	Dung disappeared between 1 year and 1.5 years

(GM and TR) and two observers (FA) with experience finding chimpanzee nests who were not aware of their location (FA1 and FA2) (Supporting Information: 17). During our revisits approximately four months following the construction of the nests, GM was able to observe two ground nests not detected by TR, whereas GM missed five of the tree nests detected by TR. FA1 and FA2 each detected 10 of the 22 nests detected by TR that were still present at the revisit. FA1 and FA2 failed to detect, respectively, 78% and 56% of the ground nests, versus 38% and 46% of the tree nests. We found a significant difference in the detectability of nests between observers (Cochran's Q test:  $\chi^2 = 24$ ,  $df = 3$ ,  $p < 0.001$ ).

## 4 | DISCUSSION

Our results highlight the importance of including night-time ground nests in density calculations of chimpanzees in areas where these apes construct them, as well as factoring in different decay rates of ground and tree nests. As an example, in their chimpanzee nesting survey of Bili-Uéré, Hicks et al. (2014) omitted ground nests from the density estimations out of caution, which likely led to a significant underestimate of chimpanzee abundance in the region, given that 10% of the nests found were terrestrial (Romani et al., 2023). The average nest half-life at a survey region should be weighted according to the relative proportion of ground and tree nests. If possible, the half-lives of ground and tree nests should be determined on a per-site basis. These are likely site-specific and impacted by a number of factors (i.e., ground wetness, vegetation availability, seasonality and the activities of animals which can disturb nests). Our study indicates that, at least at BCFR, ground nests decay significantly more rapidly than tree nests. This pattern may not be unique to Bugoma: at Bili-Uéré, there was a significant decrease in the likelihood of finding ground nests among older nests (Romani et al., 2023), indicating that a similar pattern likely operates in Northern DRC. More work is required, however, to determine whether this pattern is common across chimpanzee, and perhaps gorilla, populations. As an example of how to apply the formula to estimate chimpanzee density in a forest where the apes construct both ground and tree nests, we use our study region (BCFR), where approx. 20% were terrestrial nests (Hobaiter et al., 2022). Thus, the term “t” (nest half-life) in the density formula described in the introduction, should be calculated by weighing the half-lives by the

percentage of ground and tree nests found ( $21\% \times 238 \text{ days} + 79\% \times 276 \text{ days}$ ), thus obtaining an average half-life of 268 days.

Across research sites, studies reporting nest decay rates (Supporting Information: 18) have reported substantial variability in nest survival times, from 46 days (range 10–161) at Budongo, Uganda (Plumptre & Reynolds, 1996) to as long as 243 days (range 217–271) at Dindéfelo, Senegal (Heinicke et al., 2019). In addition, each individual study has reported some degree of uncertainty in the range of the survival times of individual nests. As an example, at Issa Valley, Stewart et al. (2011) observed average nest survival times of 210 versus 336 days in the dry versus wet season in forested habitat, respectively. Only one study, on sympatric gorilla and chimpanzee nests, has analyzed the effects of habitat type, rainfall, nest type, and construction style on nest decay (Morgan et al., 2016). Vegetation type used in nest construction also likely plays a role: as we found in this study, the nests built by the BCFR chimpanzee using the *Omusera* tree (*Maerua* sp.) lasted longer than a year (see below).

As highlighted in Romani et al. (2023), observers may miss ground nests during surveys, especially if they do not have them in their search images. As can be seen in Supporting Information: 17, during one of the revisits, FA1 missed 87% (13/15) of the ground and 58% (11/19) of the tree nests, whereas FA2 missed 74% (11/15) of the ground and 68% (13/19) of the tree nests. Such a lack of interobserver reliability is certain to have an impact not only on our understanding of the presence or absence of ground nesting at different research sites (especially when only old nests are found), but will likely lead to underestimates of chimpanzee abundance. Inconsistencies in observations can lead to inaccurate or incomplete data that can, in turn, have detrimental effects on analysis, decision-making, and project outcomes. Taking the time to ensure interobserver reliability can help to ensure the validity and reliability of the data being collected and ultimately lead to more accurate and meaningful results. We propose that survey teams be trained to look not only in the canopy for tree nests but also on the floor for ground nests, especially in areas with known ground nesting populations of nonhuman great apes. Additional training requires additional resources, but given the importance of data reliability for accurate measurements and effective interventions (Battisti et al., 2014), we encourage research groups to prioritize and support funding for capacity building and training of in-country field-teams.

Although our sample sizes were too small to test for significance, the leaves of tree nests seemed to stay green for longer than those of ground nests. Tree nests made using *Omusera* (the vernacular name for *Maerua* sp.) appeared to last longer than those constructed using other plant species, which may be due to this tree having multiple long flexible branches that do not appear to be as easily damaged or broken during nest construction. For ground nests, the use of *Acalypha neptunica* and *Argomuellera macrophylla* appeared to positively influence nest survival. Further investigation is needed to confirm that these plant species affect the life-time of a nest.

