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Developmental and Sex-Based Variation in Nest Building Among Wild Immature Chimpanzees

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ABSTRACT

All great apes build nests. Nests in trees or on the ground provide apes with a safe and comfortable place to sleep and rest at night and during the day. Nest building is a necessary skill and form of tool use that individuals learn and practice early in life, but little is known about its development and about the factors affecting the expression of nest building in infancy. We studied the development of daytime nest building of 72 wild immature chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo, Kibale National Park, Uganda. We evaluated the effects of age, sex, and maternal parity on the likelihood of infant nest building (presence or absence), as well as on the rates (frequency/hour) and durations (time from start to finish of each nest) with which infants built nests. Compared to the youngest infants (≤ 1 year), older infants were more likely to build nests, and built them at higher rates, consistent with hypotheses that nest building requires learning in early infancy and a threshold of physical development to manipulate tree branches. Female infants were more likely to build nests and built them more often than male infants, corroborating other developmental markers suggesting females attain functional independence at younger ages than males in some chimpanzee populations. Among infants who were seen to build nests at least once, rates and durations were similar, regardless of age, sex, or maternal parity, which indicated that there was little interindividual variation in nest building development once infants started practicing. The observed patterns of prior and subsequent behaviors to nest building suggested that infants > 4 years old built nests more functionally, for resting, than younger infants. This study underscores the value of nest building as a developmental measure in wild great apes. Studying factors that affect the expression of nest building in infancy allows for a better understanding of the ontogeny and evolution of learning and tool use in hominids.

1 | Introduction

Nest building, also referred to as bed building, is an essential part of a weaned great ape's daily routine, often observed around sunset and presumed to provide a place for apes to sleep and rest from dusk to dawn (Fruth and Hohmann 1996; Fruth et al. 2018). Common to all great ape species, nest building is considered a complex form of object manipulation and tool use estimated to have appeared in a common ancestor of the family Hominidae between 18 and 14 million years ago (Duda and

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Summary

- The likelihood and global rates of daytime nest building in wild infant chimpanzees varied with age and sex. Older and female infants were more likely to build nests and build them more often, than younger and male infants.
- Rates and durations were similar among infants once they started practicing nest building, regardless of age, sex, or maternal parity, suggesting little interindividual variation in the development of this skill.

Zrzavý 2013; Fruth et al. 2018), with several hypotheses used to explain its evolution. One stipulates that nest building allowed apes to sleep more comfortably and safely, improving their quality of sleep, which in turn increased individual daily net energy gains and improved cognitive function, like improving memory (Baldwin et al. 1981; Fruth and Hohmann 1996; Stewart et al. 2007). Other hypotheses attribute the selectivity of nesting locations in some great apes (e.g., tree type, nest height in trees) to improved thermoregulation when sleeping in nests, or to increased protection from predators and pathogens (Fruth and Hohmann 1996; Hernandez-Aguilar 2006; Koops et al. 2012; Lacroux et al. 2023; Largo et al. 2009; Prasetyo et al. 2009; Samson et al. 2013; Stewart and Pruetz 2013).

The process of nest building is similar in all great apes despite socioecological differences between species and populations: individuals start by twisting, breaking, and weaving larger branches and material into a circular platform, before adding smaller twigs and sometimes leaves as a rim and lining (Van Casteren et al. 2012; Fruth and Hohmann 1996; Goodall, 1968; Prasetyo et al. 2009; Stewart et al. 2007). While apes build nests in the evening to sleep in during the night, detailed data on night-time ape behavior is limited, so it is not clear whether night nests are frequently used for additional functions other than sleeping. In addition to night nests, adult and immature apes also commonly build nests during the day. Daytime nests are generally simpler than night nests and can be used for a wider range of activities outside of sleeping, including resting without sleeping, playing, grooming, and eating (wild orangutans, *Pongo pygmaeus*: Prasetyo et al. 2009; *Pongo abelii*: Permana et al. 2024; chimpanzees, *Pan troglodytes:* Brownlow et al. 2001; Fruth and Hohmann 1996; bonobos, *Pan paniscus*: Fruth and Hohmann 1993; and captive lowland gorillas, *Gorilla gorilla*: Lukas et al. 2003).

1.1 | Infant Development and Nest Building

Research on great ape ontogeny is useful when attempting to retrace the evolution of the timing of key life history events, with studies focusing on describing and comparing interspecific markers of development (e.g., weaning age) to better understand the evolution of human-specific patterns (Bădescu 2018; Kennedy 2005; Lee 1996; Lee 2012; van Noordwijk et al. 2013; Sellen 2006). While less frequently studied compared to common measures used to track development, like suckling or maternal carrying, nest building by immature apes provides researchers with another easily observable measure of the gradual acquisition of behavioral independence from the mother (Fruth and Hohmann 1993; van Lawick-Goodall 1968). Daytime nest building during development may be used as a way for infants and juveniles to gradually practice nest building skills before moving on to constructing nighttime nests (e.g., *Pongo abelii*: Permana et al. 2024).

Furthermore, since nest building is the most prevalent form of tool used in great apes (reviewed in Fruth et al. 2018), studying the development of nest building offers better opportunities to understand tool use acquisition and learning than population-specific tool use (e.g., ant dipping, nut cracking), which varies widely between ape species, populations and groups (Biro et al. 2003; Whiten et al. 1999). Research on the development of nest building in great ape infants can thus provide valuable information for comparative cognition and learning in hominids.

1.2 | Effects of Infant Age on Nest Building

Great ape infants are highly vulnerable and dependent on their mothers for at least the first few years of life, and they maintain a certain dependency on their mothers even after weaning (*G. gorilla*: Breuer et al. 2008; *P. p. abelii*: van Noordwijk and van Schaik 2005; *P. t. schweinfurthii*: Lonsdorf et al. 2014; *P. paniscus*: Toda et al. 2021). Most chimpanzees (*Pan troglodytes)* are nutritionally weaned by around 4–5 years old but can continue to behave as infants by making nipple contacts for comfort (without milk transfer) sometimes years after being nutritionally weaned (Fruth and Hohmann 1996; Bădescu et al. 2017; Bădescu, Watts, Curteanu, et al. 2022; Bădescu, Watts, Katzenberg, et al. 2022), a pattern also seen in bonobos (*Pan paniscus*), who seem to be nutritionally weaned around 6–7 years old (De Lathouwers and Van Elsacker 2006; Oelze et al. 2024).

