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The ontogeny of nest-building behaviour in Sumatran orang-utans, *Pongo abelii*

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Nest building is an important subsistence behaviour that young great apes must learn to become competent adults. Orang-utans show a remarkable degree of variability and selectivity for a broad range of features in their nest building. However, the details of when different aspects of nest-building skills emerge remain unclear. We used data on 27 immature Sumatran orang-utans and 20 mothers collected over a decade at Suaq Balimbing, Sumatra to investigate when immatures develop their nest-building skills and examine when nest tree species preferences emerge. We found that young orang-utans showed interest in nest building from 6 months of age and begin to construct day nests at around 1 year of age, whereas night nests were not practised until close to the third year of life. Nest-building practice peaked around age 3–4 years and then steadily decreased as immatures approached the age of nutritional independence, around age 8 years. By then, immature orang-utans were competent nest-builders, but their nests differed from adult nests in several aspects, such as fewer multitree nests and additional comfort elements, which seemed to be mastered later in development. All age classes demonstrated stronger selectivity towards tree species used for night nests and immatures eventually had similar preferences to mothers. We conclude that the ontogeny of nest-building behaviour and the selection of nest tree species in Sumatran orang-utans is a multiyear learning process that requires intense practice.

While the word ‘nest’ usually conjures up the constructions of birds, other species including some invertebrates and members of all classes of vertebrates, including great apes, also build nests (Deméré et al., 2002; Hansell, 2000). Functionally, nests serve a variety of purposes, protecting against fluctuations in ambient temperatures, aiding reproduction, supporting thermoregulation, and providing shelter from predators and the elements (Deacon, 2006). Some also protect against parasites and offer enhanced comfort (Biddle, Deeming, et al., 2018; Fruth & Hohmann, 1996; Hansell, 2000; Mainwaring et al., 2014; McGrew, 2004; Permana, 2022; Prasetyo et al., 2009; Samson & Hunt, 2012; Stewart et al., 2007, 2018). However, unlike the nests of birds, which are mainly constructed to protect eggs and raise altricial young (Healy et al., 2008, 2023), ape nests are primarily beds, routinely constructed daily, often multiple times, for daytime naps and nightly rest (Permana, 2022; Prasetyo et al., 2009).

Nest building in great apes involves the manipulation of vegetation to form a resting platform from branches and leafy twigs (Permana, 2022). Arboreal nests are generally a shallow, slightly elongated, bowl shapes (Permana, 2022; Rayadin & Saitoh, 2009; Stewart et al., 2018), providing a stable platform for rest and sleep and occasionally for other activities such as feeding, copulation and

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play. Although ape nests are mostly constructed in trees, some populations of chimpanzees, *Pan troglodytes* (Hernandez-Aguilar et al., 2013; Koops et al., 2007, 2012; Stewart & Pruetz, 2013; Tagg et al., 2013), gorillas, *Gorilla gorilla* (Brugiere & Sakom, 2001; De Vere et al., 2011; Fay et al., 1989; Fruth & Hohmann, 1996; Mehlman & Doran, 2002; Tutin et al., 1995) and Bornean orang-utans, *Pongo pygmaeus* (Ashbury et al., 2015) occasionally build nests on the ground.

Nests are widely referred to as the most pervasive form of material technology in the apes (Fruth & Hohmann, 1994). Moreover, there is growing evidence that the night nests of great apes (Permana, 2022; Stewart et al., 2018; van Casteren et al., 2012) and some nest structures of birds (Collias, 1986; Muth & Healy, 2011; Walsh et al., 2011, 2013) represent complex object manipulations that may involve considerable cognitive ability as in some examples of tool use (including nut cracking), which exhibit similar combinatory manipulations (Breen et al., 2016; Hansell & Ruxton, 2008; Hayashi, 2015). Field studies demonstrate a large degree of flexibility in nest-building behaviour in all great ape species, particularly with regard to nest height, rates of nest reuse, tree species selectivity and the use of additional comfort elements (reviewed in Anderson et al., 2019; Fruth et al., 2017). However, so far there has been no detailed investigation into the ontogeny of the behaviour in the wild.

Many nest-building species such as eusocial insects (termites, wasps and bees, Jeanne, 2009; ants, Moreira et al., 2004; Tschinkel, 2004) and rodents (Neely et al., 2019) can build nests from an early age, with no extensive learning period and without the presence of others. Nest building in these species is therefore traditionally viewed as a developmentally canalized, genetically anchored behaviour. In birds, there is increasing evidence that experience and learning likely also play a role, at least in some species (Breen et al., 2016). However, due to a limited number of studies, the modern view persists that nest building in birds is an instinctive behaviour (see Healy et al., 2023). Research on great apes, however, has demonstrated that nest building in these animals is not instinctive but is a learned skill. For example, when provided with nesting materials under controlled conditions, captive-born chimpanzees spent little to no time building nests compared to wild-born counterparts and in instances where an attempt at nest building was made, captive-born animals used less advanced construction techniques, such as tucking branches in, rather than weaving. Furthermore, mother-reared captives spent more time building nests than those reared in a human-led nursery (Videan, 2006). An absence of role models or a lack of opportunity for practice has also been shown to leave young captive apes as incompetent adult nest-builders, that is, not able to build functional nests (Bernstein, 1962; Lethmate, 1977; McGrew, 2004; Videan, 2006). In the wild, immature orang-utans spend years closely observing the nest-building behaviours of their mother and other models and practise building nests before becoming competent nest-builders themselves (Schuppli, Meulman, et al., 2016; van Noordwijk & van Schaik, 2005). There is thus already some evidence that young apes acquire their nest-building behaviour through some form of asocial or social learning in the wild.

As the most prolific nest-builders of all the great apes (Permana, 2022), orang-utans present an ideal model to study the behaviour. The purpose of this paper is thus to describe the details of the ontogeny of nest-building behaviour in a population of wild Sumatran orang-utans. We focus on when different elements of nest building emerge, namely, day and night nests, multitree nests, additional comfort elements and twig adjustments, but we do not attempt to explain the mechanisms underlying the development. Consistent with their arboreal lifestyle, orang-utans (*Pongo* spp.) build their nests almost exclusively in trees, so nests must be secure enough to support their large body weight (Galdikas, 1978; Prasetyo et al., 2009). Adult orang-utans build a ‘night nest’ every evening to spend the night in and often ‘day nests’ for rest during daylight hours (Prasetyo et al., 2009). Whereas most orang-utan nests are built using a single tree, at times multitree nests are made where branches from multiple trees are included in the foundation of a single nest. These nests are mostly positioned on side branches away from the main tree stem thus relying on multiple small branches, rather than one or two larger branches to secure the weight of the nest and user. Likely due to the lack of large supporting branches, multitree nests also use more complex manipulations to secure branches than single-tree nests (Permana, n.d.).

Additional comfort elements, such as linings, pillows, blankets and roofs are flexibly added to orang-utan nests (Table 1), which enhance physical comfort and serve as protection against cold and rain by increasing the insulating properties of nests (Permana, 2022; Prasetyo et al., 2009; Stewart et al., 2018). When constructing these elements, individuals may or may not pass the twig ends past their mouth sometimes lightly biting the ends, seemingly to blunt sharp ends before placing them in the nest (‘twig adjustment’). As multitree nests, additional comfort elements and twig adjustments represent features of nest building that are made in addition to what is needed to produce a functional nest foundation, the total number of actions performed by the nest-builder is greater than absolutely necessary. In this paper, we therefore refer to these aspects of nest building as ‘multistep nest features’. During the nest-building process, individuals may also regularly produce vocalizations (so called ‘nest sounds’), which are more likely to be produced during night nest construction (Hardus et al., 2009; Paul, 2007; Prasetyo et al., 2009; Schuppli & van Schaik, 2019; Wich et al., 2012). Night nest construction is arguably more critical than day nest construction because night nests are used for a longer