In addition to their construction of complex ground nests, many of which are likely night nests (Romani et al., 2023),

chimpanzees are also known to make use of simple leaf cushions (Hirata et al., 1998; Romani et al., 2023), probably to rest upon during the day. These should not be used to obtain density estimates nor in studies of night-time ground nesting behavior. To complicate matters, however, both Bugoma and Bili-Uéré chimpanzees construct what we refer to as “flimsy ground nests,” which are generally flat and involve minimal arrangement of parts and little structure (Romani et al., 2023). Given that some flimsy ground nests may also be more likely to represent day nests, perhaps investigators should use only complex ground nests (many of which at Bili-Uéré were clearly night nests, see Romani et al., 2023) to calculate densities of nonhuman great apes. Although only 8 out of the 56 ground nests analyzed in this study were flimsy nests, we considered all of the nests to have been night nests, given that they were associated with tree nests (six of the eight flimsy nests were found by the FAs in the morning as the chimpanzees left the area), and 41 of them, including five flimsy ground nests, had associated dung and/or hairs.

It is important to highlight the limitations of our study. Due to the small number of nests investigated during the wet versus dry season, we were not able to control for seasonality (changes in rainfall and temperature over the year), which can influence great ape nest decay (Morgan et al., 2016). Similarly, we did not control statistically for habitat-type (all the nest sites were found in a similar forested environment), plant species used and, for tree nests, nest height (Morgan et al., 2016). These, together with other factors (e.g., position of the nest within the crown), likely also influence nest survival, and should be the focus of further investigation.

Given that some populations of all chimpanzee subspecies construct terrestrial night nests (Tagg et al., 2013), it is crucial to understand the dynamics and factors affecting possible differences in decay rates between ground and tree nests at the different research sites. The relative abundance of ground night nests is also important when comparing chimpanzee nesting habits across different populations, given that in some regions, chimpanzee nests are exclusively found in trees and in others a significant proportion is found on the ground (Hicks, 2010; Hobaiter et al., 2022; Romani et al., 2023). It is important to be aware that ground nests may decay more quickly than tree nests, and thus may be easier to miss if mostly older nests are encountered during a survey.

We hope that by providing an average nest half-life for BCFR, our findings may help achieve more accurate assessments of chimpanzee population densities in the reserve, thus providing information crucial to informing local conservation strategies. In addition, these results highlight the importance of estimating site-specific nest half-lives, as well as the potential for differences in nest decay rates of ground versus tree nests at different study sites, which will be crucial in our efforts to estimate accurate chimpanzee population abundance, as well as document differences in chimpanzee nesting traditions across Africa.

## AUTHOR CONTRIBUTIONS

**Toni Romani:** Conceptualization (equal); data curation (lead); formal analysis (equal); funding acquisition (supporting); investigation (lead); methodology (lead); validation (lead); writing—original draft (lead); writing—review and editing (lead). **Roger Mundry:** Conceptualization (equal); data curation (supporting); formal analysis (equal); methodology (equal); validation (equal); writing—original draft (equal); writing—review and editing (equal). **Gerald Mayanja Shaban:** Data curation (supporting); investigation (supporting); methodology (supporting); validation (supporting); writing—original draft (supporting). **Marek Konarzewski:** Funding acquisition (supporting); supervision (supporting); validation (supporting); writing—original draft (supporting). **Mary Namaganda:** Investigation (supporting); validation (supporting); writing—original draft (supporting). **Catherine Hobaiter:** Funding acquisition (supporting); resources (equal); project administration (equal); validation (supporting); writing—original draft (supporting); writing—review and editing (supporting). **Thibaud Gruber:** Funding acquisition (supporting); resources (equal); validation (supporting); writing—original draft (supporting). **Thurston Cleveland Hicks:** Conceptualization (equal); data curation (supporting); formal analysis (supporting); funding acquisition (lead); investigation (supporting); methodology (equal); supervision (lead); validation (equal); writing—original draft (equal); writing—review and editing (equal).

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### CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

### DATA AVAILABILITY STATEMENT

We have made the data used in this study, as well as our R script, available at the following link: Romani, T., Hicks, T. C., Hobaiteer, C., Gruber, T. (2022). Chimpanzee ground and tree nest half-lives, Mendeley Data, V1, DOI:10.17632/jfhgf47gzf.1.

### ETHICS STATEMENT

Our research on chimpanzee nesting behavior was noninvasive and based on artifacts left behind by the apes. We conducted all of our research in accordance with national and international laws regulating the protection of endangered species. All fieldwork took place under permission from Uganda Wildlife Authority, Uganda National Council for Science and Technology and with the consent of local landowners and community members. The protocol and procedures employed were ethically reviewed and approved by the Narodowe Centrum Nauki, Poland, in accordance with decision no. DEC-2017/25/B/NZ8/O2730. In addition, adherence to the principles for ethical treatment of nonhuman primates, as set forth by the American Society of Primatologists, has been observed.

### ORCID

Toni Romani  <http://orcid.org/0000-0001-8098-553X>

Catherine Hobaiteer  <http://orcid.org/0000-0002-3893-0524>

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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