Available published data indicate that nest building behaviors in apes start around 6 months old, and individuals can become proficient in nest building by around 3 years old; however, infants continue to regularly share night nests with their mothers at least until they are weaned (at 4–5 years old in *P. troglodytes*: van Lawick-Goodall 1968; Fruth and Hohmann 1996; 6–7 years old in *P. paniscus:* Oelze et al. 2024; 6–8 years old in *P. p. abelii*: van Noordwijk and van Schaik 2005; Permana et al. 2024). In some cases, chimpanzees shared nests with their mothers until they were 10 years old (Crockford et al. 2020; Samuni et al. 2020; Walker et al. 2018). Thus, like patterns of nutritional development, sharing a nest with the mother can continue in immature great apes for years after independent nest building skills have been attained, which facilitates continued body contact with their mothers for protection and thermo-regulation, as well as enabling access to night-time nutritive or comfort nursing (Gettler and McKenna 2011; McKenna et al. 2007).

1.3 | Effect of Sex on Tool Use

Sex differences have been reported in several great ape behaviors, some of which emerge in infancy (Lonsdorf 2005; Lonsdorf 2017; Lonsdorf et al. 2004; Lonsdorf et al. 2014; Maestripieri and Ross 2003). While sex differences in nest building during infancy have not been investigated, adult female chimpanzees in some communities built more nests and spent more time building nests than males (Fruth and Hohmann 1996; Stewart and Pruetz 2020). In other forms of tool use, chimpanzee and bonobo (genus *Pan*) females showed proficiency in termite fishing and ant-dipping at younger ages, and they used tools at higher rates and for longer durations than males (Boose et al. 2013; Gruber et al. 2010; Lonsdorf 2005; Lonsdorf et al. 2004; McGrew 1979). Immature *Pan* females may learn to use tools at younger ages if they have more opportunities to learn from their mothers than males do because young *Pan* females also associate socially more closely with their mothers until dispersal at adolescence, while young males from an earlier age spend more time interacting with individuals other than the mother (Gruber et al. 2010; Hayaki 1988; Lonsdorf et al. 2004; Reddy and Sandel 2020). Additionally, immature chimpanzee females in some populations were also weaned earlier compared to males, showing that females in this species gain independence from the mother sooner, and that maternal lactational investment can be biased toward sons, the philopatric sex in *Pan* (Boesch 1997; Bădescu, Watts, Katzenberg et al. 2022; Fahy et al. 2014; Lonsdorf et al. 2020).

1.4 | Parity of Mothers and Their Effect on Development

Primiparous or young mothers often have higher infant mortality rates than multiparous and mid-aged mothers across different primates (e.g., *Papio hamadryas*: Sunderland et al. 2008; *P. troglodytes schweinfurthii*: Wood et al. 2017; *G. gorilla beringei*: Robbins et al. 2006). This is in part due to primiparous females experiencing physiological limitations with regard to lactation, especially if mothers are very young and still developing, which can hinder the growth and survival of their infants, who are consequently weaned later than those of multiparous mothers (Hinde 2009; Künkele and Kenagy 1997; Motil et al. 1997; Robbins et al. 2006; e.g., mountain gorillas, *G. beringei*; Eckardt et al. 2016: Robbins et al. 2006).

On the other hand, primiparous females have less experience caring for young, as mothering skills are often acquired through practice raising multiple offspring (Robbins et al. 2006; Stanton et al. 2014). For instance, in *P. t. schweinfurthii* at Ngogo, multiparous females more often shared premasticated food with their infants than primiparous females, a behavior that may help support infant feeding development (Bădescu et al. 2020; Bădescu, Watts, Curteanu, et al. 2022). In rhesus and pigtail macaques (genus *Macaca*), the infants of multiparous females showed independent locomotion earlier in their development than those of primiparous females, and multiparous females were more likely to encourage independent locomotion in their infants (Maestripieri 1995). While some differences in infant behavior and development relative to maternal parity have been documented in primates, it is unknown whether maternal parity differentially affects nest building behavior in infant apes.

1.5 | Objectives and Predictions

Nest building in immature great apes has been reported (e.g., Fruth and Hohmann 1996; van Noordwijk and van Schaik 2005; Permana et al. 2024; Stewart and Pruetz 2020), yet we lack detailed data on the development of nest building in different ape populations and on factors affecting its expression in infancy. We presented daytime nest building exhibited by 72 immature chimpanzees (*P. t. schweinfurthii*) in the Ngogo community at Kibale National Park, Uganda. Specifically, we compared the probability of showing nest building (presence or absence), and nest building rates (frequency/hour) and durations (mean number of seconds from start to finish) across infants, in relation to age, sex, and parity of infants' mothers. Assessing the probability of nest building allowed us to understand which infants were more likely to show this behavior, whereas behavioral rates and durations allowed us to evaluate which infants more often built nests and spent more time on each nest (Bădescu et al. 2015; Bădescu et al. 2020). These comparisons enabled us to make inferences about when nest building skills developed in chimpanzees and revealed some of the factors that influenced the expression of this behavior in early life in the wild.

We predicted that compared to younger infants, older infants would be more likely to build nests, and they would do it more often since older infants would be closer to attaining behavioral independence from the mother. We expected older infants would either spend less time building each nest, as they might be more skilled and more efficient nest builders, or that older infants would spend more time building each nest if they dedicated increasingly more time and energy to practicing this skill as they became more independent.

We predicted that female infants would be more likely than males to build nests and that they would do so more often or for longer durations, which would be in line with other forms of tools use in *Pan*, where immature females used tools at earlier ages and spent more time using tools compared to immature males (Boose et al. 2013; Gruber et al. 2010; Lonsdorf 2005; Lonsdorf et al. 2004; McGrew 1979). Additionally, immature chimpanzee females may be under greater selective pressure to gain behavioral and nutritional independence from the mother faster than males (Stumpf et al. 2009; Bădescu, Watts, Katzenberg, et al. 2022).

If mothers facilitate infant nest building, as they can do with other forms of tool use in chimpanzees (e.g., nut cracking by *P. troglodytes verus* at Taï, Côte d'Ivoire: Boesch 1991; termite fishing by *P. t. troglodytes* at Guoalougo Triangle, Republic of Congo: Musgrave et al. 2016), or encourage it like with other behaviors (locomotion in *Macaca sp.:* Maestripieri 1995), multiparous, more experienced mothers might better model or encourage nest building behavior for their young compared to primiparous females. We therefore predicted that the infants of multiparous females would be more likely to show nest building, or that they would show it more often or for longer durations, than the infants of primiparous females.