Table 1
Definitions of orang-utan behaviours and nest elements

Behaviour	Definition
Nest	A construction consisting of branches, twigs and leaves (bent, broken, transferred) manipulated to create a resting site in a tree (Fruth, 1995). We defined all nests that were used for resting $\geq$ 1 min after their construction as functional nests
Nest practice	Unsuccessful attempt to build a functional nest (by bending and intertwining leafy branches) or seemingly successful construction of a nest without using it (Schuppli, Meulman, et al., 2016)
Nest Features and Additional Comfort Elements	
Twig adjustment	Manipulating endings of twigs with the mouth before working them into the nest construction (Prasetyo et al., 2009)
Multitree nest	Several trees connected into a single nest by bending and locking branches from each tree together (Prasetyo et al., 2009)
Nest sounds	Sounds produced during nest construction. At Suaq Balimbing this commonly includes the ‘raspberry’ sound (Hardus et al., 2009)
Lining	Smaller branches with many leaves bent onto the nest foundation to create a layer (Prasetyo et al., 2009)
Pillow	Small leafy twigs arranged on one side of the nest (Prasetyo et al., 2009)
Blanket	Loose leafy branches laid on top of the body after animal lies down in the nest (Prasetyo et al., 2009)
Roof	Loose cover of braided branches woven together to make a solid, nearly waterproof, shield (Prasetyo et al., 2009)

duration and have greater requirements in terms of thermoregulation and comfort. Day nests are smaller than night nests; have fewer layers and are less likely to have additional elements such as pillows and linings (Permana, 2022). Accordingly, day nests are constructed much faster than night nests (Permana, 2022; Prasetyo et al., 2009).

Successful nest building requires two key stages: selecting an appropriate location and constructing a functional nest, that is, a nest that does not fall apart when being used (see methods, Table 1 for definitions). Orang-utans are selective in several aspects of their nest building, including disproportionately selecting nest tree species and nesting materials according to their availability (Ancrenaz et al., 2004; Cheyne et al., 2013; Permana, 2022; Rayadin & Saitoh, 2009; van Casteren et al., 2012), a phenomenon that has also been observed in other apes (reviewed by Fruth et al., 2017) and some bird species (e.g. Biddle, Broughton, et al., 2018; Blem & Blem, 1994; Quintana & Travaini, 2000). While the drivers of nest tree species selectivity in orang-utans are not yet understood, it is likely to be influenced by a number of environmental and social factors (Permana, 2022; Stewart et al., 2018). Given the extended learning time in nest building in apes (Schuppli, Meulman, et al., 2016), species selectivity in these animals may be a learned skill, dependent upon knowledge of the properties of different tree species, including wood density, fracture behaviour, leaf size and branch architecture (Permana, 2022; van Casteren et al., 2012).

Orang-utans have the longest immature period and interbirth interval of all great ape species (van Adrichem et al., 2006; van Noordwijk et al., 2009; van Noordwijk & van Schaik, 2005). Orang-utan infants receive dedicated maternal care until weaning around 6–9 years. For the first 2–3 years of life, dependent immature orang-utans are frequently carried by their mothers and remain largely within a 2 m radius of her. After weaning, immatures begin to venture further from their mothers to distances of more than 50 m (Chappell et al., 2015; Knott et al., 2009; van Noordwijk et al., 2009; van Schaik & Isler, 2021; Wich et al., 2009). Independent orang-utan immatures spend extended periods of time ranging on their own but also regularly associate with other individuals, including peers and other adults (van Noordwijk et al., 2009). Orang-utan females have their first birth around 14–16 years of age. The long dependency period provides plenty of time to develop competence in nest-building behaviour.

According to the ‘needing to learn’ hypothesis (Janson & van Schaik, 1993; Ross & Jones, 1999), by the time immature individuals reach independence they should have mastered all basic subsistence skills. This is especially true for species that do not permanently live in groups and thus cannot rely on the knowledge of others. Applied to orang-utans and the nest-building context, this means that, by independence, immatures should have all the necessary knowledge and skills required to construct fully functional day and night nests. Immature orang-utans are believed to begin to practise nest building at around 6 months of age (Prasetyo et al., 2009) and by the age of 3 years, immatures seem to be capable of building a nest good enough for a daytime nap or for play (van Noordwijk & van Schaik, 2005). In the nest-building context, practice behaviour involves the investigation of materials and repeated attempts at nest construction (Jaeggi et al., 2010; King, 1994; Schuppli, Meulman, et al., 2016; Schuppli et al., 2020). It has been suggested that skill refinement continues through repeated practice until independence from their mother and even into adulthood (see Horr, 1977; MacKinnon, 1974; Rijksen, 1978; Russon et al., 2007; Sugardjito, 1983) but this is yet to be evaluated in the field. Furthermore, we lack studies on details of the ontogeny of orang-utan nest-building behaviour, including at what age nest tree species selectivity and multistep features occur.

In this study, we aimed to investigate and describe the ontogeny of nest-building behaviour in a population of wild Sumatran orang-utans at the Suaq Balimbing monitoring station. Detailed data on nest-building activities have been collected at Suaq since 2007. The population represents the highest density of orang-utans in the world, allowing for data collection on a large number of individuals (Singleton et al., 2009; van Schaik, 1999; Wich et al., 2004). Furthermore, orang-utans at Suaq Balimbing construct day nests on a regular basis (Permana, 2022), data on which allowed us to conduct differentiated analysis of the learning trajectories for day and night nest construction.

Skills that are learned need to be practised over extended periods of time before they are fully mastered (Boesch & Boesch-Achermann, 2000; Jaeggi et al., 2010; Meulman et al., 2013; Ottoni et al., 2005; Schuppli et al., 2012). Specifically, we predicted that: (1) nest practice behaviour begins several years before functional nests are successfully constructed; (2) the construction of functional night nests and multistep nest features (i.e. multitree nests, nests with additional comfort elements and twig manipulations) appear late in development because they entail more steps that need to be learned and coordinated appropriately and thus need to be practised over longer periods; (3a) as a result of needing to learn about which trees are most suitable as nest trees, tree species selectivity will emerge only gradually during development; and (3b) due to physical proximity, young immatures will exhibit more similar nest tree species choices to mothers than older immatures, who travel independently and associate with other adults and peers more often.

METHODS

Data Collection

Data were collected by 51 experienced observers on wild Sumatran orang-utans at the Suaq Balimbing monitoring station (3°02.873′N, 97°25.013′E) between 2007 and 2020. Interobserver reliability was assessed regularly between experienced and incoming observers via simultaneous follows of the same focal animal. New observers had to reach a Cohen's kappa of $k > 0.8$ (Bakeman & Quera, 2011) with an experienced observer before their data were included. The 350 ha study area is mainly peat swamp forest, located in the South Kluet region of the Gunung Leuser National Park in Nanggroe Aceh Darussalam, Sumatra, Indonesia. Mixed dipterocarp and riverine forest border the area to the west and east. A full account of habitats in the area can be found in van Schaik (1999).

Our full data set included 45 recognized individuals: 20 mothers and 27 immatures (two of these individuals were included as mothers and immatures). Immature animals were classed as dependent (still ranging constantly with their mothers: 0 to around 8 years) or independent (observed at least once without their mother for a minimum of 3 consecutive days but not yet at reproductive age: around 8–15.5 years). The average age at independence of the individuals in our data set was 8.6 years (6.6–8.9). Previous estimates state an average weaning age at Suaq of 7–9 years and age at first reproduction as 15–16 years (van Noordwijk et al., 2018). As data collection spanned over a decade, seven dependent immatures were followed throughout their immature years and two independent immatures became mothers (this includes one female who was followed from dependency through to motherhood). Details on the focal individuals included in our analyses are summarized in Table A1.

Standardized activity data were collected by trained researchers, students and field assistants during opportunistic focal animal follows via instantaneous sampling (Altmann, 1973) at 2 min intervals. Whenever possible, focal animals were followed from their morning to their evening nest for a maximum of 10 consecutive days after which they were left alone, and another focal animal was sought. As focal animals were encountered opportunistically, our data often have gaps of several months where individuals were not seen. In addition to the activity data, we collected all-occurrence data on nest building and nest practice behaviour. For each such event, details including the nest-building duration, nest type (day nest or night nest) and nest tree species were recorded on standardized data sheets. This included information on whether the nest was made in a single or multiple trees and whether the nest-builder made additional comfort elements (lining, pillow, blanket or roof; see Fig. 1), manipulated twigs of the nests with the mouth before incorporating them (twig adjustments) and made nest sounds during the construction process (see Table 1 for definitions of the behaviours). All-occurrence data on nest practice behaviour were collected by a subset of the observers and, therefore, sample sizes vary between our different analyses (see Table A1 for an overview of the sample size).

