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RESEARCH ARTICLE

Individual Variation in Nest Size and Nest Site Features of the Bornean Orangutans (*Pongo pygmaeus*)

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Nest construction is a daily habit of independent orangutans for sleeping or resting. Data on their nests have been used in various ecological studies (e.g., density estimation, ranging behavior, evolution of material culture) because they are the most observable field signs. We investigated nest size and nest site features of Bornean orangutans in the wild during 10 months' fieldwork at three sites in East Kalimantan, Indonesia: Kutai National Park, Birawa, and Meratus. To examine individual variation, we followed 31 individual orangutans and recorded the 92 nests they made for nest size (diameter) and nest site features (height of nest above ground, tree species used for the nest site, the diameter and height of the tree, whether the nest was new or reused, and nest location within the tree). Analyses taking age–sex classes of the focal individuals into consideration showed significant age–sex differences in nest size and location, but not in nest height or nest tree features (diameter, height of tree, and height of lowest branch). Mature orangutans (adult females, unflanged and flanged males) made larger nests than immatures (juveniles and adolescents). Flanged male orangutans with larger nests used stable locations for nesting sites and reused old nests more frequently than immatures. The overall proportion of nests in open (exposed) locations was higher than in closed (sheltered) locations. Flanged males and immatures frequently made open nests, whereas adult females with an infant preferred closed locations. The good correspondence between nest size and age–sex classes indicates that nest size variation may reflect body size and therefore age–sex variation in the population. Am. J. Primatol. 71:393–399, 2009. © 2009 Wiley-Liss, Inc.

Key words: ***Pongo pygmaeus*; age–sex variation; nest size; nest site features; nest reuse; population structure**

INTRODUCTION

Nest construction is a common daily habit in all great ape species for sleeping during the night or resting during the day [Fruth & Hohman, 1996]. Nests are believed to make sleeping more comfortable [Anderson, 2000; Stewart et al., 2007] and improve thermoregulation [Fruth & Hohman, 1996]. The ability to sleep and rest more comfortably and safely in the nest may also increase the energy available the following day [Baldwin et al., 1981]. In these respects, the function of nests in great apes is more closely related to human "beds" than to the "nests" of other animals, which are usually used for breeding and as shelters for dependent young [Kappeler, 1998]. As nests are the most observable field signs of orangutan presence, nest counts are frequently used to estimate the density and distribution of orangutans in various habitats. Consequently, much attention has been given to ecological and/or behavioral factors in nest building, which affect estimates of population density (e.g., decay rate, construction rate, proportion of nest builders in the population) [Kuhl et al., 2008].

Although the basic nest-building behavior is similar among individual orangutans [MacKinnon, 1974; Rijksen, 1978; Sugardjito, 1983], nest size and nest site features vary with local ecological conditions such as forest structure and composition [Ancrenaz et al., 2004; Felton et al., 2003]. In addition, nest features may vary with the individual

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characteristics of the orangutans. It is reported that height of nest sites is lower in adult males than in other age–sex classes [Setiawan et al., 1996; Sugardjito, 1983]. Understanding the relationship between nest features and the characteristics of individual orangutans is important in order to get information about population structure from the data on nests. If there are correlations between nest size or nest site features and age–sex classes, population structure might be inferred from data on variation in nest size and/or nest site features. However, a systematic survey of variation of nest size or nest site features among age–sex classes has not yet been done. With these aims in mind, we observed 31 individual orangutans of different ages and sexes in three Bornean orangutan populations in three different types of natural forests. We examined variation in nest size and nest site features, and assessed whether the variation reflected the age–sex classes of nest users.