2 | Methods

2.1 | Study Site & Subjects

Kibale National Park in western Uganda is 795 km^2 of mostly moist evergreen and semi-deciduous forests, found at the foothills of the Rwenzori Mountains (Chapman et al. 2005; Watts et al. 2012a, 2012b). Data collection was done at the Ngogo study site, found in the center of Kibale National Park. Ngogo is situated at an altitude of 1400-1470 meters and contains old growth forests, grasslands, and swamp areas (Lwanga 2003; Struhsaker 1997). It receives 1479 millimeters of rainfall annually, usually between the two rainy seasons, March to June, and September to December (Lwanga 2003; Struhsaker 1997; Watts et al. 2012a, 2012b).

The eastern chimpanzee (*Pan troglodytes schweinfurthii)* community at Ngogo numbered between 199 and 207 individuals during the study periods, encompassing 54–57 adult females, 26–33 adult males, 30–34 juvenile and adolescent females, 33–42 juvenile and adolescent males, and 40–53 infants (Bădescu, Watts, Curteanu, et al. 2022). By the 2018 study period, this community was undergoing permanent fission and is now considered two distinct communities (Sandel and Watts 2021). Chimpanzees at Ngogo are habituated to the presence of researchers, as they have been studied since 1995 (Emery Thompson et al. 2020; Watts 2012; Watts et al. 2012a). Individual chimpanzees are recognizable by their distinguishing facial features and color patterns, body scars, missing or deformed limbs or appendages, and hair color patterns and distribution.

We included 72 immature chimpanzees aged 0–9 years old in this study. We refer to these individuals as "infants" because they were observed to make nipple contacts or ventral-ventral contact with their mothers, and they did not yet have a younger maternal sibling, so were the only dependent offspring of their mothers (Bădescu, Watts, Curteanu, et al. 2022; Bădescu, Watts, Katzenberg, et al. 2022). However, others have defined chimpanzees as "infants" up to 5 years old (Goodall 1986). Ages were calculated from infants' first appearance in the group, and the last appearance of their mothers before births. The ages of infants were most often determined to the day or several days. For a few infants who were not observed from birth, ages were estimated to within 1–2 weeks, or for one infant, to be within 4–6 weeks, and we also used comparisons of physical and behavioral developmental markers shown by other infants of known similar ages to refine age estimates for these infants.

For statistical analyses we separated infants into the following age categories: > 0–1 years, > 1–2 years, > 2–3 years, > 3–4 years, and > 4–9 years. We lumped infants over the age of 4 together because weaning usually occurs by 4 to 4.5 years old at Ngogo (although nipple contacts can continue up to 8 years with and without milk transfer; Bădescu, Watts, Curteanu, et al. 2022; Bădescu, Watts, Katzenberg, et al. 2022), and because we considered that weaned individuals are behaviorally largely independent and can thus build their own nests. Additionally, combining the oldest study subjects into one category increased the sample size for statistical analyses due to the limited number of individuals > 5 years old.

The 72 infants were the offspring of 56 adult females, with 16 females contributing two infants to the data set. Amongst them, 22 infants appeared in multiple age categories as they grew older during data collection. This resulted in a total of 99 infants-per-age-category for analyses (Table 1; data set available as Supporting Information S1: Table 1).

2.2 | Data Collection

Data on directly observed daytime behaviors of infant chimpanzees were collected from January to March 2013 and September 2013 to June 2014 by IB, and from January to April 2018 by IB, KD and CC using focal animal sampling (Altmann 1974). We obtained a total of 1318.34 focal hours (mean and standard deviation per study infant-by-age-category: 13.32 +/− 6.74 h; Table 1). Data collection occurred most days between 7:00 and 17:30, and both KD and CC were trained by IB who remained the main observer throughout both study periods to avoid differences between data due to interobserver variability. Weaned chimpanzees typically start to build their night nests around 18:00, which means our observations likely did not include the building of many, if any, nighttime nests by infants. During 1-h focal samples, observers continuously recorded the frequencies and durations of infant nest building and all other self-directed behaviors (e.g., foraging, resting) and social behaviors (e.g., nursing, playing, allo-grooming). We recorded the time and order of events and beginning and end times of each state behavior.

TABLE 1 | Focal sampling hours and characteristics of daytime nest building in all 99 chimpanzee infants-by-age-category.

			Nest building characteristics		
Infant age (Years)	Mean number of focal hours (SD) per infant	Total number of infants (female, male)	Nest building infants	Mean rate (freq/hour)	Mean duration[a] (seconds)
> 0–1	15.26 (6.29)	23 (14, 8, 1 unknown)	2 (9%)	0.01	63.50
> 1–2	13.89 (6.61)	19 (11, 8)	10 (53%)	0.07	87.91
> 2–3	12.17 (5.82)	22 (9, 13)	12 (55%)	0.13	93.64
> 3–4	11.67 (5.40)	17 (9, 8)	10 (59%)	0.09	78.54
> 4–9	13.18 (8.68)	18 (7, 11)	13 (72%)	0.13	77.58
Total	13.32 (6.74)	99 (50, 48, 1 unknown)	47 (45%)	0.09	82.30

[a] Mean durations only included infants who showed nest building.

A nest building bout, defined in this study as a single session where an individual built or attempted to build a nest, was recorded if focal subjects independently bent and manipulated branches, twigs and foliage together into a platform or similar structure (Figure 1). Given that we were interested in the development of nest building in early life, we included in this study all nest building attempts, regardless of whether they led to nests that could be functional, or were used by infants to rest in. Nest building bouts were considered distinct if infants were working on two different nests. In most cases (70%), an infant's work on one nest was the only bout of nest building recorded for the day. In 21% of cases, infants worked on two different nests separated by 3 min to 1 h. In 9% of cases, nest building bouts were separated by 1–4 h.

If the focal subject was out of view for over 10 min, sampling would cease and the time the individual spent out of view was subtracted from the total focal hours (Bădescu et al. 2016). At the end of a focal sample, observers would switch to another infant if one was in view, and they tried to cycle through collecting samples of all infants present in the same order of observation for the rest of the day. Due to the fission-fusion social dynamics of chimpanzees, daily focal infant selection was often based on which mother-infant pairs were found each day, and some infants were sampled more if no other infants were available. Whenever possible, we prioritized sampling of infants for whom data were relatively lacking.

Infant phenotypic sex was assigned unambiguously for all but one individual in this sample from observation of external genitalia. Female ($N = 50$) and male ($N = 48$) infants were observed for similar amounts of time: 13.65 +/− 6.45 focal hours per individual for females, and 13.07 +/− 7.05 focal hours per individual for males (Table 1).

The parity of mothers—i.e., whether females were first-time mothers (primiparous, $N = 36$) or had raised multiple infants (multiparous, $N = 63$)—was determined from prior demographic data collated by the research team.