Ethical Note

The research protocols in this study were approved by the Ministry of Research and Technology (RISTEK. Research Permit No.2017/FRP/SM/VIII/2008, No.: 152/SIP/FRP /SM/V/2012 and following) and adhered to all relevant legal requirements for research in Indonesia. Our study was strictly observational and researchers did not interact with study animals in any way.

Species Selectivity

In assessing the choices made regarding nest tree selectivity, a selected species is defined as one that is chosen and used with disproportionate frequency relative to its abundance in the habitat (Manly et al., 2002). We used the Manly's alpha selectivity index to assess the selection of nest tree species as it controls for the fact that nest trees remain available in the habitat for potential reuse following their initial selection. The equation for calculation of Manly's alpha is shown in the Appendix (Smith et al., 2018).

Figure 1. Sumatran orang-utan night nest in a *Sandoricum beccarianum* tree. A pile of Y-shaped pillow twigs is visible at the top edge of the nest; larger lining branches cushion the supporting frame of the nest. Some lining branches are detached (brown leaves), while some are still attached to the supporting tree (green leaves). Supporting frame branches are visible to the bottom left and bottom right of the photo. Photograph: Junaidi Jaka Permana.

Nest tree species selectivity data were separated according to nest type as a day or night nest. Manly's alpha analysis was used to identify species selected by mothers, dependent immatures and independent immatures. Tree species used by individuals followed over multiple age classes were separated into the relevant age class according to their status at the time of the nesting event, facilitating analysis of any changes in tree species choice over time. We used the frequency of species recorded from phenology plots to represent species availability. Plots included all trees with a DBH (diameter at breast height) $\geq$ 10 cm along established transects and included 43 identifiable species representing 1427 stems. We excluded nests located in climbing figs, lianas and species not found in the plots due to identification uncertainties. Owing to a lack of phenology and knowledge of botanical species in bordering riverine and hill forest zones, nests constructed in these areas were removed for the purposes of the species selectivity analysis ($N = 257$ nests, which included $N = 45$ nests in *Neesia* sp.). This left a total of 1040 day nests (Table A2) and 929-night nests (Table A3; Total $N = 1969$). Species identities were confirmed using samples collected in the field by A.P. with the National Herbarium of Indonesia in partnership with the National University of Indonesia in Jakarta (UNAS). Multitree nests constructed by mothers and immatures accounted for 11% of all nests in the sample. In most of these cases it was possible to accurately identify which of the trees represented the 'main' support tree. In the selectivity analysis we therefore only included the principal nest tree (i.e. the tree providing most of the support to the frame of the nest) as an indicator of species choice.

Data Analysis

All analyses and plots on multistep nest features and nest practice were done using the R programming language (R Core Team, 2019). To investigate development of the use of multistep nest features (prediction 2), we used generalised linear mixed models (GLMMs) with a binomial family distribution because of the binomial response variables (presence or absence of a multitree nest, comfort elements or twig adjustments) as implemented in the lme4 package (Bates et al., 2015). Nest type (day or night nest) was included as a control (in the form of a fixed effect) because previous studies have shown that the occurrence of these elements differs between day and night nests (see above). To avoid pseudoreplication and account for systematic interindividual differences, we included the individual as a random effect. To assess the overall effect of our predictors, we tested each of the full models (including all predictors, controls and random effects) against its corresponding null model (including the controls and random effects only) using a likelihood ratio test (LRT) via the anova function. When the full model was supported, in a second step we then looked at the significance of the individual predictors as directly retrieved from the model output in the lme4 package (Bates et al., 2015). We investigated differences between the multilevel categorical variable age–sex class using post hoc tests as implemented in the glht function of the multcomp package (Hothorn et al., 2016). For all GLMMs, we tested for over/under dispersion and zero inflation using the testDispersion and testZeroInflation function in the DHARMa package in R (Hartig, 2021). We found no evidence for dispersion issues or zero inflation in any of the models.

To statistically assess nest tree species selection, species identified as being selected out of proportion to their availability according to their Manly's alpha value ($\alpha \geq 1/m$; see Appendix) were tested with a two-way binomial test using the binom.test function in R. Plots of species selectivity were made in Excel version 16.75. Overlaps in nest tree species use between age classes was assessed using the Jaccard similarity index (see Appendix) and tested for significance using Fisher's exact test.

RESULTS

Does Nest Practice Begin before Functional Nest Construction?

Nest construction and practice data included 20 mothers (522 day nests and 674 night nests), 18 independent immatures (203 day nests and 404 night nests) and 16 dependent immatures (315 day nests and 44 night nests). Play with nesting materials (twigs, branches and leaves) began from 6 months of age (mean youngest and maximum ages, ± SD of minimum age: 0.5 years, 7.3 years, ± 1.7, $N = 7$ individuals). The youngest individual to build a functional day nest was 1.0 years (mean youngest and maximum ages, ± SD of minimum age: 3.2 years, 4.9 years, ± 1.5 years, $N = 6$ individuals) and the youngest individual to construct a functional night nest was 2.8 years (mean and maximum ages, ± SD of minimum age: 5.0 years, 6.4 years, ± 1.6 years, $N = 4$ individuals), although none of the night nests produced by dependent immatures were used for sleeping and it was not until the age of 6.6 years that an immature was observed to spent the whole night in their own night nest. We found that nest practice rates peak at around age 3–4 years (Fig. 2), followed by a continuous drop with increasing age. By the end of the dependency period, around 8 years, practice rates reached close to zero.

Do Multistep Features of Nesting Appear Late in Development?

Looking at when multistep features of nest building appeared, i.e. the construction of multitree nests, the construction of additional comfort elements and the use of twig adjustments, we found all the full models for multitree ness and additional comfort elements fitted the data better than the null models (LRT $_{\text{multitree}}$: chi-square = 39.057, $P < 0.001$; LRT $_{\text{comfort elements}}$: chi-square = 14.346, $P = 0.002$; see Table 2 for details of the full models) but the full model for twig adjustments did not fit the data better than the respective null model (LRT $_{\text{twig adjustments}}$: chi-square = 3.736, $P = 0.291$).

The full model on the construction of multitree nests indicated that dependent and independent immatures were significantly less likely to construct multitree nests than mothers (Table 2, Fig. 3a). The full model on the construction of additional comfort elements revealed that immatures constructed nests that contained one or more of these elements significantly less often than mothers (Table 2, Fig. 3b). Detailed analyses of individual comfort elements found that linings, pillows and blankets showed the same pattern across the age classes and that dependent and independent immatures were significantly less likely to construct individual comfort elements in their nests than mothers. There was no effect of age class on roofs, perhaps because roofs were the rarest additional element (only 5.5% of all nests had roofs), which may make detecting effects difficult (Table A4).

Does Nest Tree Species Selectivity Emerge Gradually?

