Factors affecting nest height and ground nesting behaviour in Eastern chimpanzees (*Pan troglodytes schweinfurthii*) of the northern Democratic Republic of the Congo

Toni Romani\textsuperscript{a,b,*}, Sandra Tranquilli\textsuperscript{c}, Peter Roessingh\textsuperscript{d}, Steph B.J. Menken\textsuperscript{d}, Roger Mundry\textsuperscript{e,f,g}, Marek Konarzewski\textsuperscript{a,h} and Thurston C. Hicks\textsuperscript{a}

\textsuperscript{a}The Faculty of ‘Artes Liberales’, University of Warsaw, Ulica Dobra 72, 00-312 Warsaw, Poland
\textsuperscript{b}CyberTracker Italia, 33010 Osoppo, Italy
\textsuperscript{c}Little Wildlife Explorers, 82061 Neuried, Germany
\textsuperscript{d}Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, 1098 XH Amsterdam, The Netherlands
\textsuperscript{e}Cognitive Ethology Laboratory, German Primate Center, Leibniz Institute for Primate Research, Kellnerweg 4, 37077 Göttingen, Germany
\textsuperscript{f}Department for Primate Cognition, Georg-August-University, 37073 Göttingen, Germany
\textsuperscript{g}Leibniz Science Campus Primate Cognition, 37077 Göttingen, Germany
\textsuperscript{h}Faculty of Biology, University of Białystok, 15-245 Białystok, Poland

* Corresponding author; e-mail: t.romani@uw.edu.pl

Abstract – In order to achieve a better understanding of the factors that might have led our hominin ancestors to transition to a more terrestrial niche, including sleeping on the ground, we have conducted a study on the ground nesting behavior of chimpanzees (*Pan troglodytes*). Chimpanzees, like all other species of great apes, build nests in which to sleep each night, but little is known about regional differences in their nesting habits. Previously, nesting on the ground was considered typical of gorillas, but rare in most populations of chimpanzees. Using data acquired during our extensive chimpanzee nesting survey conducted between 2004 and 2013 across a > 50,000 km\textsuperscript{2} region in northern Democratic Republic of the Congo, we report a distinctive ground nesting behaviour of eastern chimpanzees (*P. t. schweinfurthii*). We have mapped the geographical distribution of ground nesting and compared its frequency at 20 survey areas on both sides of a large river, the Uele. We found that ground nests made up more than 1% of total nests at 15 of the 20 survey regions. For a subset of 16 of these regions, we utilized statistical models to investigate whether forest type and structure, as well as the abundance of carnivores and large herbivores, and the activities of humans impacted the frequency of ground nesting and nest height. We predicted that higher encounter rates of human and dangerous animal signs would be associated with lower rates of ground nesting as well as increased nest height. Overall, 10.4% of the Bili-Uéré chimpanzee nests were terrestrial, but the frequency of ground nesting varied extensively between the survey areas (0-29% of nests). The occurrence of ground nests was positively associated with denser forests (p = 0.004), herb patches (p < 0.001), light gaps (p < 0.001), Light gaps (p < 0.001), herb patches (p = 0.044), and vine tangles (p = 0.016) also had a strong negative effect on nest height. Hunting by humans had a negative effect on the probability of the occurrence of ground nests (p = 0.001) and a positive one on nest height (p = 0.013), with a similar but likely marginal effect of large herbivores on nest height (p = 0.023). In addition, the chimpanzees nested at significantly lower heights with increasing distance from roads and settlements (p < 0.001). Carnivore
encounter rates, however, had no significant impact on ground nest frequency or nest height. Our results indicate that ground nesting can no longer be considered a rare and patchily-occurring phenomenon in *Pan troglodytes*, but is instead a major component of the chimpanzee behavioural repertoire across a considerable fraction of the range of the Eastern subspecies. Our study highlights that neither the large body size of gorillas nor the taming of fire are necessary conditions for hominids to sleep overnight on the ground, even in areas inhabited by multiple species of large carnivore. Human hunting, however, appears to reduce the probability of ground nesting, or eliminate the behavior altogether.

**Keywords** – Bili-Uéré Behavioural Realm, eastern chimpanzees, ground nesting.

**Introduction**

Following the evolutionary split of hominins from the genus *Pan* between approximately 6.5 and 9.5 million years ago (Almécija et al., 2021), our ancestors gradually transitioned to a more terrestrial lifestyle. The selective pressures leading to this shift, however, remain poorly understood. By four million years ago, the genus *Australopithecus* displayed clear anatomical adaptations for bipedal walking (White and Gen, 1987; Berger et al., 2010), although the similarity of its gait to that of modern humans is still debated (Stern, 2000; Ward, 2002), and it appeared to retain some morphological adaptations for climbing (Berge, 1994). By at least two million years ago, early members of the genus *Homo* had evolved the full suite of bipedal characters present in modern humans, including a longitudinally arched foot (Berger et al., 2010, Hatala et al., 2016). Eventually, the increased terrestriality of hominins would likely have involved sleeping on the ground, perhaps in ground nests, as we see today in the genus *Gorilla* and some populations of chimpanzees (Tagg et al., 2013; Hicks, 2010). It remains uncertain how small-bodied hominins would have managed to sleep on the ground given the large number of predators living in the Pliocene (Lewis and Werdelin, 2007), some of which are suspected of preying on hominins (Berger and McGraw, 2007; Treves and Palmqvist, 2007; Isbell et al., 2018). Wrangham (2009) hypothesized that the taming of fire approximately two million years ago may have been the necessary precondition for this innovation, although direct evidence remains lacking. To speculate, perhaps when hominins began to make use of resources in more open country habitats (Finlayson et al., 2011), they faced a shortage of suitable nesting trees and thus slept on the ground, possibly even protecting themselves with *bomas* (spikey defensive structures fashioned from thorny vegetation; Isbell et al., 2018). In addition, building nests on the ground may have decreased the hominins’ visibility to large carnivores and/or hostile conspecifics (in relation to the ‘landscape of fear’ (Bleicher, 2017)), as well as saved them energy. Given that all nonhuman great apes construct night nests (Fruth and Hohmann, 1996) and that non-lithic technology is found in several species of great apes and monkeys (van Lawick-Goodall, 1968; Mannu and Ottoni, 2009), it is likely that these behaviors were characteristic of the earliest hominins as well. Understanding behavioral variation in nest-making in our closest relatives, the African great apes, should be informative about the likely range of behaviors of our ancestors and the selective pressure that might have pushed them to spend more time on the ground. Thus we have conducted a multi-regional study of ground nesting behavior in eastern chimpanzees (*Pan troglodytes schweinfurthii*) in the northern Democratic Republic of the Congo (DRC).

In the domains of tools use, gestural communication, and self-maintenance, much evidence has been amassed over the past three decades for the existence of cultural variation between populations of chimpanzees and other nonhuman great apes (e.g., in orangutans: van Schaik (2003), bonobos: Hohmann and Fruth (2003), gorillas: Robbins et al. (2016)), to a degree likely approaching that of australopithecines and early *Homo* (McGrew, 2004, 2010). Nonhuman great apes show extensive variation in their behavioural repertoires, from food choice to tool use and gestural communication, in ways that resemble human culture (McGrew, 2004, 2010; Whiten et al., 2001). With some caution, we can thus use behavioural variation in African
Factors affecting ground nesting in chimpanzees in northern D.R. Congo

great apes to triangulate the behavior of our common ancestor.

Little is known about variation in nest-building, despite the fact that it is a fundamental aspect of great ape behaviour, distinguishing them from hylobatids and monkeys; it has even been considered to represent the ‘original tool’ of hominids (Fruth and Hohmann, 1996). The construction of a nest or bed in which to spend the night is a behaviour shared by all species of great apes (Fruth and Hohmann, 1996; McGrew, 1992). These nests are also used for other activities such as grooming, play, and sex (Fruth et al., 2018). Given our close evolutionary relationship with our fellow great apes, especially the genera Pan and Gorilla (Prüfer et al., 2012; Scally et al., 2012), the study of ground nesting in these extant species can inform our understanding of hominin sleeping patterns (Koops et al., 2012b). Most populations of nonhuman great ape species, including chimpanzees, build their nests primarily in the trees (bonobos (Pan paniscus): Serckx et al. (2016), orangutans (Pongo spp.): van Casteren et al. (2012), but see Ashbury et al. (2015) for a case of one orangutan nesting on the ground). Both species of gorilla (Gorilla gorilla and G. beringei), however, frequently build night nests in both the trees and on the ground (Brugiere and Sakom, 2001; Mehlman and Doran, 2002; Sanz et al., 2007). All gorilla populations studied to date include ground nesting in their repertoire, ranging from nearly 100% of nests at Virunga, Rwanda (Sarmiento et al., 1996), and La Belgique, Cameroon (Willie et al., 2014), to 14% in Ngotto, Central African Republic (Brugiere and Sakom, 2001) and only 7.4% at Petit Loango, Gabon (Furuichi et al., 1997). The ubiquity of ground nesting in this taxon may be related to comfort or as an adaptation to keep cool on hot nights (Mehlman and Doran, 2002), or by the large size of gorillas and their greater degree of terrestriality; silverback males in particular may have difficulties finding branches capable of supporting their weight (Yamagiwa, 2001).

At the majority of sites across their range, including at many of the long-term research sites, chimpanzees prefer to nest in trees. Ground nests appear in almost all populations of chimpanzees as a very small proportion of total nests, due to the fact that old, injured, or ill chimpanzees sometimes sleep on the ground; this falls generally below 1% of total nests, as is the case in Gombe, Tanzania (van Lawick-Goodall, 1968), Kanyawara-Kibale, Uganda (R. Wrangham, pers. comm. in Hicks, 2010), Budongo, Uganda (Reynolds and Reynolds, 1965), and Comoé, Côte d’Ivoire (J. Lapuente, pers. comm., 20 July 2021). Nevertheless, it is becoming apparent that nonhuman great apes show more flexibility in where they build their nests than was previously assumed (e.g., McLennan, 2018). Earl et al. (2020) demonstrated that, in captivity, both gorillas and chimpanzees are capable of building ground nests if conditions are appropriate.

As more chimpanzee populations have been studied in recent years, researchers have documented a significant occurrence of ground nesting in some regions (supplementary table S1). Tagg et al. (2013) showed that some populations of all four chimpanzee subspecies include frequent ground nesting in their behavioural repertoire. Koops et al. (2007) proposed mate-guarding as a possible explanation for ground nesting. In order to compare the occurrence of this behaviour at different sites, we first need to agree upon a baseline condition for which a population can be considered a ground nesting one. To account for the occasional use of ground nests by sick or old individuals that likely occurs in all chimpanzee populations, we propose that only those populations with a proportion of \( \geq 1 \) % of total nests being terrestrial be considered ground nesting ones. Using this measure, ground nests are common at only 19% (3/16) of the habituated chimpanzee populations listed in supplementary table S1 (this table is limited to sites for which we have reliable information).