This research was authorized with special permission from the Uganda Wildlife Authority, Uganda National Council for Science and Technology, Université de Montréal and University of Toronto, complied with the American Society of Primatologists' (ASP) Principles for the Ethical Treatment of Nonhuman Primates, and followed the American Society of Primatologists Code of Best Practices for Field Primatology.

FIGURE 1 | An older infant sitting in a completed nest.

2.3 | Data Analyses

First, we determined whether nest building occurred (presence or absence of at least one observed bout) for each infant, at each age category. Second, we calculated hourly rates (nest building bout frequency/focal hours) for each study subject by their age category. Third, we calculated mean nest building bout durations by subtracting the beginning time of a bout from the end, adding all the durations together, and dividing the sum of all durations by the frequency of nest building for each study subject, per age category. We analyzed mean bout durations only for complete bouts, where we observed both the beginning and the end of nest building.

For each nest building bout, we noted the behaviors displayed by each infant directly before nest building, divided the frequency of each behavior by the total number of nest building bouts in each age category, and multiplied by 100 to estimate proportions (percentage, %) of pre-nest building activities that infants engaged in per age category. The same method was applied for all behaviors following nest building bouts to obtain proportions (%) of post-nest building activities.

2.4 | Statistical Analyses

We conducted four generalized estimating equation (GEE) analyses (Liang and Zeger 1986) to evaluate how infant nest building **presence or absence** (GEE 1; who was most likely to show this behavior), **rates** with and without zero values (GEE 2; who showed this behavior most often among all infants, and also GEE 3; only among those infants who showed at least one bout of nest building) and **bout durations** (GEE 4; who engaged in this behavior longer) varied according to infant age (0–1, > 1–2, > 2–3, > 3–4, > 4 years), sex (male or female), and maternal parity (primiparous or multiparous) (fixed effects). In GEE 1 we controlled differences in observation times between study subjects by adding focal hours per infant-age-category as a covariate. For all four GEEs, we included data collection year (2013–2014 or 2018) as a covariate. In GEE 1 and 2, all infants were included, with a sample size of 99 infants-by-age-category. In GEE 3 and 4, only infants observed to build nests were included, and our sample size here was 47 infants-by-age-category. To account for repeated measurements of the same infants at different age categories, and for the females who contributed more than one infant to our data set, we included infant and maternal identities as the grouping structure in the GEEs. To account for the multiple testing of the same sample, we applied a Bonferroni correction to p-values. GEE was employed in this study due to its compatibility with ordinal data (binary and count variables) and with correlated within-group fixed effects, its ability to analyze data longitudinally, as it was able to account for multiple infants contributing data at different ages, as well as its allowance of missing values, such as the unknown sex of one infant (Ghisletta and Spini 2004; Zuur et al. 2009). Overall, GEE offers a more conservative analytical approach than Generalized Linear Models (GLM) or Generalized Linear Mixed Models (GLMM) (Zuur et al. 2009). We ran the GEE analyses using SPSS version 29, with alpha set at 0.05.

We also conducted Tukey HSD tests (Nanda et al. 2021) to compare the mean differences in the presence or absence and the rates of nest building between each of the infant age categories, as well as the mean differences in activity before and after nest building bouts in each of the age categories. Analysis of resting behavior excluded instances of infants nesting with their mothers to only include instances when they were inactive and resting by themselves. Tukey tests were conducted using Rstudio version 4.4.1, with alpha set at 0.05. All other behaviors were reported descriptively to illustrate the different behaviors that can occur in association with nest building.

3 | Results

We recorded a total of 113 nest building bouts by infants. The rate of nest building among all individuals ranged between 0 (no observed cases) and 0.66 bouts/hour, with a mean rate (± SD) of 0.09 +/− 0.12 bouts/hour. Among the 47 infants-by-age-category who were observed to build nests at least once, the mean rate was 0.18 ± 0.12 bouts/hour, and the time that these infants spent building a nest ranged between 4 s and 6 min 57 s, with a mean of 82.30 ± 50.6 s spent building a nest.

3.1 | Infants Most Likely to Build Nests

While nest building by infants younger than 1 year old was uncommon, 2 of 23 infants 6 months to 1 year old showed this behavior at least once (Table 1). There were no observed attempts of nest building by infants younger than 6 months old. Between 53% and 59% of infants older than 1 year old and younger than 4 years old built nests, and after 4 years old, 72% of infants were seen building nests. The probability (presence or absence) of nest building showed some variation with age (Generalized Estimating Equations, GEE 1: $p < 0.001$, Table 2; Figure 2), with infants in age categories greater than 1-year-old being more likely to build a nest at least once compared to those aged 1 year old and younger (Tukey HSD: $p < 0.05$; Figure 3; Table 1; Table 2). However, infants over the age of 1 year were all equally likely to build a nest at least once (Figure 3).

TABLE 2 | Generalized estimating equation (GEE) results of associations between infant age, infant sex, maternal parity and data collection period with the presence or absence of nest building behavior as a binary response variable. Significant *p*-values in bold.

	Presence or absence of nest building			
	β	**SE**	**Wald χ^2 ($df = 1$)**	***p*-value**
Infant age	0.163	0.024	45.805	**< 0.001**
Infant sex	−0.242	0.073	10.995	**< 0.001**
Maternal parity	0.096	0.082	1.369	0.242
Collection year	−0.279	0.084	11.067	**< 0.001**
Focal hours	0.018	0.006	8.326	**0.004**

Female infants were more likely to build nests than males (GEE 1: $p < 0.001$; Figure 2), as 56% (28/50) of females and 40% (19/48) of males were observed building a nest at least once.

Whether they had a primiparous, or multiparous mother did not affect the probability of nest building by infants ($p = 0.242$; Figure 2). Forty-two percent (15/36) of infants of primiparous females and 51% (32/63) of infants of multiparous females showed nest building.

Infants in 2013–2014 were more likely to be observed building a nest compared to infants in 2018 ($p < 0.001$; Figure 2), as 58% (38/66) of infants in 2013–2014 and 27% (9/33) of infants in 2018 were seen building a nest at least once.

3.2 | Nest Building Rates and Durations

Rates of nest building amongst all infants increased with age (GEE 2: $p < 0.05$, Table 3). One-year-olds built nests at an average rate of 0.01 bouts/hour, while those over the age of 4 built nests at an average rate of 0.13 bouts/hour (Table 1). However, the ranges of nest-building rates overlapped across age categories, and the observed age effects may be driven by greater differences between the rates of 1-year-olds compared to both 3-year-olds and those over 4 years old (Tukey HSD: $p = 0.01$ & $p < 0.05$ respectively). Female infants built nests at higher rates than male infants (GEE 2: $p < 0.05$), while maternal parity showed no effect.