Day nest tree species selectivity across age classes

Seventeen individual mothers used 27 species for day nest construction ($N = 522$). Manly's alpha analysis found 10 species were selected proportionally more than their availability (i.e. Manly's threshold was exceeded, or $\alpha \geq m$; Smith et al., 2018; Fig. 4a) and two species were statistically significant (two-way binomial tests: *Gymnacranthera contracta*, $P = 0.04$; *Horsfieldia polyspherulla*, $P = 0.005$). Fifteen independent immatures used 23 tree species for day nest construction ($N = 203$). Ten species were positively selected (Fig. 4a), three significantly so (two-way binomial tests: *Xylopia malayana*, $P = 0.05$*; Sandoricum beccarianum*, $P = 0.003$; *Jackiopsis ornata*, $P < 0.001$). For the eleven dependent immature individuals in our data set, 23 species were used for day nest construction or nest practice ($N = 315$). Seven species were selected (Fig. 4a), six significantly so (two-way binomial tests: *J. ornata*, $P = 0.001$; *Tetramerista glabra*, $P < 0.001$; *G. contracta*, $P = 0.03$*; S. beccarianum*, $P = 0.005$; *Brackenridgea palustris*, $P = 0.04$; *Sterculia oblongata*, $P < 0.001$). Table A2 summarizes the

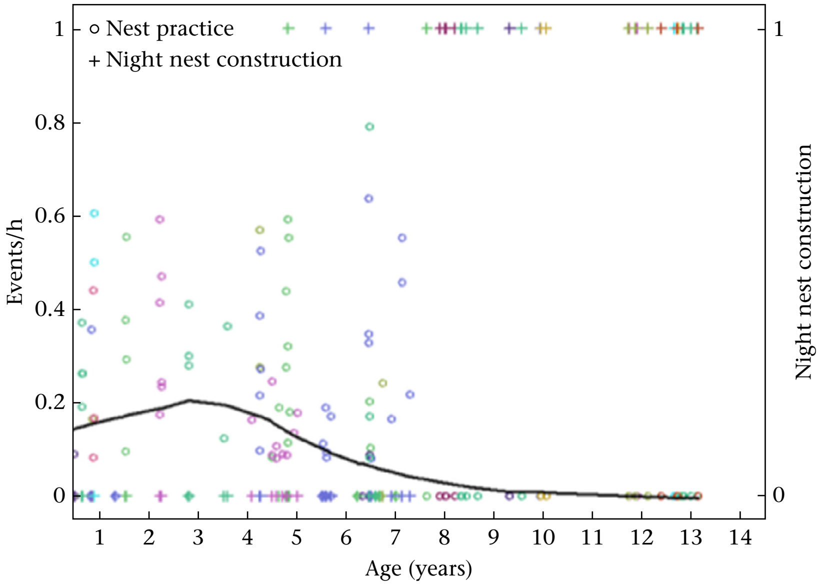

Figure 2. Nest practice and night nest construction as a function of age. Daily nest practice rates (including day and night nest practice) and successful construction of their own night nest in relation to the age (years) of the immature focal individuals. For night nest construction, 1 means that the individual did successfully build their own night nest on that day and 0 means that the individual did not build a night nest on that day (or attempted to but failed). The different colours represent the different focal individuals that contributed data to this analysis. The solid line represents the regression line for nest practice and was fitted using the loess function.

Table 2
Development of the use of multistep nest features

Response	Factor	Factor type	Estimate	SE	*P*	Dispersion	O/P
Multitree nest	Intercept	Intercept	−2.2235	0.132	<0.001	0.999	1.000
	Class:	Predictor					
	I vs M		−0.6937	0.192	**<0.001**		
	D vs M		−2.118	0.593	**0.001**		
	Nest type (night)	Control	0.5707	0.156	<0.001		
	Individual	Random	–	–	–		
Additional comfort elements	Intercept	Intercept	2.898	0.275	<0.001	1.163	1.166
	Class:	Predictor					
	I vs M		−0.565	0.257	**0.028**		
	Ds M		−1.262	0.379	**<0.001**		
	Nest type (night)	Control	0.098	0.189	0.606		
	Individual	Random	–	–	–		

The effects of the age class of the nest-builder (M = mother, I = independent immature, D = dependent immature) and nest type (day or night), on the probability of constructing a multitree nest and the construction of additional comfort elements analysed with a GLMM with a binomial family distribution. Dispersion: dispersion parameter; O/P: ratio of observed to predicted zeros. Significant *P* values of the predictors are in bold.

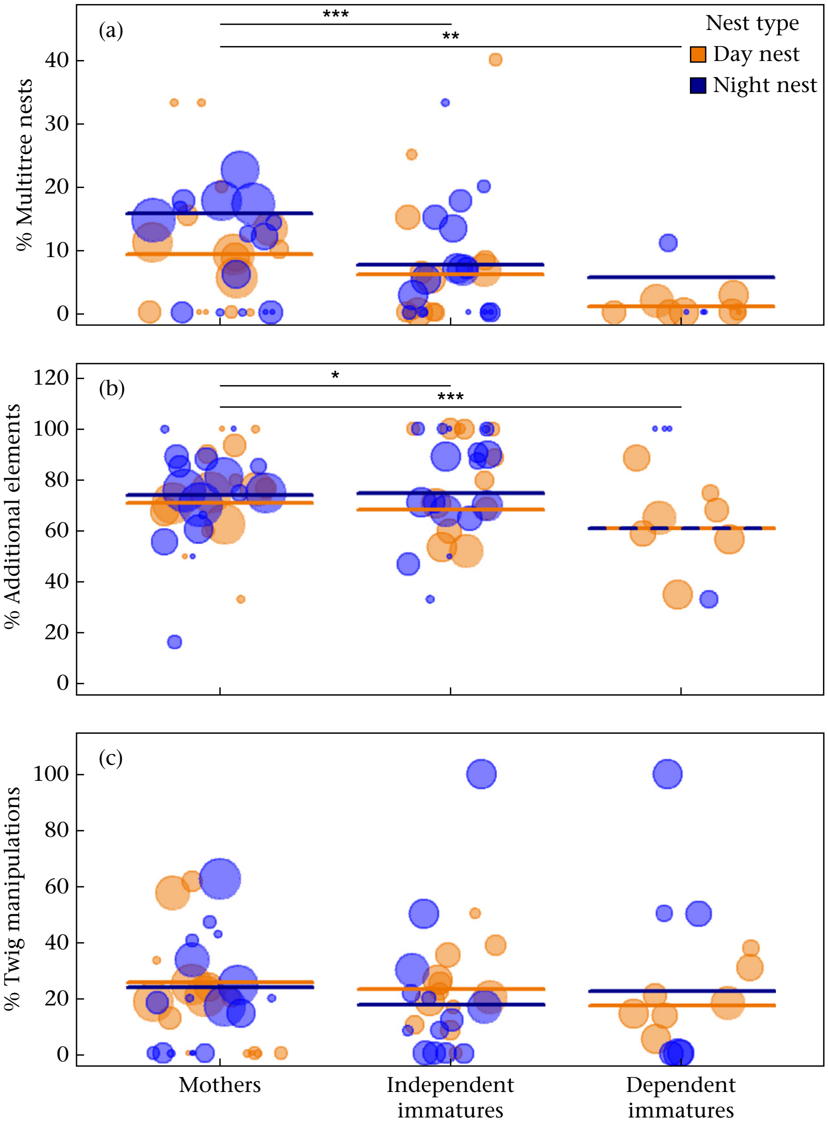

Figure 3. Multistep features of nest building across age classes and nest types. (a) Percentage of multitree nests. (b) Percentage of nests that had at least one additional comfort element (i.e. lining, pillow, blanket or roof). (c) Percentage of nests for which twig adjustments were used. Within each age class, each data point represents one individual. The symbol size represents the total number of nests constructed by each individual in each age class available in the data set following a natural logarithmic scale. Bold coloured lines represent the weighted means for day and night nests. The black lines connecting the plots indicate significance: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