METHODS

Study Sites

The study was carried out over 10 months (November 2006–August 2007) in three forest sites in East Kalimantan, Indonesia: Kutai National Park (KNP) (0°05′–0°35′S, 116°55′–117°35′E, 0–258 m a.s.l.), Birawa (00°01′S, 117°10′E, 36–102 m a.s.l.), and Meratus (00°57′S, 116°19′E, 85–1,200 m a.s.l.). KNP covers an area of 198,629 ha. In this forest the study was conducted around the Sangkima camp (00°32′S, 117°27′E, 3–76 m a.s.l.) and the Prevab camp (00°32′S and 117°27′E, 0–85 m a.s.l.); most of the area around these camps is covered by primary forest vegetation. In Birawa, the study was conducted at the Sumalindo Hutani Jaya Timber Company. This forest is a 1,500 ha area of mixed dipterocarp lowland forest and was disturbed by forest fire in 1997 and periodic logging between the 1970s and 1999. At the time of this study, most of the forest in Birawa was covered by secondary vegetation. In Meratus forest the study was conducted near the Bongan river and Meratus camp. This forest comprises 60,000 ha of lowland and hill dipterocarp forest, about half of which has been protected since 1996.

From 1997 to 2002, 93 wild and 249 rehabilitant orangutans (most of them wild-born) were released in Meratus forest by the Wanariset Orangutan Reintroduction Project [BOSF, 2007]. Although some differences in nesting behavior between rehabilitants and wild orangutans have been reported [Russon et al., 2007], all observed free-ranging rehabilitant orangutans in Meratus forest showed nesting behavior similar to wild orangutans in relation to this study: making arboreal nests, tree preference for nest sites, and making new and/or reconstructing old nests. The similarities are probably owing to the fact that 5–11 years had passed since these rehabilitants were released. Therefore, we combined data from KNP, Birawa, and Meratus for the following analyses.

Observations

Independent individual orangutans were categorized into one of six age–sex classes following Rijksen [1978] and Wich et al. [2004]: juvenile (starting to make their own nest close to their mother's nest and commonly moving with the mother during the day; the smallest body size of all independent orangutans); adolescent (completely independent but sexually immature; both sexes are smaller than adult females); adult female (independent and sexually mature, may spend some time moving with a juvenile, relatively similar in body size to unflanged males); adult female with infant (usually sleeping with an infant or older dependent offspring); unflanged (subadult) male (independent and sexually mature, similar or larger in size than adult female, undeveloped cheek pads); and flanged (adult) male (fully adult male with broad cheek pads, largest in body size).

When we encountered an individual orangutan in the forest, we followed it until it constructed a nest. We recorded the individual's sex and age class, and features of the nest the following morning. To identify nest features and age–sex classes in the field, we used a video camera (Sony DCR-TRV280, CA), a still camera (Fujifilm FinePix S304, Tokyo, Japan), and a sighting scope (Vixen Geoma Pro 82A Spotting Scope 5717, Saitama, Japan).

Nest Features

The following features were recorded for each nest: nest tree species, height, diameter at breast height (DBH) and height of lowest branch, nest height, nest size (diameter), whether the nest was new or reused, location in the tree, and whether the nest was closed (covered by one or more tree crown layers) or open (not so covered) (Fig. 1).

In most cases nest tree species were identified in the field by experienced forest staff of the Wanariset Orangutan Reintroduction Project and KNP; however, several trees were identified by comparing leaf samples taken from the nest tree with leaf samples in the herbarium of the Faculty of Forestry, Mulawarman University, and the Wanariset Herbarium (Forest Research Development Agency of Indonesia).

The tree DBH was measured using a diameter measuring tape. The height of nesting trees and their lowest branch was measured using a fiberglass measuring pole (Senshin SK 202, Osaka, Japan, total length = 12 m). We set the pole to a standard height of 10 m and placed it beside each tree as a reference from which we visually estimated the height of the tree and its lowest branch.