Among the 47 infants-by-age-category observed to build nests (i.e., excluding rates of zero: GEE 3), there were no significant effects of any of the fixed parameters (age, sex, maternal parity, data collection year) on rates of nest building (Table 4). Moreover, no significant differences were observed in the mean rates of nest building between any of the age categories.

Similarly, nest building bout durations were not influenced by age, sex, or maternal parity (Table 4) and were not significantly different between the three age categories. However, infants in 2018 spent a longer time building each nest than infants in 2013–2014 (GEE 4: $p < 0.05$, Figure 4).

3.3 | Activities Before and After Nest Building

Before nest building, infants were generally active (35% of cases), which included back-and-forth movements on a branch or on the ground or swinging slightly from a branch (Figure 5a). Infants rested before nest building bouts (inactive) in only 18% (20/113 bouts) of cases (Figure 5a). Infants also engaged in eating, grooming, and foraging before they started to build a nest (together made up 15% of cases). Infants aged 2–3 and 3–4 also showed social and solitary play behaviors before building a nest (11% of cases for 2- to 3-year-olds and 17% of cases for 3- to 4-year-olds).

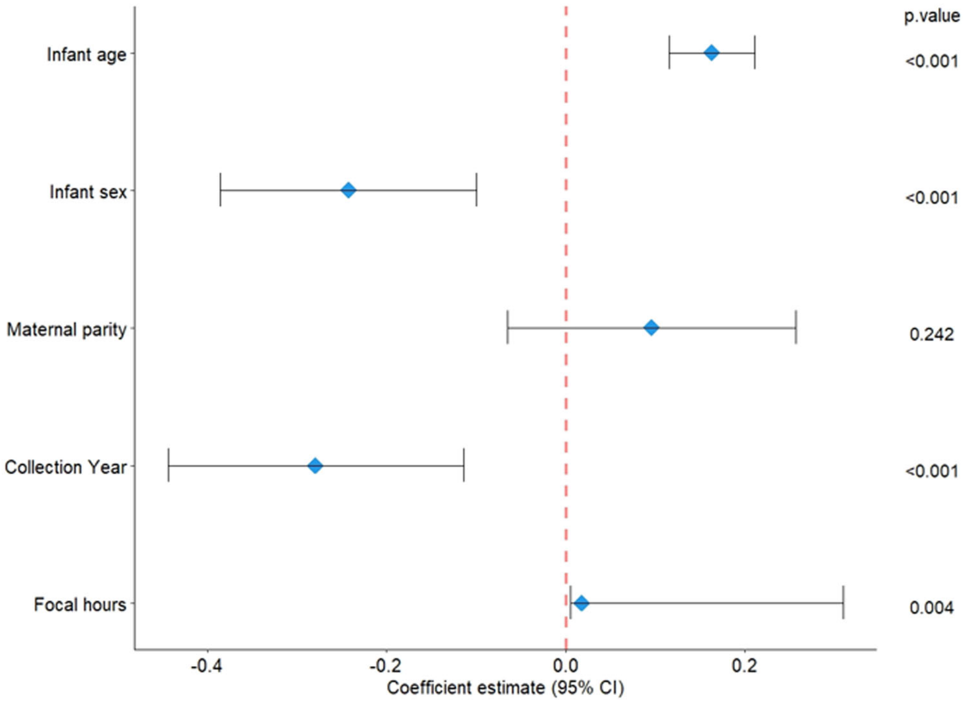


FIGURE 2 | GEE β-coefficient estimates (diamonds) and their 95% CIs (bars) for the effects of each dependent variable and covariate on the likelihood of infants building nests. Focal hours were a continuous variable, infant age was variable, while maternal parity (primiparous vs. multiparous), infant sex (female vs. male) and collection year (2013–2014 vs. 2018) were binary variables. Significant results ($p < 0.05$) do not cross the 0 threshold.

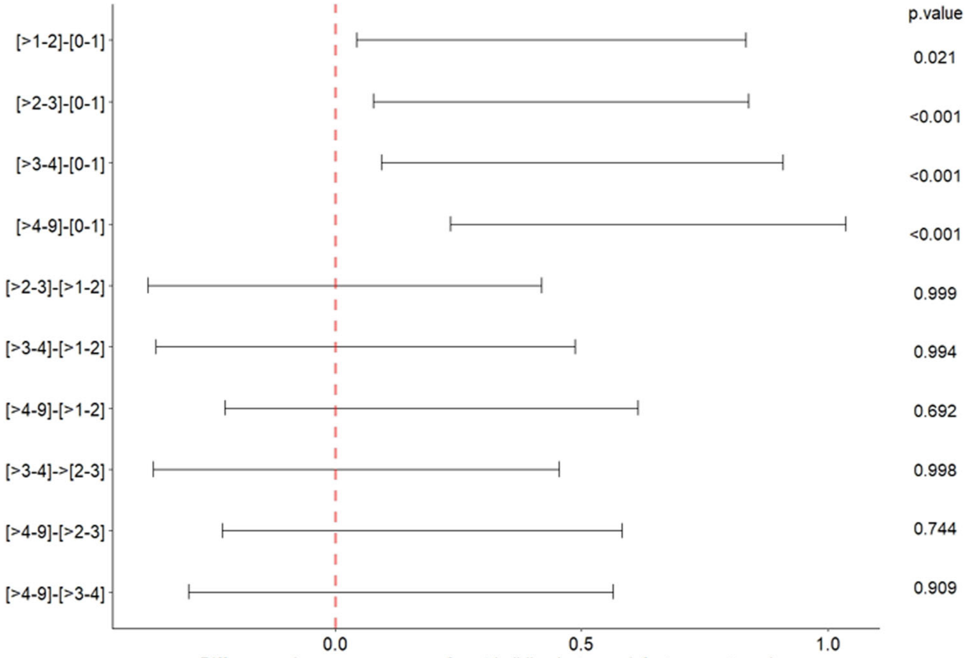


FIGURE 3 | Tukey model plots of differences in nest building presence/absence between age categories. Lines represent the 95% confidence interval for the difference of nest building presence between age groups. Significant results ($p < 0.05$) do not cross the 0 threshold.

After nest building was finished, infants usually rested (56% or 63 of 113 cases) (Figure 5b). Infants older than 1 year of age showed a decrease in being active after nest building (Tukey HSD: $p < 0.05$) and were more likely to rest after nest building than infants aged 1 year and younger (no observed cases).