It is difficult, however, to assess whether the structures that researchers at different sites have described as ground nests are consistent with one another. For example, at Tai Forest, Boesch (1995) documented a number of what he termed ‘day nests’ made on the ground, but it is unclear what percentage of total nests these are, and if they might more properly be referred to as...
'leaf cushions' (i.e., plants placed on the ground and sat on without any arrangement; Hirata et al., 1998). As another example, at Haut Niger, Guinea, Fleury-Brugiere (2002) did not mention ground nests, but they included a photograph of an old one. Consequently, it is unknown whether some of the 1074 nests they mention might have been terrestrial. These examples highlight the difficulty in interpreting the published data as to the presence or absence of ground nests at a particular site.

Although some studies have focused on the structural details of tree nests (e.g., Humle, 2003; Stewart et al., 2018), as well as the influence of habitat type in the context of hominin nesting sites (Hernandez-Aguilar, 2009), very little comparative work has been conducted on the construction styles of chimpanzee ground nests, nor of the raw materials used to build them. Some evidence suggests, however, intersite variability in ground nest construction styles. For example, at two sites in Senegal, Fongoli (Stewart, 2011b) and Bagnomba Hill (Badji et al., 2018), researchers documented ground nests made of elephant grass (Andropogon sp.). Such nests were never found in the current study in northern DRC, despite the fact that savanna grass was abundant, including species of the genus Andropogon (Hicks, 2010). No ground nests were found at Ishasa (DRC), despite abundant elephant grass (J. Sept, pers. comm., 19 July 2021). Of course, such differences in vegetation choices may reflect differences in availability or abundance of construction materials.

An important aspect of any study of ground nests is to define what a ground nest is used for and how it is constructed, especially given that their definition varies between studies. With habituated chimpanzees, it is often possible to observe directly whether a ground nest is made during the day for resting or in the evening for sleeping at night (e.g., at Bulindi, Uganda, M. McLennan (pers. comm., 1 September 2022) observed a pregnant chimpanzee making a ground nest to rest in during the day). For non-habituated subjects, however, researchers must infer how the nest was used based on the presence of other nests, as well as dung, hairs, and urine (Hicks, 2010), or, if they are lucky, by encountering the chimpanzees at their nest groups in the early morning or observing them resting in day nests. To compound the confusion, at a number of sites, chimpanzees also sometimes sit on leaf cushions. This is the case at Kibale (Kanyawara), Uganda (R. Wrangham, pers. comm., 18 January 2010 in Hicks, 2010), and Kalinzu, Uganda (Furuichi and Yashimoto, 2000), Bossou, Guinea (Hirata et al., 1998), Taï, Côte d’Ivoire (Boesch, 1995), Goualougo, the Republic of Congo (Sanz and Morgan, 2007), as well as at Tenkere, Sierra Leone, in the latter case to protect themselves from thorns (Alp, 1997). At some research sites, it is not clear that these are categorized separately from ground nests, as we do here.

Another problem arises from a failure of researchers to observe ground nests, perhaps because the structures are not included in their ‘search image’. This can be the case especially during nesting surveys, where ground nests may be missed by surveyors who keep their eyes in the canopy scanning for tree nests.

Finally, another difficulty is that at some research sites where gorillas and chimpanzees share the same forest, distinguishing ground nests made by the two species is difficult (e.g., in Petit Loango, Gabon (Furuichi et al., 1997), Ngotto, Central African Republic (Hicks et al., 2009), and Goualougo, the Republic of Congo (Sanz et al., 2007)). This is, however, not an issue in the current study, as gorillas do not occur at Bili-Uéré.

HYPOTHESES PROPOSED TO EXPLAIN GROUND NESTING IN CHIMPANZEEs

Ground nesting represents a divergence from what is considered the ‘standard’ and likely ancestral arboreal nesting behaviour in chimpanzees, and a number of hypotheses have been postulated to explain its occurrence (table 1). Here, we briefly review those tested in the current study.

Ecological factors (seasonality, climate, elevation above sea level, and vegetation availability) may play a role in the frequency of ground nesting or nest height. Pruetz et al. (2008), for example, found that chimpanzees built their
Table 1. Hypotheses postulated to explain the occurrence of ground nesting behaviour in chimpanzees.

<table>
<thead>
<tr>
<th>Category</th>
<th>Specific factor</th>
<th>Prediction</th>
<th>Supporting evidence</th>
<th>Counter evidence</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ecology and environment</td>
<td>Seasonality</td>
<td>Dry season = ↑ GNs (in seasonally-flooded forests less ground is available for nesting during the wet season)</td>
<td>At Bili, DRC, where the gallery forests are often seasonally flooded, GNs were significantly more common during the dry season, but only when considering fresh and recent nests.¹ At La Belgique, Cameroon, GNing occurred significantly more frequently during the dry season.² At Andu, Cameroon, more GNs were found during the wet season.⁵ GNs made in swamps are likely less detectable by humans, thus GNs may be undercounted in the wet season.⁶</td>
<td>At several sites, season had no effect on the proportion of GNs.⁴⁻⁷</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Wet season = ↑ GNs</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elevation above sea level</td>
<td>↑ altitudes = ↑ GNs</td>
<td>GNs at Yealé, Côte d’Ivoire, were more common at higher altitudes (possibly to allow the chimpanzees to avoid strong winds).⁷</td>
<td></td>
<td>GNs are common at Bili-Uégré¹, which lies at a much lower altitude than Nimba.</td>
</tr>
<tr>
<td></td>
<td>↓ altitudes = ↓ GNs</td>
<td>GNs were more commonly found in riparian forest and in swamps in the Budongo-Bugoma corridor.⁶ At Seringbara, Guinea, they occurred at lower altitudes during the dry season when there were stronger winds.⁴</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Climate</td>
<td>↑ humidity/temperature = ↓ GNs</td>
<td>At Seringbara, Guinea, higher humidity and daily temperature resulted in fewer GNs.⁸</td>
<td></td>
<td>–</td>
</tr>
<tr>
<td>Availability of vegetation</td>
<td>Lack of suitable trees or ↑ abundance of preferred GNing materials = &gt; GNs</td>
<td>↑ GNs occur where suitable nesting trees are rare⁷⁻⁹ or in swamps next to settlements.²⁻⁶ In the Budongo-Bugoma corridor, reduced availability of trees may explain the presence of GNs.⁶</td>
<td>Researchers found no clear impact of tree density on GN frequency.³⁻⁴</td>
<td></td>
</tr>
</tbody>
</table>
### Table 1. (Continued.)

<table>
<thead>
<tr>
<th>Category</th>
<th>Specific factor</th>
<th>Prediction</th>
<th>Supporting evidence</th>
<th>Counter evidence</th>
</tr>
</thead>
<tbody>
<tr>
<td>Human impact</td>
<td>Human pressure</td>
<td>Hunting pressure and/or human activity = ↓ GNs</td>
<td>Areas with fewer hunting signs were associated with more GNs.¹-⁵</td>
<td>↑ GNs were found near settlements (Budongo-Bugoma corridor)² and in association with higher levels of human activity (La Belgique).²</td>
</tr>
<tr>
<td>Dangerous fauna</td>
<td>Predators</td>
<td>↑ Density of carnivores = ↓ GNs</td>
<td>GNs have been found at multiple sites lacking potential predators.³</td>
<td>GNs have been found at some sites inhabited by large carnivores.¹-²⁻⁸⁻¹⁰</td>
</tr>
<tr>
<td></td>
<td>Large herbivores</td>
<td>↑ Density of large herbivores = ↓ GNs</td>
<td>GNs have been found at sites lacking large herbivores.⁴</td>
<td></td>
</tr>
<tr>
<td>Parasites</td>
<td>TNing is an anti-malaria (Plasmodium sp.) adaptation, thus ↓ parasites = ↑ GNs</td>
<td>At Toro-Semliki, Uganda, and Fongoli, Senegal, nest height¹¹⁻¹²⁻¹³ and the use of anti-mosquito vegetation¹³, were correlated with a low density of vectors. At Fongoli, Senegal, higher mosquito densities on the ground¹² suggests that fewer GNs should be found.</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

¹-²-³⁻⁸⁻¹⁰-¹²-¹³
<table>
<thead>
<tr>
<th>Category</th>
<th>Specific factor</th>
<th>Prediction</th>
<th>Supporting evidence</th>
<th>Counter evidence</th>
</tr>
</thead>
<tbody>
<tr>
<td>Genetic and morphological</td>
<td>Differences in body size</td>
<td>↑ body size = ↑ GNs</td>
<td>Large-bodied apes may require more stable nests. Groves argued that the Bili-Uéré chimpanzees, who frequently make GNs, may differ morphologically from other populations of the species.</td>
<td>For most GNing populations, there is no evidence that the chimpanzees are larger than elsewhere.</td>
</tr>
<tr>
<td>Genetics</td>
<td>Genetic differences between populations or subspecies may lead to higher propensities for making GNs in some populations</td>
<td>Genetic differences between populations or subspecies may lead to higher propensities for making GNs in some populations</td>
<td>Genetic differences between populations or subspecies may lead to higher propensities for making GNs in some populations</td>
<td>Genetic differences between populations or subspecies may lead to higher propensities for making GNs in some populations</td>
</tr>
<tr>
<td>Category</td>
<td>Specific factor</td>
<td>Prediction</td>
<td>Supporting evidence</td>
<td>Counter evidence</td>
</tr>
<tr>
<td>---------------------</td>
<td>-------------------</td>
<td>-----------------------------------------------------------------------------</td>
<td>--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------</td>
<td>-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>Social and cultural</td>
<td>Mate-guarding</td>
<td>GNing is a mate-guarding strategy; GNs are mostly built by males in association with estrus females</td>
<td>65% of GNs at Seringbara, Guinea, were made by adult males, with only 9% made by adult females (sex was not determined for 26% of the GNs), and were most likely to be found in association with TNs made by estrous females.⁴</td>
<td>At Seringbara, females also made some GNs.⁸ In Koops and colleagues’ follow-up study, no support was found for the mate-guarding hypotheses, as the majority of the males who made GNs were maternally related to the tree nesting individuals (or they were possibly the same individuals).</td>
</tr>
<tr>
<td>Culture</td>
<td>GNing is a socially-transmitted behavior that varies between populations. Cultural differences are more likely when ecological, seasonal and other factors are ruled out. If connected chimpanzee populations are ground nesters despite differing habitats, diffusion of culture is a likely explanatory factor</td>
<td>The fact that GNs occur across all of northern DRC despite notable differences in habitat-types between the different areas is at least consistent with culture.¹⁷ In addition, these chimpanzees are genetically similar to other populations of eastern chimpanzees who are not known to be GNers.¹⁶</td>
<td>It is difficult to rule out ecological differences between study sites¹⁴ in available vegetation, human and carnivore pressure, parasite density etc., as well as the impact of genetic or morphological factors.</td>
<td></td>
</tr>
</tbody>
</table>
nests significantly higher during the wet season at Fongoli. At their respective sites in northern DRC and Cameroon, Hicks (2010) and Tagg et al. (2013) reported that chimpanzees made more ground nests during the dry season. Differences in elevation (Matsuzawa and Yamakoshi, 1996), forest type, and forest structure (Tagg et al., 2013) may also influence whether chimpanzees build ground nests.