Nest height and nest size (diameter) were measured by several methods: (1) for nests located

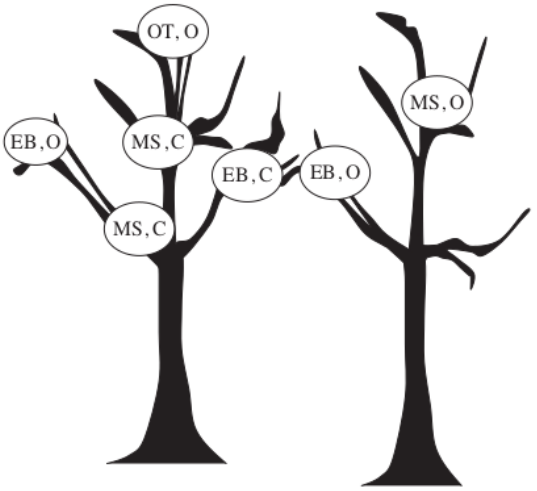

Fig. 1. Nest site locations (OT, at top of tree crown; MS, at the main stem; EB, at the end of a branch; O, open; C, closed). MS and OT were categorized as stable locations and EB as unstable location.

below 15 m, height was measured directly using a fiberglass measuring pole and an aluminum ladder (Krisbow, KW20b 606, Jakarta, Indonesia, total length 5.0 m); (2) for nests located above 15 m, height was measured by climbing trees (sometimes by local climbers); (3) for nests near the ends of branches or at the top of the tree, methods (1) and (2) were combined. Nest diameter was measured using a 1 m aluminum ruler marked at 10 cm intervals, which was fixed horizontally at the end of a pole. Nests were not exactly circular but had irregularities in their shape. To minimize measurement error, we measured the diameter from two angles: maximum diameter (including solid but not marginal area) and the dimension at right angles to the maximum diameter from the center position (representing minimum diameter). The "nest diameter" measure was calculated as the average of the two measurements and is a proxy for the true size.

New and reused nests were identified by direct behavioral observation; nests were categorized as reused if orangutans renewed old nests. In a few cases we were not able to observe nest construction directly because orangutans made their nest close to nightfall. In those cases we identified them the following day as follows: nests that consisted of fresh leaves (green) were categorized as new nests and nests with old (dry and brown leaves) as well as fresh leaves were categorized as reused nests.

Nest locations were coded in three categories: (1) at the top of the tree crown (OT), (2) at the main stem (MS), and (3) at the end of branches (EB) (Fig. 1). OT and MS were regarded as stable locations and EB as unstable. Nests at stable locations were made on the main stem or on a larger branch (diameter >5 cm), whereas nests at unstable locations were usually made on the end of a smaller branch (diameter <5 cm). The research complied with Indonesian legal requirements and was approved by the relevant institutional animal care committees of the nation of Indonesia.

TABLE I. The Number of Orangutans and Nests Observed in Different Age-sex Classes in the Three Study Forests

	KNP		Birawa		Meratus		Total	
Age–sex classes	n_o	n_b	n_o	n_b	n_o	n_b	n_o	n_b
Juvenile	1	1	2	10	0	0	3	11
Adolescent	2	2	5	12	1	1	8	15
Adult female	0	0	2	4	1	3	3	7
Unflanged male	0	0	1	2	1	4	2	6
Adult female with infant	3	10	3	10	1	3	7	23
Flanged male	2	7	3	9	3	14	8	30
Total	8	20	16	47	7	25	31	92

KNP, Kutai National Park; n_o, number of orangutans; n_b, number of nests.

Statistical Analysis

Kruskal–Wallis tests were performed to assess differences in nest and nest site features between six age–sex classes using JMP 7.0.1 (SAS Institute, NC). We also used a Fisher exact test to assess differences in frequency between nest locations, between new and reused nests, and between open and closed nests. Wilcoxon tests were used to compare nest sizes between nest locations, new and reused nests, and open and closed nests.

RESULTS

Number of Nests

Representing 77 actual days of orangutan observation from November 2006 to August 2007, we observed 92 nests made by 31 different independent orangutans (Table I): 90 nests were made for night sleeping and 2 for day rest. Generally, orangutans made one nest a day (95.7%, 88/92), only one juvenile and one adolescent made two nests in one day (4.3%, 4/92). In the majority of cases, they used one tree for one nest (87.0%, 80/92) but sometimes shared one tree with other orangutans (13.0%, 12/92; four cases of an adult male sharing a tree with a mother–infant pair, four cases by two adolescents, and four cases by a juvenile with a mother–infant pair). We also observed, in Birawa, one case of two adolescents sleeping in one nest.