4 | Discussion

4.1 | Effects on Infant Nest Building

Nest building is a skill that began developing early in chimpanzees, as almost half of the infants showed this behavior at

TABLE 3 | Generalized estimating equation (GEE) results of associations between infant age group, infant sex, maternal parity and collection year with the rates of nest building as continuous response variables in all infants. Significant p-values are in bold.

	Rates of nest building			
	β	SE	Wald χ^2 ($df = 1$)	p-value
Infant age	0.016	0.006	6.593	**0.010**
Infant sex	−0.046	0.023	4.205	**0.040**
Maternal parity	0.020	0.0224	0.834	0.361
Collection year	−0.059	0.023	6.642	**0.010**

least once. The youngest chimpanzees who built nests or attempted to do so were between 6 months to 1 year old. While chimpanzee infants aged 1 year and younger were seen building nests, they were significantly less likely to do so than older infants, partly in line with our prediction that the probability of nest building would correlate positively with age. Contrary to our prediction, however, the probability of nest building seemed to plateau after the age of 1, such that older infants were equally likely to show this behavior. A similar pattern was reported for orangutan (*P. pygmaeus*) infants, who also showed interest in nest building at around 6 months old and a peak in the occurrence of daytime nest building between 1 and 2 years old, with similar nest building behaviors to adults (e.g., functional night nests, nesting calls) reported after this age (reviewed in Fruth and Hohmann 1996; Mendonça et al. 2017; Prasetyo et al. 2009).

Nest building requires physical force sufficient to bend and twist branches of various sizes, which would be harder for younger infants to accomplish and may have contributed to the lower presence of nest building we found in the youngest chimpanzee infants (Fruth and Hohmann 1996; Anderson et al. 2019). In addition, in immature chimpanzees and orangutans, tool use and nest building skills are acquired gradually, presumably by first observing their mothers and other more experienced group members before attempting to practice the skill themselves, showing a potentially important role of social learning in great ape development (*Pongo* spp.: Schuppli et al. 2016; *Pan troglodytes schweinfurthii*: Lonsdorf 2005; Biro et al. 2003; Boose et al. 2013; van Lawick-Goodall 1968; Videan 2006). Infant chimpanzees less than 1 year old in our study could have been less likely to build nests and practiced them at lower rates because they were still in a process of learning by observing others (Videan 2006). We did not collect data on infants observing others build nests to test this theory, nor did we evaluate the quality or size of nests according to age to be able to infer which bouts resulted in functional nests.

That nest building measures did not seem to differ significantly between the ages of 1 and 9 suggests that most chimpanzees by around 1 year old performed this skill at similar rates and for similar durations over several years once it was learned, presumably until they built and slept in their own night nests after reaching independence. However, infants older than 1 spent on average 1 min and 24 s building a nest (range: 8 s to 3 min and 46 s), which is quicker than adult great apes, who take on average 2–5 min to complete a night nest (*P. paniscus* at Lomako: Fruth and Hohmann 1993; *P. troglodytes* at Gombe: Goodall, 1968; reviewed in Fruth and Hohmann 1996). Since young chimpanzees do not need to sleep in their own nests until they are fully independent and sometimes share nests with their mothers until 10 years old (Crockford et al. 2020; Samuni et al. 2020), nest building by infants in our study may have included many short bouts either because (1) infants did not build complex nests that took longer to build, as day nests are usually less complex in structure than night nests (Fruth and Hohmann 1993), or (2) infants did not complete their nest because they could more conveniently share their mother's completed nest when resting. This could suggest that the observed bouts were indeed practice attempts that did not result in a fully functional nest.

The sex of infants influenced the probability and rates of nest building, as female infants were more likely to build nests, and built them more often, than males. This finding supports our predictions and is in line with other developmental markers suggesting females gain independence from their mothers at younger ages than males in some ape populations. For instance, female chimpanzees were weaned earlier than males at Ngogo and at Taï (Boesch 1997; Fahy et al. 2014; Bădescu, Watts, Curteanu, et al. 2022). At Gombe, chimpanzee females survived longer than males if orphaned both before and after weaning, which indicated that young females could meet their own needs independently sooner, compared to males (Nakamura et al. 2014; Stanton et al. 2020). Findings from mountain gorillas (*Gorilla beringei beringei*) similarly suggested that females were weaned earlier than males (Robbins and Robbins 2021). Thus, if female infants generally gain independence sooner than males in some species, this means that females could start to build nests sooner than males.

Contrary to our prediction, however, the rates and durations of nest building did not significantly differ between chimpanzee males and females among infants who showed this behavior at least once. Since nest building is not a sex-specific behavior, as all independent chimpanzees make nests to sleep in every day, it is likely that during infancy, individuals showed nest-building behaviors at similar rates and durations regardless of their sex because they all needed to learn this skill eventually. Indeed, in captive lowland gorillas (*G. gorilla*), neither age nor sex influenced nest building behavior (Lukas et al. 2003). Wild bonobos (*P. paniscus*) at Lomako showed no significant differences in the durations of nest building (including both day and night nests) between adult males and females (Fruth and Hohmann 1993). However, during the daytime alone, adult male bonobos took less time to build their nests than females did (Fruth and Hohmann 1993). Among adult chimpanzees, females built more day nests than males (reviewed in Fruth and Hohmann 1996) and spent more time building night nests (at Fongoli; Stewart and Pruetz 2020). Thus, previous studies showed mixed results regarding sex differences in nest building in adults.

We could reasonably expect to see differences between the sexes in the overall quality or size of the nests built, as most adult

TABLE 4 | Generalized estimating equation (GEE) results of associations between infant age group, infant sex, maternal parity and collection year with the rates and duration of nest building as continuous response variables in infants that showed a presence of nest building. Significant *p*-values are in bold.

	Rate				Duration			
	β	SE	Wald χ^2 ($df = 1$)	*p*-value	β	SE	Wald χ^2 ($df = 1$)	*p*-value
Infant age	−0.101	0.061	2.752	0.097	−7.309	6.027	1.470	0.225
Infant sex	0.043	0.064	0.454	0.500	11.117	16.550	0.451	0.502
Maternal parity	−0.039	0.063	0.392	0.531	20.476	12.328	2.759	0.097
Collection year	−0.113	0.091	1.537	0.215	48.608	18.052	7.250	**0.007**