Human activities such as hunting, agriculture, and logging likely also affect the frequency of ground nesting, but this is complex and may be linked to differences in the relationships between chimpanzees and humans at different research sites (for examples of some of these differing patterns of interaction, see Hicks et al., 2012 and McLennan and Hill, 2010). In addition, van Dijk et al. (2021) observed that at Bulindi, western Uganda, chimpanzees nested at lower heights after a substantial portion of their forest had been cleared for agricultural fields. Tagg et al. (2013) found a higher frequency of ground nesting with increased human encounter rate, whereas Hicks (2010) and Last and Muh (2013) found the opposite. Chimpanzees in western Uganda preferred to build ground nests in swamps, likely in order to avoid detection by humans (McCarthy et al., 2017).

At some research sites, ground nesting may be favored by a lack of large carnivores (e.g., Fongoli, Senegal: Pruetz et al. (2008), Seringbara, Côte d’Ivoire: Koops et al. (2012a)) and potentially large dangerous animals like elephants, but this is not always the case (Hicks, 2010). Absence of predators and large herbivores is, however, often a result of human hunting, and it is thus difficult to disentangle the effects of these factors.

The final factor that might explain ground nesting is culture, defined as ‘a behavior that is transmitted repeatedly through social or observational learning to become a population-level characteristic’ (McGrew, 1992). Ground nesting as a socially-transmitted behavior may explain the scattered distribution of the phenomenon in chimpanzees (Hicks, 2010). If we can rule out the potential impact of genetic, morphological, or ecological factors (see table 1) as well as of humans and other fauna on ground nesting, then the ‘method of exclusion’ (Whiten et al., 2001) would make the cultural explanation more likely. This can be a challenge, however, as most primate behavior is shaped by a complex mix of genetic, ecological, and social influences (McGrew, 1992; Whiten et al., 2001).

GROUND NESTING IN THE CHIMPANZEES OF NORTHERN DEMOCRATIC REPUBLIC OF THE CONGO

The frequent construction of complex ground nests by chimpanzees has now been documented at multiple areas in northern DRC (Hicks, 2010), as well as approximately 500 km to the southeast at Epulu (Hart, unpubl. data; Hicks, unpubl. data), and along the border with Uganda in the Relict Altitude Forest Fragment of the Albert Lake Escarpment (RAFALE) (A. Laudisoit, pers. comm., 20 September 2021). They also occur just across the border at Bugoma, Uganda (Hobaiter et al., 2022). Frequent ground nesting thus represents a potential large-scale behavioural variant (Hicks et al., 2019a).

In order to better understand the distribution of chimpanzee ground nesting across the Bili-Uéré landscape in northern DRC, we used data collected by Thurston Hicks (TH) and team over a 9-year period from 20 survey areas to map the proportion of ground nests out of total nests. We then used data collected at 16 of these survey areas to investigate the impact of the factors detailed below on the frequency of ground nesting behaviour across the region, as well as the height at which chimpanzees built their nests (see a map of the surveyed area in supplementary fig. S1, as well as Hicks et al. (2014, 2019a and 2020) for more details).

HABITAT-TYPE AND SEASONALITY

We investigated whether ecological factors such as seasonality and rainfall had an impact on the frequency of chimpanzee ground nesting and nest height in northern DRC. We also examined whether forest type, structure, and density influenced the likelihood of a nest being a ground nest, as well as nest height. We predicted that ground nests would make up a
larger proportion of nests during the dry season, as was found at Dja, Cameroon (Tagg et al., 2013; see also Hicks, 2010). This we considered to be especially likely given that during the dry season in northern DRC, many swamps and streambeds dry up completely, thus leaving more ground available for nesting (Hicks, 2010). Due to the fact that chimpanzee ground nests have been documented in a variety of habitats and altitudes (e.g., swamps (McCarthy et al., 2013), and mountain slopes (Koops et al., 2012)), we had no specific predictions about the impact of forest structure and density on ground nesting and nesting height.

**CARNIVORES AND LARGE HERBIVORES**

Chimpanzees are known across Africa to fall prey to large carnivores such as leopards (*Panthera pardus*) (Boesch and Boesch-Achermann, 2000) and lions (*Panthera leo*) (Tsukahara, 1993). Based on their known danger to humans, hyenas (*Crocuta crocuta*) represent a potential predator as well. All three carnivores are present in northern DRC (see Materials and methods). Large herbivores such as forest buffaloes (*Syncerus caffer nanus*) and African forest elephants (*Loxodonta cyclotis*) are potentially dangerous to chimpanzees, as they are to humans, and these species are present at multiple sites in northern DRC (Hicks, 2014). We hypothesized that increased abundance of these large mammal species would dissuade chimpanzees from nesting on the ground and encourage them to nest higher in the trees. We hence tested whether the encounter rates of large carnivores and herbivores affected the frequency of chimpanzee ground nesting as well as nest height at the 16 survey areas.

**HUMAN IMPACT**

Human disturbance is known to affect the behaviour of nonhuman great apes (e.g., orangutans (van Schaik, 2002), chimpanzees (Hicks et al., 2013; Kühl et al., 2019; Tédonzong et al., 2020). Hicks (2010) reported a negative impact of human hunting on ground nesting in northern DRC, and this was also observed at Lebialem-Mone, Cameroon (Last and Muh, 2013). We thus predicted that increased levels of human impact and close proximity to roads would reduce the occurrence of ground nesting as well as lead to an increase in nest height.

**Materials and methods**

**THE STUDY REGION**

Over a total non-consecutive period of 41 months between 2004 and 2013 (see supplementary table S2 for details), TH and coworkers conducted surveys for chimpanzees and other mid-to-large-sized mammals across an approximately 50,000 km² region in northern DRC. These surveys took place in 20 areas between the Tele River in the south and the Mboomu River in the north with the towns of Bondo and Bambesa representing the western and eastern limits, respectively (supplementary fig. S1). This area was bisected by a major river, the Uele. Eight of the survey areas were to the north of the Uele River and 12 were to the south. Survey regions were relatively cohesive geographic areas, separated from other sites by roads, rivers, or settlements, and generally sharing the same major habitat type. In three cases (Akuma-Yoko, Nawege-Zaza and multiple locations at Bili South), because satellite maps revealed them to be connected as a unit and relatively homogeneous, we combined geographically separate forest regions to achieve an adequate sample size. Conversely, for analysis we separated two adjoining areas in the Bili-Gangu area because their predominant habitat types differed substantially: Camp Louis is mostly composed of savanna, savanna-woodland and regenerating forest, whereas Gangu is made up of mostly old growth moist tropical forest, drier to the north of the Gangu River and more seasonally flooded to the south. Given the complex farmland-forest mosaic nature of Bambesa, the region was counted as one unit (Hicks et al., 2019a).

We found chimpanzee nests in all of the surveyed regions (Hicks et al., 2014). The chimpanzee population appeared to be continuous across the area. The chimpanzees were unhabituated, and in most of the regions they were fearful of humans, likely due to heavy hunting.
Factors affecting ground nesting in chimpanzees in northern D.R. Congo

pressure (Hicks et al., 2010, 2012). The exception was the Gangu Forest, where human pressure was very low (see supplementary table S3), and the chimpanzees behaved in a naïve way towards researchers. In the Camp Louis Forest, we estimated the density of weaned chimpanzees per km² to be 0.46-1.43, and as high as 1.01-2.95 in the Gangu Forest. The population was stable between 2005 and 2012 (Hicks et al., 2014). Nest encounter rates were comparable across the entire region surveyed, and the chimpanzees shared elements of a single widespread material culture (termite mound and snail pounding, lack of tool-assisted predation on termites of the genus *Macrotermes*, frequent ground nesting and the use of tools to prey on epigaec *Dorylus* and ponerine ants (Hicks et al., 2019a, 2020)).

Hicks (2010) and Hicks et al. (2019a) provide detailed descriptions of the climate across the Bili-Uéré region, using data their team collected at several sites as well as from the historical record. Annual rainfall is similar across the region (1652 mm at Hicks’ weather station at Aketi vs 1644 mm at Tukpwo further north (Gerard, 1960), with a wet season lasting from April to November. The seasonality of rainfall was more extreme to the north (Hicks, 2010): during two dry seasons at Bili, for instance, no rain fell and streams that had been over two meters deep during the wet season dried up completely.

The predominant habitat to the north of the Uele River was a mosaic of savanna woodland and moist tropical forest intersected by large patches of open grassland (Hicks, 2010). The forests and savannas were interlaced with streams; in the grasslands, these were surrounded by gallery forests. The moist tropical forest to the south of the Uele River lacked savannas. Mono-dominant stands of *Gilbertiodendron dewevrei* were present but rare to the north of the Uele and occurred more extensively along streams to the south (Hicks, 2010). Near settlements and alongside roads across the region, slash-and-burn agriculture had created large areas of farmland and regenerating forest, characterized by oil palms (*Elaeius guineensis*), introduced species of bamboo such as *Bambusa vulgaris* and, at a later stage of succession, stands of *Musanga cecropioides*.

We found leopard traces on both sides of the Uele River (Hicks, 2014). We encountered evidence (encounters, scats, and tracks) of hyenas and (more rarely) lions only to the north of the Uele River (supplementary table S3; Hicks, 2010, 2014). Forest elephants and buffaloes occurred in a patchy distribution across the survey region, with both species being more common to the north than the south (supplementary table S3), where they were absent at a number of sites, likely due to human hunting (Hicks, 2010; Hicks et al., 2019b). As reviewed in Hicks (2010), the human population density to the south of the Uele River was roughly triple that in the north. Artisanal mining for diamonds and gold was concentrated in the south, especially in proximity to the city of Buta. On our surveys, we found much higher encounter rates of human activities to the south than to the north of the Uele River (10.2 times higher for hunting evidence and 6.4 times higher for other human signs). Camp Louis, Gangu, and Leguga had the lowest human encounter rates, whereas Mbane West, Ngume, and Zongia had the highest (supplementary table S3). Gangu was the only region in which we surveyed distances >15 km from the nearest road or settlement, up to 41.8 km. Prior to 2007, Gangu had lower human encounter rates than Camp Louis (0.07 vs. 0.09 signs per km walked (Hicks et al., 2013), and for both of these areas, the majority of human signs were limited to a few old, abandoned mining pits. At Gangu, we found these pits only on the eastern edge of the forest; deeper inside, the forest was nearly pristine.