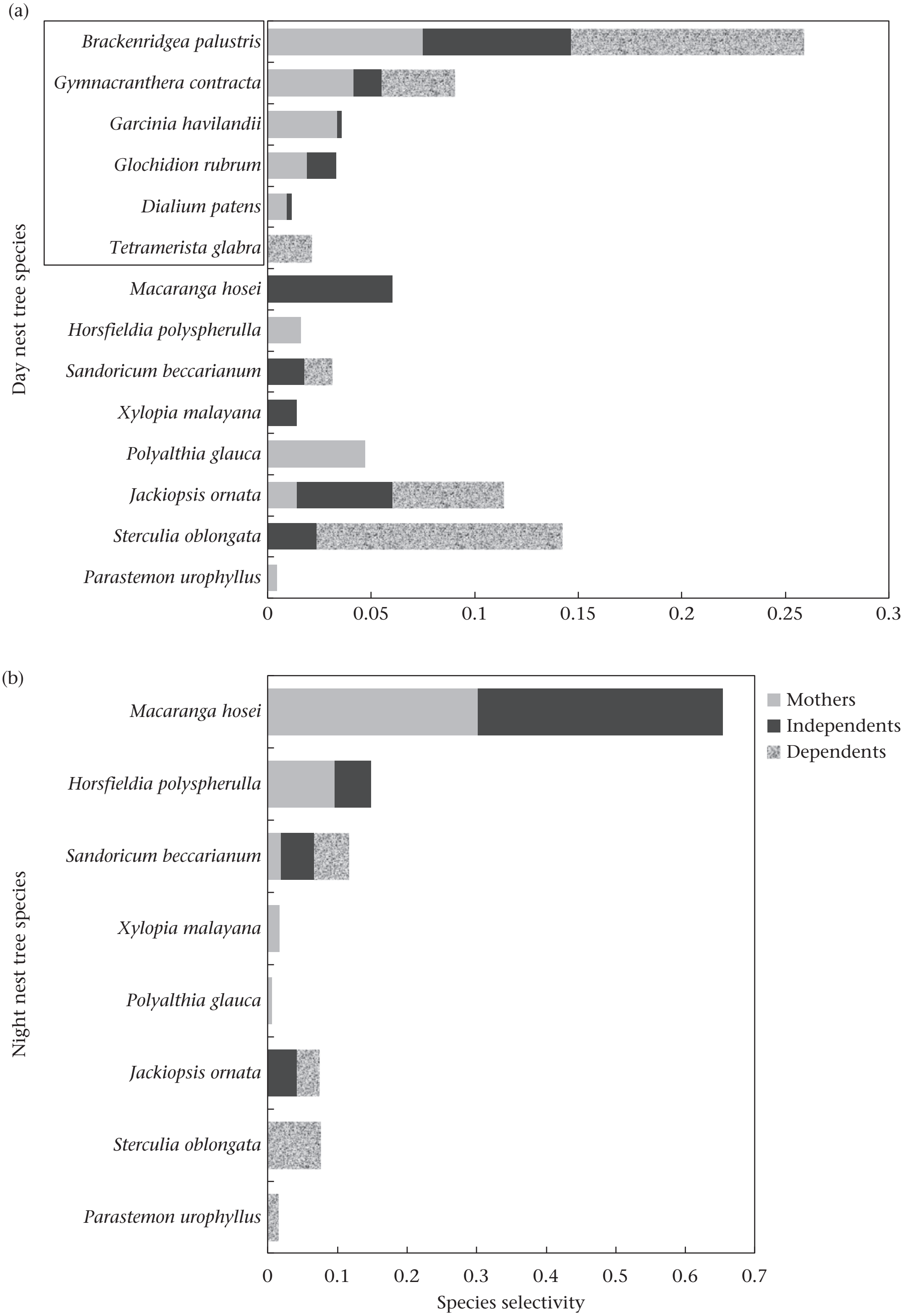

Figure 4. Selectivity strength for tree species used for (a) day nests and (b) night nests by mothers, independent immatures and dependent immatures. Bars are stacked to show the total strength of the Manly's alpha selectivity index for each species. The black box indicates tree species selected exclusively for day nests. The strength of the selectivity for each nest tree species was calculated by subtracting the threshold value ($1/m$) for each age class's nest type from the Manly's alpha of each species (see Appendix).

results showing all species positively selected for the day nest constructions of mothers, independent immatures and dependent immatures.

Night nest tree species selectivity across age classes

Nineteen individual mothers used 25 species for their night nests ($N = 655$). Manly's alpha analysis found six of these were positively selected. Statistically, three were significant (two-way binomial tests: *S. beccarianum*, $P < 0.001$; *Macaranga hosei*, $P < 0.001$; *H. polyspherulla*, $P < 0.001$). From our sample of 19 independent immatures, 19 species were used within a sample of 257 night nests. Four tree species produced alpha values above the Manly's threshold and statistically all were significant. Three of those species were the same as those significantly selected by mothers (two-way binomial tests: *J. ornata*, $P = 0.006$; *S. beccarianum*, $P < 0.001$; *M. hosei*, $P < 0.001$; *H. polyspherulla*, $P < 0.001$). Seventeen dependent immature night nests were available for analysis; these included eight tree species used by six individuals. Of the eight species, four were positively selected from the habitat (Fig. 4b) but we found no statistical significance to the selections. Table A3 summarizes the results on species selectivity analysis for the night nests of mothers, independent immatures and dependent immatures.

How Do Immatures' Tree Species Choices Compare to Mothers'?

We compared the tree species used for day and night nests made by immature animals with the species used by mothers. Jaccard's similarity index showed that species used for dependent immature day nest building were 85% similar to those used by mothers and tree species used for night nests were 32% similar. Tree species used by independent immatures displayed a 79% overlap with mothers for day nest building and a 76% overlap in the tree species used for night nest building.

Dependent and independent immatures shared 77% of day nest tree species and 42% of night nest tree species. The proportions of tree species shared between the three classes are illustrated in Fig. 5. A Fisher's exact test confirmed that the tree species used for day nests between the three classes were similar ($P = 0.11$) but the tree species used for night nests were significantly different between the three classes ($P = 0.0001$).

DISCUSSION

Does Nest Practice Begin before Functional Nest Construction?

We found that infants began to investigate nest materials, including adding leaves and twigs to the mother's nests, bending and breaking branches and making initial attempts at forming circular nest foundations from 6 months of age, progressing to attempted construction of day nests at around a year of age. This interest in nest-building practice continued until it peaked around age 3–4 years before trailing off as the age of independence approached. In our data set, attempts at night nest construction were observed from 2.8 years. Wild chimpanzees similarly make their first attempts at day nests between 8 and 12 months of age and night nests at 3–5 years (Van Lawick-Goodall, 1968). Captive chimpanzees also demonstrate simple object–object combinations (relating an object with another object) at a similar age (Hayashi & Matsuzawa, 2003), while captive orang-utan infants may begin to use objects as tools (relating an object with a substrate, Bard, 1992) around age 2 years. By 3 years of age, all captive great apes display a marked increase in play and trial-and-error behaviour (Parker & Gibson, 1977, 1982). In human children, this is observed around the age of 2–6 years (Piaget, 1967). All in all, this evidence suggests that the development of orang-utan nest building in the wild closely mirrors manipulative and trial-and-error behaviours as they appear in captive animals and humans.

Our observations of immatures around weaning age found that despite being capable of building functional night nests, it was not until age 6.6 years that an immature was observed to spend the whole night in their own night nest. This coincided with a sharp drop in nest practice rates (Fig. 2). A possible explanation for these results may lie in our field observations of weaning-age immatures at night nesting time. Often, immatures constructed a functional night nest a few metres above the mother's nest. However, after entering their own nest for a while, they would regularly move to their mother's nest; where they might, or might not, stay for the remainder of the night. Occasionally, we would find immatures who went to sleep in their own nest but then were observed waking in their mother's nest the following morning. Sometimes, immatures were also observed to ‘nest-hop’, where they would make their own night nest but move several times between it and their mother's nest over the course of a night. Viewed with our results on the ontogeny of night nest construction, this suggests that the transition from co-sleeping with the mother to solitary sleep is likely a gradual process. Delaying the move to solitary nocturnal sleep may be adaptive, as it could improve survival by delaying total separation from the caregiver. In primates, this can cause a decrease in body temperature, the release of stress hormones, cardiac arrhythmias, compromise of the immune system