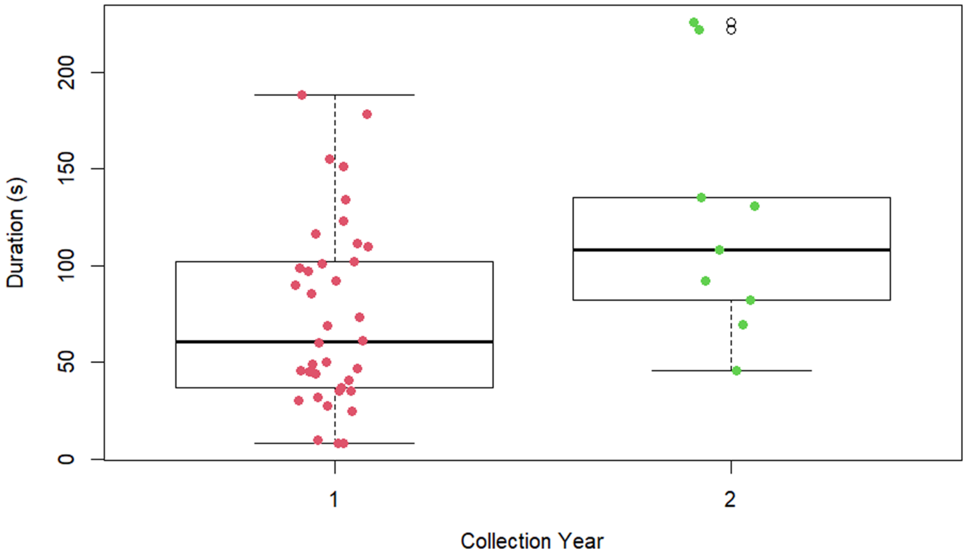


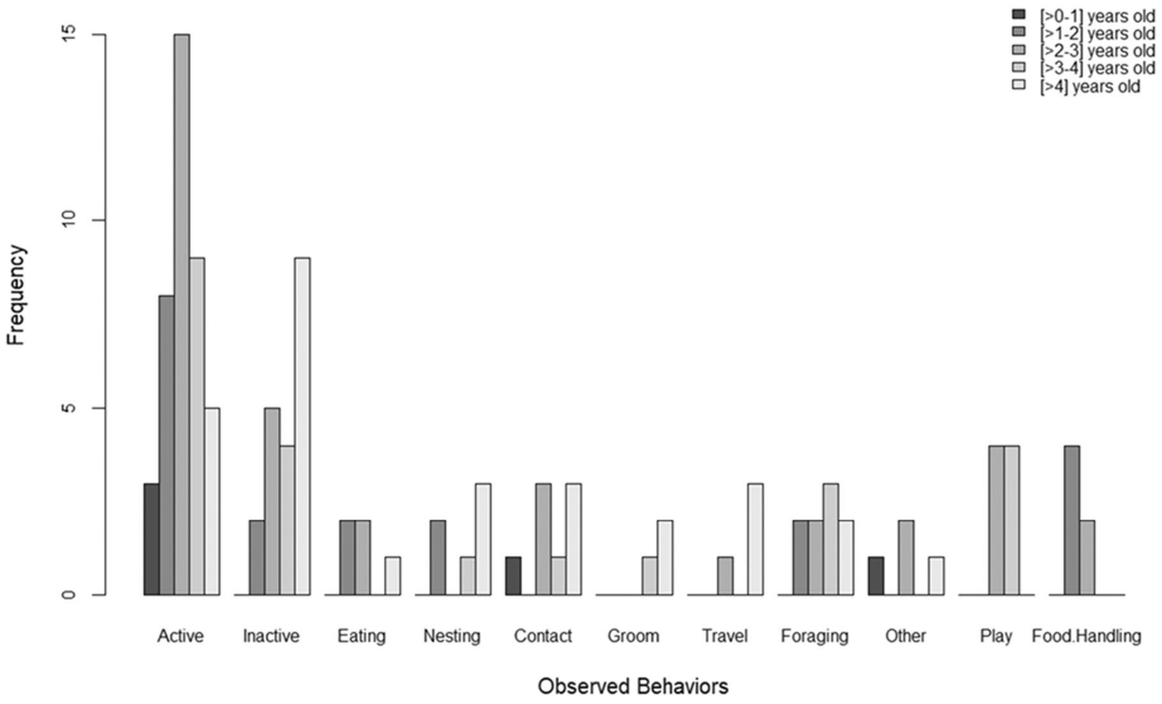
FIGURE 4 | Distribution of durations of nest building bouts by infants who showed this behavior at least once, by year of data collection. 1 = 2013–2014 study period, 2 = 2018 study period.

females make nests not just for themselves, but also for their dependent offspring. For instance, females in all great ape species built nests higher in the trees than males, presumably for increased safety from predators for females and their young (Fruth and Hohmann 1993; Fruth and Hohmann 1996; Rayadin and Saitoh 2009; Stewart and Pruetz 2013; Stewart and Pruetz 2020). Since we did not evaluate the quality of nests in this study, future research will benefit from evaluating qualitative measures of nests built by immature chimpanzees.

Whether mothers were primiparous or multiparous did not affect nest building in infant chimpanzees. While rare, chimpanzee females have been reported to teach their young to use tools (Boesch 1991; Musgrave et al. 2016), but we did not observe mothers at Ngogo teach or correct infants while they built nests. Thus, if this behavior is learned independently by infants through trial-and-error or imitation of others (Carvajal and Schuppli 2022; reviewed in Maestripieri 2018), greater maternal experience may not accord infants extra benefits in the development of nest building. In fact, infants in most primates take the initiative to learn new skills either through trial-and-error or via observational social learning, while their mothers show passive tolerance, such as we see with foraging and food-sharing behaviors in monkeys and apes (Rapaport and Brown 2008; Bădescu et al. 2020) and termite fishing and ant-dipping in chimpanzees (reviewed in Lonsdorf 2013; reviewed in Maestripieri 2018).

We found that the year of data collection, one of the covariates in the analyses, was associated with the probability of observing nest building by infants, as we were more likely to see this behavior in 2013–2014 than in 2018. The decline in incidences of nest building in 2018 may suggest that infants were more likely to share nests with their mothers instead of attempting to build their own nests, possibly due to changes in group dynamics and increased community aggression associated with the intra-community split that occurred between 2013–2014 and 2018 (Sandel and Watts 2021). Future research will focus on evaluating how infant nest building at different ages relates to changes in nest sharing by infants with their mothers. It is unknown why amongst the infants who built nests, those in 2018 spent more time building each nest than those in 2013–2014. Further research is required to understand the causes of differences in nest building between study years, but this result highlights the importance of accounting for study period in analyses aimed at understanding primate behavior longitudinally. This would provide a more nuanced understanding of the range in behaviors over time and offer insights into behavioral changes that can occur after natural or anthropogenic events in long-lived species.