In 2007, there was a rapid incursion of thousands of gold miners into the formerly isolated Gangu area in the north, leading to a 4-year disruption of research in the area. During this time, elephant densities plummeted in the Gangu Forest, and in 2011, researchers encountered a bushmeat camp in Gangu with a chimpanzee carcass (Hicks, 2014). TH and team also documented such disturbances upon their return to the area in 2012, with recent hunting and fishing camps present in both Camp Louis and
Gangu, and abundant signs of elephant poaching (Hicks, 2014). This led to an increased number of human signs observed in Gangu, compared to Camp Louis. Between 2005 and 2012, however, Hicks et al. (2014) found no significant change in chimpanzee nest encounter rates in the Gangu and Camp Louis regions, indicating that no population decline had occurred, and this continued to be the case during surveys in 2016 and 2019 ([Funk et al., 2022]). South of the Uele River, Hicks et al. (2010) documented a thriving market for bushmeat, including chimpanzee meat and infants.

SURVEYS

During our Bili-Uéré surveys, we collected data on nesting behaviour (Hicks et al., 2019a), as well as encounter rates of humans and other mammalian species (Hicks et al., 2013; Hicks, 2014). Our surveys consisted of reconnaissance forest walks, generally following the path of least resistance and actively searching for chimpanzees (recces: 2627.1 km to the north of the Uele River and 476.7 km to the south). In 2005, to collect data on chimpanzee nest encounter rates, we conducted 160 km of line transects through the Camp Louis-Gangu regions (consisting of three parallel lines randomly placed on the map, separated from one another by 4 km), and repeated 26 km of these in 2012. In 2012, we conducted an additional 45 km of line transects in the Bambilo and Dume areas (supplementary fig. S1). In addition to nests, we recorded data (dung, prints, sightings) on carnivores and other mid-to-large herbivores as well as signs of human presence and impact, including agriculture, hunting, and mining (for more details on the methodology of these surveys, we refer the reader to supplementary tables S2 and S3, Hicks (2010, 2014), Hicks et al. (2013, 2019a)). The use of recces may have led to a bias in nest encounter rates, but this is of little concern given that the focus of this paper is on the proportion of ground nests to total nests, not chimpanzee density (see Discussion).

CHIMPANZEE NEST SURVEYS

We recorded GPS points for all chimpanzee nest groups encountered on both recces and line transects. We excluded from our encounter rates any nests to which we had been led by local guides who had encountered them prior to the surveys. We considered nests as belonging to the same group if they were of the same age (age categories adapted from Tutin and Fernandez (1984): fresh, recent, old, and rotten, with the addition of skeleton for old nests with only leafless branches remaining). We refer to nest aggregations of the same age and within 20 m of one another (Tutin and Fernandez, 1984; Furuichi et al., 1997; Blom et al., 2001; Dupain et al., 2004; Kouakou et al., 2009) as ‘nest groups’. This threshold distance has varied between studies: 30 m (Furuichi and Hashimoto, 2000; Humle, 2003; Dupain et al., 2004; Koops et al., 2012b; Tagg and Willie, 2013; Tagg et al., 2013), 50 m (White and Edwards, 2000; Morgan et al., 2006; Hicks et al., 2009), and 100 m (Stewart and Pruetz, 2013; Badji et al., 2018). Hicks and the other observers on his team estimated nest height by eye, following a period of training together. We recorded for each nest whether it was covered by canopy (fully or partially) or open to the sky, in addition to habitat type and whether or not feeding remains, chimpanzee dung, hair, or urine were present. We considered a nest to be a ground nest when its height was ≤50 cm above the ground (for details on the definition of nests at different research sites, see additional data 1 of the online repository), including when a nest at this height had been built on a root or fallen tree with no open space between it and the ground. We consider 50 cm a reasonable cut-off point, as any nest constructed higher than this would likely have required the chimpanzee to climb up off the ground. In a few cases, although components of old ground nests had over time sprung up >50 cm, when they were reconnected as they had originally been, we could verify that the nests had touched the ground.

We categorized ground nests according to the degree of complexity of their construction as flimsy or complex. Complex ground nests involved the use of multiple components (branches, vines and/or herb samplings) woven together into a complicated structure,
Factors affecting ground nesting in chimpanzees in northern D.R. Congo

often in a circular bowl shape. ‘Flimsy’ ground nests involved minimal arrangement of multiple parts, lacking interweaving of branches and/or herbs, usually flat and with little discernable structure (although often roughly circular in shape). The latter possibly represent ‘day nests’ used for resting or feeding, as described for the Taï Forest by Boesch (1995). We also documented a previously undescribed nest type: half ground nests, a subcategory of complex ground nest constructed in a half-circle shape, often with the built side raised like a chair back (fig. 1). We also documented leaf cushions, which are not ground nests but consist of one or more leaves or branches simply placed on the ground with no arrangement or construction (fig. 1 and Hirata et al., 1998). Given the possibility that leaf cushions or flimsy ground nests may be used for different purposes than complex ground nests, and thus might show different patterns of usage and wear, we recorded data on dung, hair, and feeding remains associated with these artifacts.

FAUNA

Following Hicks et al. (2013), in order to assess the effect of the abundance of carnivores and large herbivores on the likelihood of chimpanzees building ground nests, on our forest walks we systematically recorded direct sightings as well as dung, tracks and feeding remains of all mid-to-large-sized mammal species. See supplementary table S3 for the number of kilometers walked per species.

HUMAN ACTIVITIES

In order to compare the impact of human activities on chimpanzees in the different regions, we systematically recorded observations of human evidence along the transects and recce, following the methodology used by Hicks et al. (2013). ‘Hunting evidence’ includes bushmeat carcasses or skins, hunting camps, snares, and cartridges as well as gunshots heard or hunters encountered, while ‘Other human evidence’ refers to cultivated fields, footpaths, mining camps, fishing huts, graffiti, signs of fishing and honey collection, machete cut marks, encounters with unarmed people, and any other direct or indirect signs. Some of these categories, such as mining, were likely associated with hunting as well (Hicks et al., 2010).

HABITAT TYPE AND FOREST DENSITY

Following Hicks et al. (2013), in order to assess the impact of forest density on ground nesting, we categorized forest into dense (visibility ≤ 1 m), medium (visibility > 1 m, but ≤ 5 m), and open (visibility > 5 m). In addition, based on Gerard (1960), Doumenge (1990), and Hicks (2010), we grouped habitat types into the categories listed in tables 2 and 3, and supplementary table S4.

STATISTICAL ANALYSES

We fitted two statistical models to test the impact of the environmental and faunal-related factors detailed below on the proportion of ground nests out of total nests. We then reran the same models with nest height as the response variable. We did not include leaf cushions in these analyses, since they were likely only used to be sat upon during the day (see online repository additional data 2 for a description of the leaf cushions found at Bili-Uéré). For the two models, we included only 16 of the 20 survey areas, omitting Difongo, Dume, Membulu, and Bambilo. Although the nest encounter rates were accurate for these areas, we lacked data for one or more of the predictors.

MODEL 1: FACTORS IMPACTING THE LIKELIHOOD OF A NEST GROUP CONSISTING OF GROUND OR TREE NESTS

In our first model, we evaluated the impact of ecological and human impact factors on the likelihood that a nest group consisted of ground nests or tree nests. Originally, we aimed to fit this model on the level of the individual nests. In the majority of nest sites, however, either all or none of the nests were a ground nest. As a consequence, the corresponding model revealed an extreme estimate for the random intercepts effect of nest group, which led to various issues with regard to the estimation of the fixed effects. More precisely, for most of the
estimates the model revealed identical and also very small standard errors. As a consequence, almost all p-values were unrealistically small. As it seemed likely to us that this was caused by the extremely large random intercept effect of the nest group, we omitted the 80 groups containing both ground and tree nests together (7% of the nest groups). We also omitted an additional 63 nest groups in which our four categorical predictors (presence of vine tangle, herb

Figure 1. (A) Fresh chimpanzee tree nest in the Gangu Forest, North Uele, January 2007 (accompanied by a Cercopithecus ascanius). (B) Local guide Chipula with a freshly-constructed complex ground nest made of herbs in the Zapay Forest, North Uele, December 2006. (C) Old complex ground nest made of herbs in the Mbange East Forest, January 2008. (D) Half ground nest, Gangu Forest, North Uele, September 2012. (E) Flimsy ground nest, Gangu Forest, January 2007. (F) Leaf cushion, Mbange East Forest, March 2008.
Factors affecting ground nesting in chimpanzees in northern D.R. Congo

Table 2. Definitions of habitat types used for nesting by chimpanzees.

<table>
<thead>
<tr>
<th>Habitat Type</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Active field</td>
<td>An active agricultural field, usually in the context of slash-and-burn agriculture.</td>
</tr>
<tr>
<td>Subcategories: field edge; oil palm plantation</td>
<td></td>
</tr>
<tr>
<td>Old field/Regenerating forest</td>
<td>An abandoned field, often dominated by oil palms, bamboo stands, and the colonizing tree <em>Musanga ceccropiodes</em>; the forest may be partially regenerated.</td>
</tr>
<tr>
<td>Subcategories: abandoned field; <em>Musanga grove</em></td>
<td></td>
</tr>
<tr>
<td>Secondary forest</td>
<td>Forest recovering from previous human exploitation or fire.</td>
</tr>
<tr>
<td>Mixed forest</td>
<td>Primary forest with mixed species of trees and little evidence of recent human intervention.</td>
</tr>
<tr>
<td>Subcategories: clearings</td>
<td></td>
</tr>
<tr>
<td>Riparian forest</td>
<td>Forest lining a stream. Subcategories: <em>stream bed</em>; <em>stream-edge</em></td>
</tr>
<tr>
<td>Swamp forest</td>
<td>Forest associated with extensive swamp (deep mud and, in the wet season, water).</td>
</tr>
<tr>
<td>Subcategories: flooded swamp; swamp edge; vine tangle swamp</td>
<td></td>
</tr>
<tr>
<td>Savanna-associated habitat</td>
<td>Open grassland, savanna woodland, and intermediate stages of the two.</td>
</tr>
<tr>
<td>Subcategories: savanna associated forest; savanna woodland; savanna edge</td>
<td></td>
</tr>
<tr>
<td><em>Gilbertiodendron</em></td>
<td>Mono-dominant forest composed of <em>Gilbertiodendron dewevrei</em>, often found alongside stream banks. In some cases, this tree can be found in mixed forests as well.</td>
</tr>
<tr>
<td><em>Laccosperma</em></td>
<td>Mono-dominant thickets composed of <em>Laccosperma</em> spp., often found in swampy areas.</td>
</tr>
</tbody>
</table>

For the analysis we included a total of 20 subcategories, which we have grouped here into major habitat types.