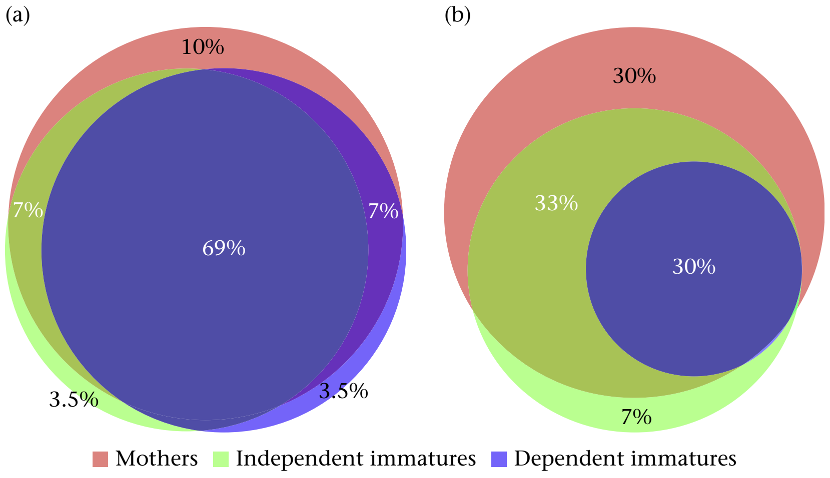

Figure 5. Area-proportional percentage overlap of nest tree species used by mothers, independent immatures and dependent immatures. (a) Day nest trees, total number of species used: mothers, $N = 27$; independent immatures, $N = 23$; dependent immatures, $N = 23$. (b) Night nest trees, total number of species used: mothers, $N = 25$: independent immatures, $N = 19$; dependent immatures, $N = 8$. The size of each circle corresponds to the number of species used by each group. Percentage values show the percentage of species overlap between or unique to each group (area-proportional Venn diagrams; Hulsen et al., 2008).

and sleep disturbance (McKenna et al., 1993). The results presented in this study do not facilitate any conclusions regarding the underlying mechanisms involved. However, the data and observations presented suggest that the development of nest-building skills may follow stages in physical, cognitive, physiological and emotional development. Further investigation into underlying mechanisms is warranted to fully understand the development of nest-building behaviour in the great apes.

Do Multistep Features of Nesting Appear Late in Development?

In line with our predictions, we found that functional day nests were constructed before functional night nests. Day nests used fewer and more simple manipulations, had fewer layers and, when made by adults, were also less likely to incorporate additional comfort elements (Table 1, Table A4; Permana, 2022). We also found that even when controlling for nest type (i.e. day versus night nest), multitree nests were less likely to be constructed by immatures than mothers (Table 2, Fig. 3a) and while the inclusion of additional comfort elements such as pillows and blankets appeared during the dependency period, these elements occurred less frequently in dependent and independent immature nests compared to those of mothers (Table 2, Fig. 3b). These results support our prediction that these nest features require more time to master. This may be because they involve multiple steps to produce, potentially requiring multiple decision-making steps, increasing the demand on working memory, which may still be developing in younger apes (Lacreuse et al., 2020; Manrique & Call, 2015; Zhou et al., 2016). Further investigation into the mechanisms involved here is required to fully explain these patterns.

A similar developmental trajectory is seen in the development of complex foraging skills: Immature orang-utans first develop competence with food items that require low levels of preingestive processing before they master ones that require multistep processing (Jaeggi et al., 2010; Schuppli, Forss, et al., 2016). In the realm of tool use, simple tools are mastered before more complex ones after reaching independence (Meulman et al., 2013; Schuppli, Meulman, et al., 2016). In the nest-building realm, data on lining, pillow and roof structure (Permana, n.d.) imply that the construction of multistep nest features by young orang-utans may be constrained by the manipulative complexity required to assemble them. Our results are in line with findings across species, which show that many of the manipulative skills of larger-brained species require extended periods of maturation due to their developmental trajectories (Heldstab et al., 2020; Schuppli et al., 2012). Adult levels of skill competence and dexterity also take longer in larger-brained primate species compared to those with smaller brains (Heldstab et al., 2020). We did not find an age effect for the occurrence of twig adjustments (Fig. 3c). However, upon analysis of the data, we found that it was impossible to distinguish undirected oral twig biting resulting from trial-and-error during the nest-building process from skilled, goal-oriented twig adjustment. As twig adjustment is a cultural variant the functional significance of which is poorly understood, this is another area of nest-building behaviour that warrants further investigation.

Advanced physical development (i.e. body growth and thus also strength) may also be required for the manipulation and construction of certain nest features. This may explain to some extent why day nests were mastered before night nests and why multitree nests and nests with additional elements appeared late in development. Pulling trees together for the construction of multitree nests certainly often requires physical strength that may be beyond the ability of small immatures. Furthermore, immatures tend to nest much higher (where branches tend to spread wide and canopies overlap less) than adults, particularly at night (Permana, 2022), which may also explain the low levels of practice and occurrence of multitree nests in this age class. A detailed study of nest-building behaviour at Suaq found that multitree nests and additional comfort elements are more commonly constructed by flanged males and mothers compared to unflanged males and adult females without infants (Permana, 2022). Differences in the construction of multitree nests and nests with additional elements may therefore also reflect differences in body weight or physiological changes driving the need and ability to construct additional comfort elements. Detaching small twigs and branches needed for the construction of additional comfort elements such as pillows or blankets does not require physical strength beyond an immature's ability, however, making a lack of physical ability alone unlikely to explain their low occurrence.

Night nest construction is more critical than day nest construction due to constraints on thermoregulation and comfort. As additional comfort elements increase the thickness of a nest and contribute to its thermal capacity, they would be especially beneficial to independent immatures, for whom the need to stay warm during the night is more pertinent, due to their higher surface area-to-volume ratio and poorer ability to conserve heat (Permana, 2022). It therefore seems reasonable to suggest that, although the beginning of night nest construction practice and use of additional nest elements may be constrained by the development of the brain and nervous system, it may also be driven by the onset of weaning and a drop in parental investment and attachment (see above).

Does Nest Tree Species Selectivity Emerge Gradually?

Studies on the great apes are greatly lacking information regarding the ontogeny of nest tree species selection. We found that for day (Table A2) and night nest trees (Table A3), species repertoires and species selectivity increased with age, with mothers showing the largest species repertoires and the largest numbers of preferred species. Orang-utans (van Casteren et al., 2012) and some birds (e.g. *Turdus merula*, Biddle et al., 2015) are known to select thicker, stronger and more rigid branches for their nest foundations, which increase the structural stability of their nests. For both night and day nests, selecting a suitable species may therefore be crucial for the construction of a functional nest. Using the wrong species could result in a ‘malfunctioning’ nest, for example if the wood is too weak to support the body weight or if branches are not flexible enough to manipulate and remain secured. We found dependent immatures use species most common in the habitat, rather than those selected by mothers (Table A3), which likely have specific nest tree qualities, such as suitable wood density and insecticidal properties (Permana, 2022). Indeed, field observations often report that young immatures' nests fall apart as soon as they are left, or even while the immatures are using them and remain in the landscape for much shorter lengths of time.

Across all classes, species selectivity was stronger and involved fewer species for night nests than for day nests (Fig. 4). This supports preliminary work on a subset of our data, which found that day nests are made more often in trees with fruit and are always closer to fruiting trees than night nests and that species selectivity is stronger for night nest trees (Permana, 2022). Given that night nests need to be sturdier and more stable for longer periods of use than day nests, it follows that fewer species may be suitable for them. Furthermore, dependent immatures overlapped more with mothers regarding night nest tree species choice than day nest tree species choice (Fig. 5), which may reflect the proximity of dependent immatures to their mother but may also indicate that independent animals are less adventurous in species exploration for their night nest practice.

Our results on species selectivity suggest that species exploration for night nest trees most likely takes place during the day. Tree species most selected by immatures for their night nests were also strongly selected for their day nest constructions, while some of the tree species that mothers only used for their night nests were used by immatures for their day nests. As day nests are only used for short periods of time, this may represent immatures playing it safe: it is less risky to construct a malfunctioning day nest than a malfunctioning night nest when risks of predation, falls and thermal stress become more pertinent. In other words, independent immatures use species used by their mother, which they know are suitable for overnight use for their night nests, so that they are less likely to make errors and only broaden their tree species repertoire once they are confident with the species they know. It is also likely that competent nest-building immatures begin to investigate other tree species as they increase their independence and their physical distance from their mother, when their tendency and opportunities to explore increase. Such explorative behaviour is more common following the observation of trusted expert models (Schuppli, Meulman, et al., 2016; van Schaik et al., 2016). Thus, it remains a plausible explanation for the development of night nest tree species selection and the broader repertoire of independent immatures.