a) Frequency of behaviors observed before nest building bouts



b) Frequency of behaviors observed after nest building bouts

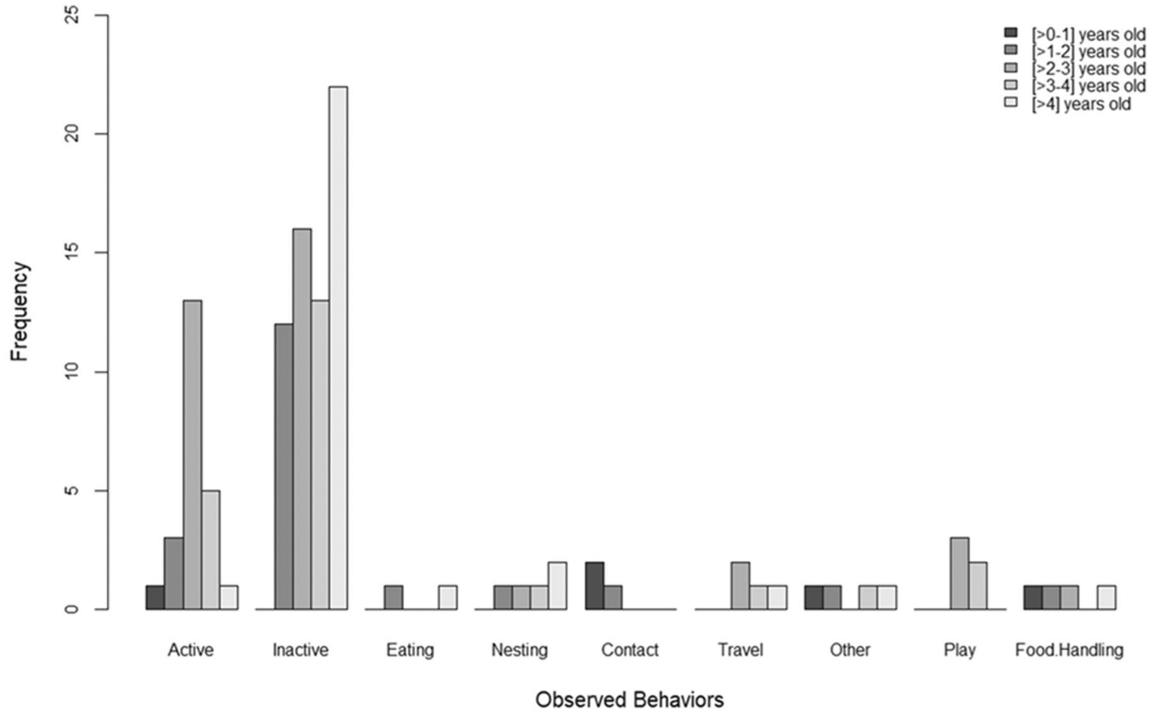


FIGURE 5 | Frequency of observed behaviors by infant age (a) before nest building bouts, (b) after nest building bouts. Nesting and Contact were done with mother. Infants were resting when they were inactive and alone before or after nest building.

This study was limited to daytime nest building and likely included little to no building of night nests. However, chimpanzees nest with their mothers even after infancy (Crockford et al. 2020), and night nests are also more elaborate as they need to support individuals and be comfortable for them to sleep in all night (Brownlow et al. 2001), and thus require more skill to complete, so it is unlikely that we would have observed nighttime nest building by infants that would have been any more functional (i.e., used for sleeping) than daytime nest building. It is therefore unclear whether missed bouts of nest building in the evenings would differ in the likelihood of their occurrence, rates or durations compared to daytime nest building.

4.2 | Behaviors Before and After Nest Building

As infants aged, they rested more after nest building, which may indicate that compared to younger infants, older infant chimpanzees more often built nests functionally, for resting or sleeping, which would be like adults (Fruth and Hohmann 1996). Moreover, like adult chimpanzees, who – in addition to resting – can use day nests for a variety of behaviors (Brownlow et al. 2001; Fruth and Hohmann 1996), we found that infants played, groomed, and ate food after nest building bouts. Infants 2 to 4 years old were the only ones who played before or after nest building, which is in line with published reports on the development of play behaviors in this species, which showed playing peaked around 2 years old (15% of the observed time) and decreased around 4 years old (Lonsdorf et al. 2014). Interpretation of these qualitative results on the behaviors of infants before and after nest building is difficult, however, since we did not consistently collect data on whether infants engaged in the described activities or rested inside the nests, therefore using them, or simply displayed the behaviors nearby after attempting to build their nests. Future studies should focus on investigating in more detail infants' motivations behind nest building, as well as the functionality and use of nests built by infants.

5 | Conclusions

We documented nest building in wild immature chimpanzees and highlighted the possible factors that impacted this behavior during development. While age and sex predicted the likelihood and global rates of infants building nests, once chimpanzee infants at Ngogo started to show this behavior, they built nests at similar rates and for similar amounts of time. There may therefore be less intraspecific variation in the ontogeny of nest building in chimpanzees once infants start practicing this skill. We did not evaluate the building process or quality of nests, however, which could differ between infants according to their age, sex, or experience of their mothers.

This study demonstrated that the development of nest building is a feasible measure of ontogeny in wild apes and that its practice varies according to age and sex, similar to other forms of tool use in chimpanzees and bonobos (Boose et al. 2013; Gruber et al. 2010). Further investigations of ape nest building in early life could yield insights into the mechanisms of tool and object use development, exploration and learning in great apes aside from chimpanzees, especially for *Gorilla* and *Pongo* spp. where other forms of tool use have been documented (e.g., Masi 2023; Meulman and van Schaik 2013) but to a lesser extent compared to *Pan* spp. As nest building occurs in all great apes but might still show some cultural components (reviewed in Fruth and Hohmann 1996), further studies on the process of how it is learned and developed in each species (e.g., trial-and-error, imitation, teaching) will confer valuable information on the acquisition of tool use, skill transfer and cultural traits in hominids.

Author Contributions

Tara Khayer: conceptualization (equal), formal analysis (equal), writing–original draft (lead), writing–review and editing (equal). **Kelly J. Desruelle:** data curation (equal). **Cassandra Curteanu:** data curation (equal). **Daniel W. Sellen:** investigation (equal), project administration (equal), resources (equal), supervision (equal), writing–review and editing (equal). **David P. Watts:** conceptualization (equal), project administration (equal), resources (equal), supervision (equal), writing–review and editing (equal). **Iulia Bădescu:** conceptualization (equal), data curation (equal), funding acquisition (equal), investigation (equal), methodology (equal), project administration (equal), resources (equal), supervision (equal), visualization (equal), writing–original draft (equal), writing–review and editing (equal).

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that supports the findings of this study are available in the Supporting Information section of this article.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.