Table 3. Definitions of the additional categories of habitat types which we included as fixed effects in Models 1 and 2.

<table>
<thead>
<tr>
<th>Habitat Type</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hillside</td>
<td>Forest on the side of a hill, with a slope of &gt;10 degrees.</td>
</tr>
<tr>
<td>Light-gap</td>
<td>An area with &gt;10 m² of the forest floor exposed to direct sunlight due to a gap in the canopy.</td>
</tr>
<tr>
<td>Herb-patch</td>
<td>An open area of &gt;10 m² dominated by herbaceous vegetation instead of trees, often found in a light gap or in a swamp.</td>
</tr>
<tr>
<td>Vine tangle</td>
<td>A &gt;10 m² area of forest ensnarled with a dense, nearly impenetrable network of vines.</td>
</tr>
</tbody>
</table>

patch, light gap, and hill side) and forest density varied between nests at the same nest site. We then averaged the other predictors per nest group and considered as the response whether we found only tree nests or only ground nests at the nest site.

In order to estimate the effects of forest density, habitat type, forest structure (operationalized as ‘yes’ or ‘no’ for each of hillside, herb patch, and light gap; see table 4), distance from roads, encounter rates of human hunting and ‘other activities’ signs, and encounter rates of carnivore, buffalo and elephant signs (the latter two pooled; see below) on the likelihood of a nest group consisting of ground nests, we used a Generalized Linear Mixed Model (GLMM (Baayen, 2008), Model 1a) with binomial error structure and logit link function (McCullagh and Nelder, 1989). We included all of the above-mentioned predictors, with the exception of habitat type, as fixed effects (supplementary table S5). Given that ‘habitat type’ had multiple levels, we included this factor as a random intercept effect to control for its potential impact (for details, see table 2, supplementary table
S5, and additional data 3 of the online repository). Given that we expected that predation threat from large carnivores might have a different effect on ground nesting than that of accidental encounters with elephants and buffaloes, we separated large herbivores from carnivores. We pooled elephants and buffaloes as ‘large, potentially dangerous herbivores’ because both can be dangerous to humans, and we reasoned that they would also likely represent a threat to chimpanzees they encountered sleeping on the ground.

Generally, the forests in northern DRC are seasonally-flooded, which means that the chimpanzees likely have more dry ground available for ground nesting during the dry season. This initially led us to consider seasonality as a predictor of the likelihood of a nest group consisting of ground nests. A visual inspection of the distribution of the residuals of the full model against date did not, however, reveal any pattern of temporal autocorrelation. Seasonal variation in the probability of ground nesting, on the other hand, would lead to temporal autocorrelation in these residuals. Thus, we did not include seasonality as a predictor (supplementary fig. S2).

To test the combined impacts of the nine fixed effects and to avoid cryptic multiple testing (Forstmeier and Schielzeth, 2011), we compared the full model with a null model lacking the fixed effects but being otherwise identical using a likelihood ratio test (Dobson, 2002). Prior to fitting the model, we checked the distribution of all of the predictors. As a consequence, we log-transformed ‘distance from road’ and ‘human signs’ in order to achieve a more symmetrical distribution and to avoid leverage issues. An additional reason for log-transforming these two predictors was that they otherwise could have a non-linear effect: as an example, one kilometer further away from the road is likely to have a larger effect at smaller distances from the road as compared to the same measure at larger distances. We then z-transformed forest density, distance from road and human and carnivore signs to a mean of zero and a standard deviation of one to ease model convergence. We assessed model stability by comparing the estimates obtained from the model based on all of the data with those obtained from models based on subsets of the data with habitat types excluded one at a time (Nieuwenhuis et al., 2012). This revealed the models to be fairly stable (tables 5 and 6).

To rule out collinearity, we determined Variance Inflation Factors (VIF; Field, 2005) using the function vif of the R package car (version 3.0-10; Fox and Weisberg, 2011) and applied a standard linear model excluding the random effects, which revealed maximum VIFs well under 2.6 for all factors except elephant and buffalo signs (2.6), distance from road (2.7) and for other human signs encounter rates (3.1) (supplementary fig. S3). To check whether the correlation between hunting evidence and other human signs could distort inference, we fitted two additional models excluding each of these two predictors one at a time. For hunting evidence, the two models with and without other human signs revealed essentially the same results. For other human signs, however, the model without hunting evidence revealed a coefficient of the opposite sign as compared to the full model, and in this model, the effect of other human signs was also significant whereas it was not in the full model (see supplementary table S6 for details). Since there was little variation in the fixed effect predictors within the levels of the random effects, it was not possible to include random slope into the model. As we had no predictions regarding interactions between the predictors, we did not include interactions in the models. In addition, we fitted a second GLMM (Model 1b), pooling both hunting evidence and other human signs into the more general predictor of human activity and combining large carnivores and herbivores into the general predictor of ‘dangerous animals’ (supplementary table S6).

MODEL 2: FACTORS IMPACTING NEST HEIGHT

Given that there is an arbitrary dimension to our classification of ground nests as nests ≤50 cm elevation, and given the substantial amount of variation in the heights of the tree
nests (0.51-40 m), we fitted a second model in which we substituted the binomial response of ground nests (yes – no) with the Gaussian response of nest height. The dataset used for this model comprised one data point for each individual nest. We used a Linear Mixed Model (LMM (Baayen, 2008), Model 2 a) to evaluate the effects of the same predictors as in Model 1 and included again habitat type, but this time also nest group random intercept effects (supplementary table S5). Degrees of collinearity were almost identical to that of Model 1, and we determined model stability and the significance of the full model as described for Model 1 (for assessing model stability, we also excluded nest sites one at a time). We also fitted a second LMM (Model 2b) to test the same predictors as in Model 2a, but lumped together all human signs and all large carnivore/herbivore signs, respectively, as described for Model 1b.

Results

GROUND AND TREE NESTING ACROSS THE REGION

Ratio of ground nests to tree nests

Across the region, we found 2991 chimpanzee nests in 1277 nest groups. Of these, 311 (10.4%) were ground nests in a total of 179 nest groups (14% of groups) (range: 0-29% of all nests; and 0-60% of all nest groups) (supplementary tables S2 and S7). Although ground nests occurred in the majority of the survey areas (15 of the 20), both to the north and south of the Uele River, we did not find them at the South Uele sites of Buta, Ngume, Lingo, and Mbang West, nor at Nawege-Zaza to the north of the Uele (table 4, fig. 2, supplementary tables S2 and S7). In 10 of the 20 survey regions, we found 5% or more ground nests, and in six we found 10% or more.

CHARACTERISTICS OF NEST GROUPS ACROSS THE REGION

Overall, we found an average of 2.3 nests per nest group (median = 1; Q1 = 1; Q3 = 3; range: 1-26). Limiting ourselves to only the 179 nest groups with ground nests present, there was an average of 4.1 nests per group (median = 2; Q1 = 1; Q3 = 4.8; range: 1-26), averaging 2.4 tree nests (median = 0; Q1 = 0; Q3 = 3; range: 0-24) and 1.7 ground nests per group (median = 1; Q1 = 1; Q3 = 2; range: 1-13). In 52% (93/179) of the nest groups containing ground nests we found no associated tree nests, and in 36% (64/179) of the nest groups with ground nests present there were two or more ground nests; 5% (9/179) had 5 or more (supplementary table S8). We found two nest groups at Bambesa with large numbers of ground nests of the same age: one had a mix of 9 ground nests and 9 tree nests and another consisted entirely of 12 ground nests. One nest group in the Gangu Forest contained 13 ground and 11 tree nests of the same age. The average height of nests across the region was 9.0 m (median = 8.0; Q1 = 5.0; Q3 = 12.0; range: 0-40; n = 2649); excluding ground nests, it was 10.2 m (median = 8.0;
Table 4. Number of ground nests encountered (by complexity) and number of leaf cushions per survey area. Ground nests include complex, flimsy and half ground nests, the latter being a subset of the complex ones.

<table>
<thead>
<tr>
<th>Survey area</th>
<th>No. GNs</th>
<th>No. FGNs</th>
<th>No. CGNs</th>
<th>No. HGNs</th>
<th>No. LCs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Camp Louis</td>
<td>88</td>
<td>5</td>
<td>83</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Gangu</td>
<td>121</td>
<td>4</td>
<td>117</td>
<td>5</td>
<td>6</td>
</tr>
<tr>
<td>Bili South</td>
<td>7</td>
<td>0</td>
<td>7</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Zapay</td>
<td>10</td>
<td>0</td>
<td>10</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Gbangadi</td>
<td>3</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Nawege-Zaza</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Bambilo</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Dume</td>
<td>6</td>
<td>5</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Total north Uele</td>
<td>236</td>
<td>14</td>
<td>222</td>
<td>7</td>
<td>9</td>
</tr>
<tr>
<td>Leguga</td>
<td>33</td>
<td>2</td>
<td>31</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Buta</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Ngume</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Akuma-Yoko</td>
<td>2</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>Mbangue East</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Mbangue West</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lingo</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Zongia</td>
<td>3</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Lebo</td>
<td>4</td>
<td>1</td>
<td>3</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Bambesa</td>
<td>34</td>
<td>0</td>
<td>34</td>
<td>13</td>
<td>1</td>
</tr>
<tr>
<td>Total south Uele</td>
<td>77</td>
<td>3</td>
<td>74</td>
<td>17</td>
<td>13</td>
</tr>
<tr>
<td>Total</td>
<td>313</td>
<td>17</td>
<td>296</td>
<td>24</td>
<td>22</td>
</tr>
</tbody>
</table>

GN, ground nest; LC, leaf cushion; CGN, complex ground nest; FGN, flimsy ground nest; HGN, half ground nest.

In this table, we include only nests for which we gathered data on complexity, thus we have excluded data from the Membulu and Difongo regions.

Q1 = 6.4; Q3 = 13.0; range: 0.6-40; n = 2334) (supplementary table S9).

The majority of ground nests found both to the north (94% of 236 ground nests) and south (96% of 77 ground nests) of the Uele River were complex ground nests (table 4). To the north of the Uele River, 3% (7/236) of ground nests were half ground nests, vs. 22% (17/77) south of the Uele; all of these were of complex construction. Gangu, Bambesa, Mbangue East and Lebo had the highest percentage of half ground nests; these were also found at Leguga, and Camp Louis, but not at the other survey areas. Eight of the 24 half ground nests (35%) were found on hillsides, compared to only 8% (25/311) of other ground nests and 7% (185/2639) of tree nests. In four cases, we found ground nests built on logs that were touching the ground. In 23 cases, the trees used to make ground nests had sprung up into the air with the passage of time, which made it difficult to estimate precisely their original height, although it was below 0.5 m.