Compared to some of the tree species selected by mothers, tree species selected by immatures such as *J. ornata* and *S. oblongata* tend to have lower wood densities (see Chave et al., 2009; Zanne et al., 2009) and large soft leaves, offering bushy, pliable branches, which may be more readily manipulated into a nest. Most of the day nest tree species selected by immatures were favoured fruiting trees suggesting that they select day nest trees based on their location during the day while feeding, rather than some other physical or chemical characteristic of the tree. It is possible that persistence with the act of trial-and-error night nest building may therefore be facilitated more by the characteristics of the trees selected, rather than their fruit content because orang-utans do not generally forage overnight. Together with physical maturation, cognitive aspects such as motivation, curiosity and memory are probably also important when naïve individuals are faced with years of error-prone practice (Meulman & van Schaik, 2013), which may include misidentification of tree species. Although it has been shown that orang-utans exploit the natural fracturing properties of wood to build strong nests (van Casteren et al., 2012), further work is needed to establish whether it is physical characteristics of tree species or the maturation and strength of the individual that contribute to the delay in preferences for suitable night nest tree species.

Conclusion

Our results showed that orang-utans acquire expertise at nest-building only gradually during development. Specifically, we found that (1) immatures practise with nesting materials from 6 months of age and begin to build nests themselves around the age of 1 year when the tree species used for nesting correspond with those selected by the mother. (2) Night nests are not constructed until around the third year of life, when nest practice also peaks, but they are not exclusively used until weaning at around age 7 years. (3) At weaning age nest practice rates drop sharply, indicating that nest-building skills are likely mastered by this time. (4) By independence, immature orang-utans are competent nest-builders, although the development of multistep skills continues beyond this age. (5) During independence, nest tree species choices continue to develop, and older immatures begin to incorporate species outside their mothers' repertoires.

The results of this study show that orang-utans acquire nesting skills after an extended period of practice and maturation in the wild. Single-step nest-building skills appear before multistep ones, which has also been evidenced in previous studies on object manipulation and tool use in wild and captive great ape populations (e.g. Heldstab et al., 2020; Meulman et al., 2013; Schuppli, Meulman, et al., 2016). As other nest-builders, for example mice and birds, do not exhibit extended ontogenetic periods in the development of manipulative and technological skills (Breen et al., 2021), we suggest that the need to learn subsistence skills and the high energetic demands of their large brain (Mink et al., 1981) may influence the extended immature phase of orang-utans, while the development of multistep skills, perhaps better referred to as 'complex skills', may be attributable to the needing to learn hypothesis. Nest building in some birds, which reach adult size much faster but still delay breeding by some time, suggests a similar need to learn skills (Schuppli et al., 2012) but a stronger innate element (see Healy et al., 2023) and less physiological influence (see McKenna et al., 1993). A full explanation of the evolution of skilled technological behaviour in orang-utans thus remains unclear and open to further investigation.

This study has answered many questions on the development of nest-building behaviour in orang-utans and allows the formulation of hypotheses to be tested in the future regarding the acquisition and development of learnt skills. The fact that skills involved in nest building take around 7 years to develop in the wild requires detailed investigation of the underlying learning mechanism, including forms of social learning.

Author Contributions

A.P. co-conceptualized the study, collected data, wrote the manuscript, did statistical analyses and plots and secured funding. J.J.P. collected data and commented on the manuscript. L.N. collected data and commented on the manuscript. D.P. and S.W. commented on the manuscript. C.v.S. co-conceptualized the study, commented on the manuscript and secured funding. C.S. collected data, co-wrote the manuscript, did statistical analyses and plots and secured funding.

Data Availability

Data are provided in the Supplementary Material.

Declaration of Interest

None.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2024.02.018.

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Appendix

Equations used for nest tree species similarity:

$$\propto_i = \frac{r_i}{ni} * \frac{1}{\Sigma_{j=1}^{m}\left(\frac{r_j}{nj}\right)}, i = 1, \ldots, m$$

α_i = Manly's α for tree species i

r_i = Proportion of species i used for nesting (i and j = 1, 2, 3, …, m)

n_i = Proportion of tree species i available in the habitat

j = an index of summation

m = Total number of tree species available for nesting, established from plots.

Equation 1: Calculation of Manly's alpha

The 'alpha' measures a nest-builder's perception of a species' value as a function both of its abundance and of the abundance of other species present in the forest. Species are considered selected if alpha is greater than $1/m$, and not selected if values are less than $1/m$. A neutral preference is suggested where the value of alpha is equal to $1/m$.

Equation 2: Calculation of the Jaccard Similarity Index

The Jaccard similarity index was used to calculate the percentage overlap of species used between groups.

$$\text{Jaccard similarity index} = \frac{\text{Number of species shared by both sets}}{\text{Total number of species in both sets}} \times 100$$

Table A1

Focal orang-utans

Focal orang-utan name	Sex	Age class	Mother's name	No. of nests included in species analysis	Contributed data to nest practice development	Contributed data to analysis on multistep nest features
Alice	F	Mother	–	19	No	Yes
Bebita	F	Mother		0	No	Yes
Cheech	M	Dependent	Chick	2	No	Yes
Chick	F	Mother		5	No	Yes
Chindy	F	Dependent	Cissy	8	Yes	Yes
		Independent		28	Yes	Yes
Cinnamon	F	Dependent	Cissy	41	Yes	Yes
		Independent		6	Yes	Yes
Cissy	F	Mother		151	No	Yes
Diddy	M	Dependent	Dodi	1	No	Yes
		Independent		12	No	Yes
Dodi	F	Mother		13	No	Yes
Eden	F	Dependent	Ellie	56	Yes	Yes
Ellie	F	Independent	Friska	91	Yes	Yes
	F	Mother		253	No	Yes
Frankie	M	Dependent	Friska	81	Yes	Yes
Fredy	M	Dependent	Friska	35	Yes	Yes
		Independent		13	Yes	Yes
Friska	F	Mother		287	No	Yes
Gani	F	Mother		4	No	Yes
Guntur	M	Independent	Gani	4	No	Yes
Helga	F	Mother		3	No	Yes
Inky	M	Dependent	Infant	1	No	Yes
		Independent		1	No	Yes
Intai	F	Mother		4	No	Yes
Karma	F	Mother		10	No	Yes
Kronos	M	Dependent	Karma	3	No	No
Lilly	F	Dependent	Lisa	27	No	Yes
		Independent		41	Yes	Yes
		Mother		23	No	Yes
Lisa	F	Mother	Cissy	297	No	Yes
Lois	M	Dependent	Lisa	47	Yes	Yes
		Independent		47	Yes	Yes
Luther	M	Dependent	Lisa	0	Yes	No
Nibla	M	Independent		1	No	Yes
Nora	F	Mother		2	No	Yes
Nuk	M	Dependent	Nora	0	No	Yes
Nuzari	F	Independent	Nora	3	No	Yes
Okume	F	Mother		4	No	Yes
Pauline	F	Independent		9	No	Yes

(*continued on next page*)

Table A1 (*continued*)

Focal orang-utan name	Sex	Age class	Mother's name	No. of nests included in species analysis	Contributed data to nest practice development	Contributed data to analysis on multistep nest features
Pepito	M	Dependent	Piniata	0	Yes	No
Piniata	F	Mother		4	No	Yes
Raffi	F	Mother		42	No	Yes
Rendang	M	Dependent	Raffi	5	Yes	No
Sarabi	F	Mother		31	No	Yes
Sazu	M	Independent	Sarabi	7	No	Yes
Shera	F	Independent	Chick	51	Yes	Yes
Simba	M	Dependent	Sarabi	0	Yes	Yes
Sonya	F	Mother		1	No	Yes
Tiara	F	Mother		24	No	Yes
Tina	F	Independent	Rafi	40	No	Yes
Tornado	M	Independent	Tiara	0	Yes	No
Trident	M	Independent	Tiara	25	Yes	Yes
Yulia	F	Independent	–	65	Yes	Yes

Focal orang-utan individuals' names, age class, sex (F: female; M: male), known relationships, the number of their nests included in the nest tree species selectivity analyses and to which analyses they contributed data.