We found that 19% (27/141) of fresh and recent complex ground nests were associated with hairs only, 6% (8/141) with dung only, 13% (18/141) with dung and hairs, and 10% (14/141) with feeding remains. No fresh and recent flimsy ground nests were associated with hairs, 17% (1/6) were associated with dung, and 50% (3/6) with feeding remains (supplementary table S10).

As can be seen in supplementary table S11, ground nests made up 13% (220/1712) of the nests which had been made recently enough.
Factors affecting ground nesting in chimpanzees in northern D.R. Congo

Figure 2. Proportions of ground nests (in black) out of total nests per survey area. Circle area represents the number of nests found per survey area (range: 23 to 934). See supplementary table S7 for more details.

to retain their original form (age categories 1-3), whereas for older, decayed nests (age categories 4 and 5), only 7% (87/1222) were terrestrial, a significant difference (Mann-Whitney U-test: \(W = 375\ 233, p = 0.008\)). This may indicate that ground nests at Bili-Uéré decay more quickly than tree nests, as has been documented at Bugoma, Uganda by Romani et al. (in press).

Concerning habitat types, to the north of the Uele River we found the majority of tree nests (52% (972/1857)) in mixed forest. To the south but not to the north of the Uele, the majority of tree nests were in *Gilbertiodendron* monodominant forest (51% (396/770) in the south vs. 6% in the north (115/1857)) (supplementary table S4), and only 38% (293/770) of tree nests were in mixed forest in the south. Of the 292 ground nests for which we recorded data on habitat type, the majority were also in mixed forest (71% (122/173) north vs. 52% (62/119) south). We also found ground nests in riparian forest (27% (46/173) north vs. 1% (1/119) south), swamp forest (28% (33/119), in the south only), and *Gilbertiodendron dewevrei* monodominant forest (1% (2/173) to the north vs. 19% (23/119) to the south). We found 29% (82/286) of the ground nests in dense forest and 53% (151/286) in medium dense forest, compared to 19% (451/2400), and 63% (1510/2400), respectively, for tree nests (see supplementary table S4 and additional data 4 of the online repository).

**Leaf Cushions**

We found leaf cushions in 8 of the 20 survey areas (table 4); 50% (11/22) of these were associated with chimpanzee nests, 9% (2/22) with tree nests and 41% (9/22) with ground nests. Considering only the fresh leaf cushions, 44% (7/16) were associated with feeding remains, 31% (5/16) with hairs, and 31% (5/16) with dung (supplementary table S10).
FACTORS POTENTIALLY IMPACTING GROUND NESTING AND NEST HEIGHT IN THE CHIMPANZEEs OF NORTHERN DEMOCRATIC REPUBLIC OF THE CONGO

Ground vs. tree nest groups (Model 1)

In Model 1a, we evaluated the impacts of forest structure, habitat type, human presence, distance from road, and dangerous animals on the probability of a nest group consisting of ground nests (table 5). Overall, the model showed that several fixed effects had a clear impact on the likelihood of a nest group consisting of ground nests (likelihood ratio test comparing full and null model: \( \chi^2 = 97.549, \text{df} = 9, P < 0.001 \)).

Habitat-type

Ground nest groups were significantly associated with herb patches and light gaps (table 5, supplementary fig. S4A, B), as well as with dense forest (supplementary fig. S5). The model revealed little variation in the random effect of habitat type in relation to the fixed effects (estimated standard deviation in link space: 0; see supplementary table S12 for more information).

Impact of large fauna

We found no significant impact of encounter rates of carnivores or large herbivores on the likelihood of a nest group consisting of ground nests, whether combined or divided into carnivores and herbivores (table 5, and see additional data 5 of the online repository), although there was a trend for fewer ground nest groups to be found in association with carnivores. We provide more information on the distribution of these carnivores, elephants, and buffaloes across the region in supplementary table S3.

Human impact on ground nesting

The model revealed a significant negative impact of human hunting on the probability of a nest group consisting of ground nests (table 5, and fig. 3A). In three of the areas most impacted by hunting (Mbange West, Buta, and Ngume; supplementary table S3), we found no ground nests at all (supplementary table S2). At Mbange East, which had a high impact of human hunting, only one of the 47 nests was terrestrial. Also, Gangu and Leguga, two of the areas with the lowest levels of human impact, hunting or otherwise, had some of the highest proportions of ground nests out of total nests (13% (119/934) and 29% (33/115), respectively; see supplementary table S2 for details). Encounter rates of non-hunting human signs, however, had no impact on the proportion of ground nest sites (table 5, and fig. 3B).

Factors impacting nest height (Model 2)

In addition, we modelled nest height using the same predictors included in Model 1 (table 6). We present the results for each group of predictors separately: habitat type, large fauna and human signs. Overall, the combined impact of the 10 fixed effects had a clear impact on nest height (full-null model comparison: \( \chi^2 = 100.234, \text{df} = 10, P < 0.001 \)).

Habitat type

The model showed considerable variation in the random effect of habitat type in relation to the fixed effects (estimated standard deviation = 4.02; supplementary table S12). Furthermore, we found that light gaps, vine tangles, and herb patches had a negative effect on the height chosen by the chimpanzees to build their nests (table 6; see also additional data 6 of the online repository).

Impacts of large fauna and humans

We found a significant positive impact of large herbivores, but not carnivores, on nest height (table 6, and supplementary fig. S6). This impact of herbivores was, however, very small. Nest height significantly decreased with increasing distance from roads (table 6, fig. 4, and supplementary table S13), and significantly increased with higher encounter rates of hunting evidence, but not with other human signs (table 6, and supplementary table S3; see also additional data 7 of the online repository).
Table 5. Effects of ecological factors, human activities, carnivores and large herbivores on the probability of a nest group being composed only of ground nests (Model 1a).

<table>
<thead>
<tr>
<th>Term</th>
<th>est</th>
<th>SE</th>
<th>Lower CI</th>
<th>Upper CI</th>
<th>$\chi^2$</th>
<th>P</th>
<th>min$^b$</th>
<th>max$^b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>−3.253</td>
<td>0.233</td>
<td>−3.986</td>
<td>−2.945</td>
<td></td>
<td></td>
<td>−3.717</td>
<td>−3.059</td>
</tr>
<tr>
<td>Hillside ($1 = y, 0 = n$)</td>
<td>−1.079</td>
<td>1.027</td>
<td>−10.882</td>
<td>0.298</td>
<td>1.544</td>
<td>0.213</td>
<td>−17.006</td>
<td>−0.842</td>
</tr>
<tr>
<td>Herb patch ($1 = y, 0 = n$)</td>
<td>2.315</td>
<td>0.512</td>
<td>1.263</td>
<td>3.388</td>
<td>19.274</td>
<td>$&lt;$0.001</td>
<td>1.701</td>
<td>3.709</td>
</tr>
<tr>
<td>Light gap ($1 = y, 0 = n$)</td>
<td>2.639</td>
<td>0.609</td>
<td>1.395</td>
<td>4.097</td>
<td>18.498</td>
<td>$&lt;$0.001</td>
<td>2.211</td>
<td>2.891</td>
</tr>
<tr>
<td>Forest density$^1$</td>
<td>0.354</td>
<td>0.125</td>
<td>0.112</td>
<td>0.623</td>
<td>8.198</td>
<td>0.004</td>
<td>−0.032</td>
<td>0.428</td>
</tr>
<tr>
<td>Distance from road$^2$</td>
<td>0.309</td>
<td>0.268</td>
<td>−0.180</td>
<td>0.931</td>
<td>1.497</td>
<td>0.221</td>
<td>0.182</td>
<td>0.561</td>
</tr>
<tr>
<td>Hunting evidence$^3$</td>
<td>−2.000</td>
<td>0.712</td>
<td>−3.766</td>
<td>−0.854</td>
<td>11.356</td>
<td>0.001</td>
<td>−3.107</td>
<td>−0.738</td>
</tr>
<tr>
<td>Other human signs$^4$</td>
<td>0.519</td>
<td>0.390</td>
<td>−0.208</td>
<td>1.376</td>
<td>1.778</td>
<td>0.182</td>
<td>−0.274</td>
<td>0.89</td>
</tr>
<tr>
<td>Carnivores$^5$</td>
<td>−0.366</td>
<td>0.196</td>
<td>−0.817</td>
<td>−0.002</td>
<td>3.684</td>
<td>0.055$^t$</td>
<td>−0.548</td>
<td>−0.121</td>
</tr>
<tr>
<td>Large herbivores$^6$</td>
<td>−0.063</td>
<td>0.221</td>
<td>−0.523</td>
<td>0.387</td>
<td>0.082</td>
<td>0.775</td>
<td>−0.424</td>
<td>0.175</td>
</tr>
</tbody>
</table>

$^a$ $\chi^2$ values from a likelihood ratio test df was 1 in all cases.

$^b$ Range obtained when including nest sites and habitat types one at a time.

$^1$ z-transformed to a mean of 0 and a standard deviation of 1; mean and sd of the original variable were 2.01 and 0.59, respectively.

$^2$ Log and then z-transformed to a mean of 0 and a standard deviation of 1; mean and sd of the log-transformed variable were 2.28 and 0.99, respectively.

$^3$ Log and then z-transformed to a mean of 0 and a standard deviation of 1; mean and sd of the log-transformed variable were 0.16 and 0.24, respectively.

$^4$ Log and then z-transformed to a mean of 0 and a standard deviation of 1; mean and sd of the log-transformed variable were −1.22 and 1.09, respectively.

$^5$ z-transformed to a mean of 0 and a standard deviation of 1; mean and sd of the original variable were 0.04 and 0.03, respectively.

$^6$ Log and then z-transformed to a mean of 0 and a standard deviation of 1; mean and sd of the log-transformed variable were 0.35 and 0.27, respectively.
Figure 3. Effect of signs of hunting evidence per km (A), and other human signs per km (B) on the proportion of ground nest groups/total nest groups. The area of the dots represents the number of nests found at each area (min = 5; max = 735). The dashed lines depict the fitted model (Model 1a) and the dotted lines its upper and lower confidence limits for all other predictors centered to a mean of zero. GN, ground nest.
Table 6. Results of the LMM model of the effects of environmental factors, humans and animals on nest height (Model 2).

<table>
<thead>
<tr>
<th>Term</th>
<th>est</th>
<th>SE</th>
<th>Lower CI</th>
<th>Upper CI</th>
<th>$\chi^2$</th>
<th>P</th>
<th>min$^b$</th>
<th>max$^b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hillside ($1 = y, 0 = n$)</td>
<td>0.764</td>
<td>0.67</td>
<td>–0.504</td>
<td>2.024</td>
<td>1.316</td>
<td>0.251</td>
<td>0.161</td>
<td>1.088</td>
</tr>
<tr>
<td>Herb patch ($1 = y, 0 = n$)</td>
<td>−1.785</td>
<td>0.886</td>
<td>−3.584</td>
<td>−0.080</td>
<td>4.063</td>
<td>0.044</td>
<td>−3.007</td>
<td>−0.959</td>
</tr>
<tr>
<td>Light gap ($1 = y, 0 = n$)</td>
<td>−4.855</td>
<td>0.877</td>
<td>−6.385</td>
<td>−3.062</td>
<td>30.627</td>
<td>&lt;0.001</td>
<td>−6.500</td>
<td>−3.838</td>
</tr>
<tr>
<td>Vine tangle ($1 = y, 0 = n$)</td>
<td>−3.879</td>
<td>1.618</td>
<td>−7.173</td>
<td>−0.642</td>
<td>5.771</td>
<td>0.016</td>
<td>−5.740</td>
<td>0.362</td>
</tr>
<tr>
<td>Forest density$^1$</td>
<td>−0.174</td>
<td>0.158</td>
<td>−0.462</td>
<td>0.138</td>
<td>1.201</td>
<td>0.273</td>
<td>−1.006</td>
<td>−0.056</td>
</tr>
<tr>
<td>Distance from road$^2$</td>
<td>−1.198</td>
<td>0.299</td>
<td>−1.806</td>
<td>−0.601</td>
<td>15.572</td>
<td>&lt;0.001</td>
<td>−1.740</td>
<td>−0.997</td>
</tr>
<tr>
<td>Hunting evidence$^4$</td>
<td>0.634</td>
<td>0.256</td>
<td>0.124</td>
<td>1.117</td>
<td>6.192</td>
<td>0.013</td>
<td>0.497</td>
<td>0.763</td>
</tr>
<tr>
<td>Other signs (humans)$^3$</td>
<td>−0.016</td>
<td>0.328</td>
<td>−0.653</td>
<td>0.624</td>
<td>0.006</td>
<td>0.937</td>
<td>−0.353</td>
<td>0.101</td>
</tr>
<tr>
<td>Carnivores$^5$</td>
<td>−0.091</td>
<td>0.221</td>
<td>−0.542</td>
<td>0.338</td>
<td>0.163</td>
<td>0.686</td>
<td>−0.369</td>
<td>0.011</td>
</tr>
<tr>
<td>Large herbivores$^6$</td>
<td>0.620</td>
<td>0.274</td>
<td>0.070</td>
<td>1.159</td>
<td>5.186</td>
<td>0.023</td>
<td>0.022</td>
<td>0.908</td>
</tr>
</tbody>
</table>

$^a$ $\chi^2$ values from a likelihood ratio test df was 1 in all cases.

$^b$ Range obtained when including nest sites and habitat types one at a time.

$^1$ $z$-transformed to a mean of 0 and a standard deviation of 1; mean and sd of the original variable were 2.32 and 0.61, respectively.

$^2$ Log and then $z$-transformed to a mean of 0 and a standard deviation of 1; mean and sd of the log transformed variable were 0.14 and 0.96, respectively.

$^3$ Log and then $z$-transformed to a mean of 0 and a standard deviation of 1; mean and sd of the log transformed variable were 0.14 and 0.22, respectively.

$^4$ Log and then $z$-transformed to a mean of 0 and a standard deviation of 1; mean and sd of the log transformed variable were −1.25 and 1.10, respectively.

$^5$ $z$-transformed to a mean of 0 and a standard deviation of 1; mean and sd of the original variable were 0.04 and 0.03, respectively.

$^6$ Log and then $z$-transformed to a mean of 0 and a standard deviation of 1; mean and sd of the log transformed variable were 0.35 and 0.27, respectively.
Figure 4. Nest height as a function of distance from road (Model 2a; significant: p-value < 0.001). Note that the model depicted lacks the random effect of nest group as its inclusion led to a very small intercept. We binned the predictor into 49 bins and the circle area is proportionate to the number of nests per bin (range: 7-320). The dashed line depicts the fitted model and the dotted lines its confidence intervals for all other predictors centered to a mean of zero.

Discussion

We found ground nesting to be an important component of chimpanzee behaviour across the Bili-Uéré landscape: in 75% (15/20) of the surveyed areas, 1% or more of the nests were ground nests, and overall 14% (179/1277) of nest groups contained ground nests. We categorized 95% (296/313) of these ground nests as being of complex construction, and thus likely night nests (for more evidence that some of these nests were slept in at night, see supplementary text S1). At 10 of the 20 survey regions, 5% or more of the nests were ground nests, and at 6 regions ground nests made up 10% or more of total nests. These results indicate that ground nesting in northern DRC is a widespread and consistent behaviour spanning two sides of a major river, and is common in both the savanna woodland mosaic habitat to the north and the moist tropical forest habitat to the south. This is to be contrasted with the distribution of ground nesting in other chimpanzee populations, which is much more sporadic (supplementary table S1). Bili-Uéré appears to be the largest continuous area which has been surveyed over which chimpanzee ground nesting occurs (10.4% (311/2991) of all nests, with a fairly evenly distribution across the > 50 000 km² area surveyed; fig. 2, table 4, supplementary table S2 and S7). This behaviour is found as well in the Epulu and RAFALE regions of DRC further east (Hart, unpubl. data; Hicks, unpubl. data; Laudisoit, unpubl, data), and ground nests are common at some localities in Uganda along the border with DRC (Maughan and Stanford, 2001; McCarthy et al., 2017; Hobaiter et al., 2022). This supports the inclusion of ground nesting into the widespread suite of behaviours described by Hicks et al. (2019a) as the Bili-Uéré Behavioural Realm. Given that forest density increased the likelihood that a nest group would contain one or more ground nests (table 5), and that on our recce walks we generally followed the path of least resistance (thus sometimes avoiding...
Factors affecting ground nesting in chimpanzees in northern D.R. Congo

denser vegetation), it is possible that we under-counted ground nests across the region.

The relatively uncommon flimsy ground nests may have been used, like leaf cushions, to rest in or feed in during the day (Koops et al., 2007). In fact, when looking at fresh and recent nests, a substantial proportion of the flimsy ground nests and leaf cushions (50% (3/6) and 44% (7/16), respectively) were associated with feeding remains, whereas only 10% (14/141) of complex nests were. More work remains to be done investigating the styles of ground nest construction in these different regions, the plant types used, and the sex of the nesters, which will help us to determine whether this represents one continuously-distributed behavior or rather multiple independent evolutions of ground nesting, based on happenstance, similar ecology or genes. In addition, more nesting surveys should be conducted in the vast forests between these areas to ‘connect the dots’, if indeed they can be connected. It should be remembered, though, that surveys carried out conveniently close to roads or in areas with high levels of human hunting may only uncover sub-populations of chimpanzees that have recently lost ground nesting due to human threat.

Regarding the potential social role of terrestrial night nesting (e.g., mate guarding) we observed that more than half of the nest groups containing ground nests lacked any associated tree nests. In addition, 36% (65/179) of the ground nest sites had two or more ground nests, and 2% (3/179) of nest groups containing ground nests had 9 or more ground nests, including a group of 12 ground nests found with no associated tree nests (supplementary table S8). This makes it unlikely that mate guarding alone can explain the prominence of this behavior in northern DRC.

MODELS

We used statistical models to investigate the potential impact of several factors on the ratio of ground nests to tree nests and also nest height. These can be grouped into habitat type, dangerous fauna and human activities.

HABITAT TYPE

Our results revealed that in northern DRC, chimpanzees nested more often on the ground in mixed forest (63% (184/292) of ground nests vs 48% (1265/2627) of tree nests), but they also used riparian forests (16% (47/292) of ground nests vs 20% (517/2627) of tree nests) and swamps (11% (33/292) of ground nests vs 10% (266/2627) of tree nests) (supplementary table S4). South of the Uele River, but not to the north, chimpanzees often built both ground nests (19% of the total) and tree nests (51% of the total) in Gilbertiodendron dewevrei monodominant forest: given that this forest type is much more common to the south of the Uele (Hicks, 2010), this is perhaps not surprising. We cannot rule out that differences in vegetation availability, as we could expect to find in remote forests vs. more anthropogenic ones, might impact ground nesting. Although at Bili-Uéré trees and herbs used to construct tree and ground nests are common close to the road as well as in the deep forest, future studies should attempt to assess the impact of vegetation type on terrestrial nesting. Considering the major differences in the predominate habitat types on the two sides of the Uele River (forest-savanna mosaic to the north vs. semi-deciduous moist tropical forest to the south), it is unlikely that any particular environmental factor is sufficient to explain the unusually high frequency and wide distribution of ground nesting behaviour in northern DRC. Nevertheless, dense forests as well as light gaps and herb patches were strongly associated with ground nests across the region. Given that light gaps and herb patches were often associated with abundant herb presence, and that 44% (137/311) of ground nests used herbs in their construction (Hicks, unpublished data), perhaps the pattern is driven by availability of resources. Future studies should take into account more detailed information on the availability of preferred nest construction materials between survey areas, which may influence the frequency of ground nests.

In addition, several factors might affect nest decay rates (e.g., vegetation-type and/or nest complexity) (see Bessone et al. (2020) for such an analysis of bonobo nests), and these have
not been investigated at Bili-Uéré. Morgan et al. (2016) analyzed the factors affecting the decay of arboreal and terrestrial nests of western lowland gorillas, finding that decay was influenced by forest structure and habitat type, as well as number of components. To address the lack of information on nest decay in chimpanzees, we have recently carried out a study on chimpanzee ground nest decay in the Bugoma Forest, Uganda (Romani et al., in press).