Table A2

Selected day nest tree species according to age class

Species	Family	Observed no. of nests	Proportion of nests in which species used (r_i)	Observed no. of trees available in habitat	Proportion of available trees used (n_i)	Manly's alpha	P	Part eaten
Mothers								
Horsfieldia polyspherulla	Myristicaceae	67	0.12	95	0.07	0.055	**0.005**	F
Gymnacranthera contracta	Myristicaceae	15	0.03	15	0.01	0.079	**<0.05**	S
Garcinia havilandii	Clusiaceae	16	0.03	19	0.01	0.071	0.08	F
Gluta renghas	Anacardiaceae	166	0.32	371	0.26	0.038	0.06	X
Parastemon urophyllus	Chrysobalanaceae	51	0.10	103	0.07	0.042	0.15	F
Dialium patens	Fabaceae	33	0.06	60	0.04	0.046	0.16	F
Brackenridgea palustris	Ochnaceae	4	0.01	3	0.002	0.113	0.16	F
Polyalthia glauca	Annonaceae	5	0.01	5	0.003	0.084	0.20	F
Jackiopsis ornata	Rubiaceae	14	0.03	23	0.02	0.051	0.27	X
Glochidion rubrum	Euphorbiaceae	2	0.003	3	0.004	0.056	0.39	F
Independent immatures								
Jackiopsis ornata	Rubiaceae	12	0.06	23	0.02	0.090	**<0.001**	X
Sandoricum beccarianum	Meliaceae	22	0.11	62	0.04	0.061	**<0.005**	F
Xylopia malayana	Annonaceae	5	0.03	15	0.01	0.058	**0.05**	F
Dialium patens	Fabaceae	16	0.08	60	0.04	0.046	0.07	F
Macaranga hosei	Euphorbiaceae	3	0.02	5	0.004	0.104	0.08	X
Sterculia oblongata	Sterculiaceae	7	0.04	18	0.01	0.067	0.09	S
Brackenridgea palustris	Ochnaceae	2	0.01	3	0.002	0.115	0.13	F
Gymnacranthera palustris	Myristicaceae	5	0.03	15	0.01	0.575	0.20	F
Garcinia havilandii	Clusiaceae	5	0.03	19	0.01	0.454	0.27	F
Glochidion rubrum	Euphorbiaceae	1	0.06	3	0.002	0.058	0.41	F
Dependent immatures								
Sterculia oblongata	Sterculiaceae	25	0.08	18	0.01	0.162	**<0.0001**	S
Tetramerista glabra	Tetrameristaceae	43	0.14	78	0.06	0.064	**<0.0001**	F
Jackiopsis ornata	Rubiaceae	19	0.06	23	0.02	0.096	**<0.001**	X
Sandoricum beccarianum	Meliaceae	30	0.10	62	0.04	0.056	**<0.005**	F
Gymnacranthera contracta	Myristicaceae	10	0.03	15	0.01	0.078	**<0.05**	F
Brackenridgea palustris	Ochnaceae	4	0.01	3	0.002	0.155	**<0.05**	F

Tree species selection by mothers (alpha threshold ($1/m = 0.037$, $N = 522$ nests, 27 species used), independent ($1/m = 0.044$, $N = 203$ nests, 23 species used) and dependent immatures ($1/m = 0.043$, $N = 315$ nests, 23 species used). The Manly's alpha threshold indicates a selected species was positively used out of proportion to its availability ($\alpha \geq 1/m$). Statistical significance was assessed using two-tailed binomial tests; significant results are in bold. Part eaten refers to which part of the tree is eaten by orang-utans (F = fruit, S = seed, X = not eaten).

Table A3
Selected night nest tree species according to age class

Species	Family	Observed no. of nests	Proportion of nests in which species used (r_i)	Observed no. of trees available in habitat	Proportion of available trees used (n_i)	Manly's alpha	*P*	Part eaten
Mothers								
Horsfieldia polyspherulla	Myristicaceae	227	0.35	95	0.07	0.136	**<0.00001**	F
Macaranga hosei	Euphorbiaceae	30	0.005	5	0.004	0.342	**<0.00001**	X
Sandoricum beccarianum	Meliaceae	64	0.10	62	0.05	0.059	**<0.001**	F
Shorea teysmanniana	Dipterocarpaceae	67	0.10	90	0.07	0.042	**0.02**	X
Xylopia malayana	Annonaceae	15	0.02	15	0.01	0.06	0.15	F
Polyalthia glauca	Annonaceae	4	0.006	5	0.004	0.046	0.55	F
Independent immatures								
Horsfieldia polyspherulla	Myristicaceae	64	0.25	95	0.07	0.105	**<0.0001**	F
Macaranga hosei	Euphorbiaceae	13	0.05	5	0.004	0.404	**<0.0001**	X
Sandoricum beccarianum	Meliaceae	40	0.16	62	0.04	0.100	**<0.0001**	F
Jackiopsis ornata	Rubiaceae	14	0.06	23	0.02	0.095	**0.01**	X
Dependent immatures								
Sandoricum beccarianum	Meliaceae	3	0.18	62	0.04	0.101	0.15	F
Jackiopsis ornata	Rubiaceae	1	0.06	23	0.02	0.136	0.40	X
Parastemon urophyllus	Chrysobalanaceae	4	0.24	103	0.07	0.139	0.26	F
Sterculia oblongata	Sterculiaceae	1	0.06	18	0.01	0.173	0.29	S

Tree species selection by mothers ($1/m = 0.04$, $N = 655$ nests, 25 species used), independent ($1/m = 0.053$, $N = 257$ nests, 19 species used) and dependent immatures ($1/m = 0.125$, $N = 17$ nests, 8 species used). The Manly's alpha threshold indicates a selected species was positively used out of proportion to its availability ($\alpha \geq 1/m$). Statistical significance was assessed using two-tailed binomial tests; significant results are in bold. Part eaten refers to which part of the tree is eaten by orang-utans (F = fruit, S = seed, X = not eaten).

Table A4
Effects of age class and nest type on the construction of additional comfort elements

Response	Factor	Factor type	Estimate	SE	*P*	Dispersion	O/P
Lining	Intercept	Intercept	3.134	0.310	**<0.001**	1.123	1.123
	Nest type (night nest)	Predictor	0.080	0.207	0.700		
	Class: M–I	Predictor	−0.803	0.279	**0.004**		
	M–D		−1.374	0.409	**<0.001**		
	Individual	Random	–	–	–		
Pillow	Intercept	Intercept	0.782	0.148	**<0.001**	1.021	1.044
	Nest type (night nest)	Predictor	−0.046	0.124	0.709		
	Class: M–I	Predictor	−0.180	0.171	0.294		
	M–D		0.738	0.252	**0.003**		
	Individual	Random	–	–	–		
Blanket	Intercept	Intercept	−1.941	0.302	**<0.001**	0.863	1.030
	Nest type (night nest)	Predictor	0.238	0.191	0.214		
	Class: M–I	Predictor	−0.750	0.332	**0.024**		
	M–D		−1.212	0.538	**0.024**		
	Individual	Random	–	–	–		
Roof	Intercept	Intercept	−2.375	0.167	**<0.001**	0.994	1.001
	Nest type (night nest)	Predictor	0.149	0.202	0.459		
	Class: M–I	Predictor	−0.275	0.233	0.238		
	M–D		−0.532	0.419	0.205		
	Individual	Random	–	–	–		

The effects of the class of the nest constructer (M = mother, I = independent immature, D = dependent immature) individual and nest type on the probability that the nest includes a lining, a pillow, a blanket and a roof, analysed with a GLMM with a binomial family distribution. Dispersion: dispersion parameter; O/P: ratio of observed to predicted zeros. Significant *P* values of the predictors are in bold.