**DANGEROUS ANIMALS**

We predicted that the threat of large dangerous animals such as carnivores, buffaloes, and elephants would dissuade chimpanzees from sleeping on the ground, as suggested by Pruetz et al. (2008), Hicks (2010), Stewart and Pruetz (2013) and Badji et al. (2018). The literature on this relationship is contradictory: Tagg et al. (2013) found no influence of abundance of potential predators and large herbivores on ground nesting, whereas Pruetz et al. (2008), and Koops et al. (2012a) documented abundant ground nests in forests where large carnivores were rare or absent. In northern DRC, especially in the remote Gangu Forest, we often encountered ground nests in the same swamps in which we found the dung and footprints of large carnivores and herbivores. Comparing the different survey areas, we found that encounter rates of large herbivores had no impact on the frequency of ground nesting, but that there was a trend for carnivore encounter rates to be associated with a greater likelihood of a nest site being composed of ground nests (this trend disappeared when carnivores and large herbivores were combined) (table 5). In addition to this being only a trend, it was a very small effect. When considering the impact of these factors on nest height (Model 2), only large herbivores had a significant positive effect, although this small difference in heights was likely to have been of minimal biological importance: when the encounter rate of elephant and buffalo signs increased by one standard deviation of its log transformed predictor, nest height increased by only 0.62 m (SE = 0.3, table 6, and supplementary fig. S6). Ground nests were particularly common at Gangu (13% of total nests), which also had the highest encounter rates of these potentially dangerous animals. Other localities such as Buta, Ngume, Mbange West, Lebo, and Lingo had very few or no large mammals and also few or no chimpanzee ground nests. Given that large terrestrial mammals were also much less common near roads and in association with human signs, probably due to hunting pressure, this factor is likely linked to human activities. In addition, elephants, unlike the other large mammals under study, are capable of migrating en masse across the landscape, disappearing from one area and appearing in another over a short period of time (Hicks, pers. observ.). We observed this pattern in the forests of Camp Louis and inferred it in Mbange East (Hicks, 2010, 2014). To speculate, perhaps this unpredictability of the movement of elephants (and to a lesser degree buffaloes) might have led to the observed minor effect on chimpanzee nest- ing habits.

**HUMAN IMPACT**

Human disturbance is known to have an impact on the behavior of non-human great apes (orangutans: van Schaik (2002), chimpanzees: Hicks et al. (2013), Kühl et al. (2019)), often leading to impoverishment or loss of their traditions, but sometimes producing innovations (McLennan et al., 2019). Across Africa, the impact of human activities on ground nesting can be complex. At La Belgique, Cameroon, ground nests were positively associated with human evidence (Tagg et al., 2013), whereas the opposite was the case at Lebialem-Mone (Last and Muh, 2013). In northern DRC, we found, in accordance with Hicks (2010), but using an expanded data set, a significant negative effect of hunting signs, but not of non-hunting human signs or distance from roads, on the likelihood of a nest group consisting of ground nests (table 5, and fig. 3); similarly, for nest height we found a significant negative impact of hunting (table 6) and a positive one of distance from roads (table 6, and fig. 4). When the log-transformed distance from road increased by one standard deviation of its log-transformed predictor, nest height decreased by 1.2 m (SE = 0.3, table 6). In addition, when the log-transformed number of
Factors affecting ground nesting in chimpanzees in northern D.R. Congo

hunting signs increased by one standard deviation of its log-transformed predictor, nest height increased by 0.63 m (SE = 0.3, table 6); the latter is small and likely of minimal biological importance. Taken together with the absence or rarity of ground nests in the areas most impacted by human hunting (Buta, Ngume, Akuma-Yoko, and Mbang East and West) and their abundance in two of the least human-impacted areas (Gangu and Leguga), these results provide modest support for the hypothesis that the northern DRC chimpanzees build their nests slightly lower with a greater distance from human hunting activity, and appear to cease building ground nests altogether in areas where they experience extreme danger from hunting.

Ground nesting could also be a result of high rates of injury from snares or hunting in a particular forest region (chimpanzees missing hands or feet may have trouble climbing into the trees) or a larger number of old or sick individuals. This is also unlikely, however, given that ground nests were found at 15 out of our 20 survey areas, in multiple nest groups, and that a number of nest groups contained multiple ground nests. TH observed large groups of healthy-looking chimpanzees across the Bili-Uéré region, often actively climbing through or displaying in the treetops, and saw none that were afflicted with missing hands or feet or other obvious snare injuries (see supplementary video S1 for links to clips of uninjured Bili-Uéré chimpanzees). In addition, as already mentioned, snares and other hunting signs were rare or absent at the sites with the largest percentages of ground nests, such as Gangu and Leguga. The lack of human impact on chimpanzees in Gangu is actually more pronounced than our analysis revealed, because we found the overwhelming majority of human signs at the far eastern edge of what was otherwise a mostly pristine forest.

**Potential Social Factors**

At Nimba, Guinea, and Fongoli, Senegal, ground nesting has been proposed to be a sex-linked behaviour (Koops *et al.*, 2007; but see Koops *et al.*, 2012b). We have not included any genetic analysis in this paper. Nevertheless, given that we found more than half of the ground nests in nest groups lacked tree nests, and that we found multiple nest groups with large numbers of ground nests, we consider it unlikely that the behaviour was limited to one or the other sex, and thus it cannot be fully explained by mate-guarding. In the future, however, this should be tested with genetic analyses on dung and hair samples gathered from the nests.

**Conclusions**

The implications of our results are that neither the large body size of gorillas nor the taming of fire (Wrangham, 2009) are necessary for medium-sized hominids such as chimpanzees to regularly construct night nests on the ground, even in areas with high densities of carnivores. Chimpanzees have been documented to attack leopards (Hiraiwa-Hasegawa et al., 1986; Boesch, 2009), pirate prey from them (Nakamura *et al.*, 2019; and possibly Hicks *et al.*, 2020b), and consume a leopard carcass (Hicks *et al.*, 2020b). They can, however, also fall prey to these carnivores (Boesch, 1991). In addition, chimpanzees at Loango, Gabon have been observed to attack gorillas (Southern *et al.*, 2021). Thus, it is possible that in northern DRC some as-yet-unknown behavioural anti-predator adaptation may contribute to the apes’ increased comfort in sleeping on the ground, and it is notable that they frequently sleep together in multiple ground nests. The only dangerous predator that seems to limit chimpanzee ground nesting is their close cousin, *Homo sapiens*: in areas where human hunting was heaviest, ground nesting disappeared completely.

The Bili-Uéré region of northern DRC, with its complex mix of ecotones, provides us with a perfect natural laboratory in which to study the impact of factors that, millions of years ago, may have also pushed our own ancestors towards the gradual transition to a more terrestrial life. Hominins of the genera *Ardipithecus*, *Australopithecus*, and the earliest *Homo* were roughly similar in body size to modern chimpanzees and may have experienced some of the same selection pressures (McHenry, 1992), including niche competition with fellow hominids (Haile-Selassie *et al.*, 2016) as occurs...
between chimpanzees and gorillas in many areas today (Oelze et al., 2014; Deblauwe, 2009; Southern et al., 2021). They likely faced more abundant large terrestrial predators than chimpanzees do today (Turner, 1990), but they did not have to reckon with the most dangerous hunter of all, Homo sapiens. These results add significantly to our knowledge of the behavioural diversity in the sleeping habits of one of our closest cousins. Given the enormous geographical area over which chimpanzee ground nesting occurs in northern DRC, and its distribution across a diverse range of habitats, P. troglodytes now joins G. gorilla and H. sapiens as a great ape species that, in at least some populations, frequently nests on the ground. Nonhuman great ape cultures are fragile and easily diminished by human encroachment (Kühl et al., 2019), and we now know that ground nesting disappears quickly in areas with increased human hunting pressure. To safeguard this fascinating aspect of chimpanzee behavioural diversity, it is essential that we provide protection for the Bili-Uéré chimpanzees to ensure that ground nesting does not disappear.

Acknowledgements

We thank the Ministère de l’Environnement of the DRC and the Institut Congolais pour la Conservation de la Nature (ICCN) for granting us permission to work in the DRC. We thank Chief Zelesi Yakisi for inviting us to set up a field site in his collectivity. Laura Darby-Singh and Adam Darby-Singh assisted with the South Uele surveys, and Karsten Dierks and Jeroen Swinkels assisted in the north. Field assistant Chipula verbally agreed that his photograph could be used in fig. 1. We thank the following supporters of our project: The Wasmoeth Wildlife Foundation, Lucie Burgers Foundation, International Primate Protection League, The African Wildlife Foundation, Le Centre de Rehabilitation des Primates de Lwiro, US Fish and Wildlife Service, the Panafri- cian Programme of the Max Planck Institute for Evolutionary Anthropology, Karl Ammann, Hans Wasmoeth, Jan Sevink, and Jan van Hooff. We also thank Terese and John Hart, Christophe Boesch, Hjalmar Kühl, Claudia Nebel, Andreas Walther, and Rainer Benz. At The Faculty of ‘Artes Liberales’, we thank Jerzy Axer, Robert Sucharski, Dorota Łagodzka, Joanna Pijanowska, Joanna Romanowicz, Ewa Jakubi ec, Robert Przybysz, Tatiana Lewińska, Ilona Szewczyk, Jan Miernowski, and Monika Stobiecka. We are grateful to the hard work and knowledge of our field assistants, in particular Team Leaders Ephrem Mpaka, Henri Silegowa, Gilbert Pakulu, Bebe Bofenda, Ligada Faustin, Chief Mbolibie Cyprian, and Kisangola Polycarpe, as well as Olivier Esokeli, Seba Koya, Dido Makeima, Makassi Constant, Likambo, Likongo, Garavura Roger, and Kongoyesi. Anne Laudisoit, Alejandra Pascual-Garrido, Anna Nekaris, Vittoria Estienne, Lydia Luncz, Jan van Hoff and Carel van Schaik provided useful ideas in discussions which helped us interpret the data. Last but not least, we are thankful to the four anonymous reviewers for providing a number of invaluable remarks and comments.

Statement of ethics

Our research on chimpanzee nesting behaviour was non-invasive 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 with the permission from L’Institut Congolais pour la Conservation de la Nature (ICCN), the Ministère de l’Environnement of DRC and with the consent of local landowners and community members.

Conflicts of interest

The authors have no conflicts of interest to declare.

Funding sources

This work has been developed within the project “A Survey of Chimpanzee Material Culture in Eastern DR Congo” financed by the National Science Center of Poland on the basis of the Decision no. DEC-2017/25/B/NZ8/
Factors affecting ground nesting in chimpanzees in northern D.R. Congo


Author contributions

In addition to the tasks listed below, TR organized the data and co-wrote the manuscript. TH conceived the research, led the Bili-Uéré survey missions, organized the data and co-wrote the manuscript. Statistical analyses, maps and figures: RM and TR, with input from TH. Research protocol design: TH, RM and SM. Comments on the manuscript: ST, PR, AM, RM and MK.

Data availability

All data used in the analyses, including the basic script for the two models, are available at the following link: Romani T, Hicks TC (2023), Data Bili-Uere chimpanzee ground nesting, Mendeley Data, V1, doi: 10.17632/ssdftsv88y.2 (https://data.mendeley.com/datasets/ssdftsv88y/2).

Supplementary material

Supplementary material is available online at: https://doi.org/10.6084/m9.figshare.22093430

References


Factors affecting ground nesting in chimpanzees in northern D.R. Congo


van Lawick-Goodall J (1968). The behaviour of free-living chimpanzees in the Gombe Stream Vol. 0(0), 2023 33