Trees Used for Nest Sites

Thirty-one tree species in 20 families were used for 92 nests (Table II). The most selected five tree

TABLE II. Family and Species of Trees Used for Nest Sites by Different Age-Sex Classes

Tree family	Tree species	Juvenile	Adolescent	Adult female	Unflanged male	Adult female with infant	Flanged male
Anacardiaceae	*Dracontomelon dao*					2	1
Annonaceae	*Polyalthia* sp.			1	1		
	Monocarpia euneura					1	2
	Canangium odoratum						1
	Mezzettia parviflora						1
Bombacaceae	*Durio testodinanum*			1			
Dipterocarpaceae	*Shorea* sp.			1	1	1	2
	Dipterocarpus sp.						2
Dilleniaceae	*Dillenia suffruticosa*					1	
Ebenaceae	*Diospyros borneensis*			1		2	1
	Diospyros lanceolata						1
	Diospyros sp.						1
Euphorbiaceae	*Croton argyratus*	2	1			2	
	Drypetes longifolia						1
	Baccaurea sp.	1				1	
Fagaceae	*Quercus gaharuensis*	2					1
	Lithocarpus sp.						1
Hypericaceae	*Crotoxylon sumatranum*		1				
Lauraceae	*Eusideroxylon zwageri*	3	2	1	3	10	8
	Alseodaphne obovata						1
	Alseodaphne parakensis						1
Meliaceae	*Aglaia odoratissima*		2				
Melastomataceae	*Memecylon* sp.	1				1	1
Polygalaceae	*Xanthophyllum* sp.						2
Moraceae	*Ficus* sp.		4				
Myrtaceae	*Syzygium* sp.	1	2	1	1	1	1
Myristicaceae	*Myristica maxima*	1					
Sterculiaceae	*Pterospermum diversifolium*		2				
Sapotaceae	*Palaquium sericeum*		1				
Sapindaceae	*Paranephelium* sp.			1			
Tiliaceae	*Pentace triptera*					1	1
Total		11	15	7	6	23	30

families (Lauraceae, Myrtaceae, Euphorbiaceae, Ebenaceae, and Dipterocarpaceae) accounted for 63% of the total number of nest sites. *Eusideroxylon zwageri* was used by all age–sex classes and accounted for 29.3% (27/92) of nest sites. Adult females carrying an infant used this tree species more frequently than other tree species (43.5%, 10/23). There was some variation in nest tree height (mean = 21.6 m, range: 11–36, SD = 6.4), height of lowest branch (mean = 9.3 m, range: 2–20, SD = 4.0), DBH (mean = 33.9 cm, range: 12–87, SD = 15.0), and nest height (mean = 17.7 m, range: 9–34, SD = 5.5), but Kruskal–Wallis tests did not show significant differences between age–sex classes in nest tree height ($\chi^2 = 4.97$, $P = 0.419$), height of lowest branch ($\chi^2 = 4.44$, $P = 0.488$), DBH ($\chi^2 = 5.85$, $P = 0.321$), or nest height ($\chi^2 = 5.40$, $P = 0.369$). Nest site preferences will be analyzed in a separate paper [Rayadin, in preparation].

Nest Size

We measured nest size (diameter) directly for 86 of 92 nests; for the remaining 6 nests, size was estimated. The average nest diameter was 114.5 cm (range: 50–170, SD = 29.7, $n = 92$). Average nest diameter was smallest for juveniles (mean = 64.1 cm, SD = 11.8, $n = 11$) and largest for flanged males (mean = 139.3 cm, SD = 17.4, $n = 30$). Nest size differed significantly between age–sex classes (Kruskal–Wallis test: $\chi^2 = 67.88$, $P < 0.0001$), and increased from juveniles to flanged males (Fig. 2). The number of nests observed for each individual ranged from one (for one juvenile and one adolescent) to eight (one adult male). To remove effects of sample size variation among individuals, average nest sizes of each individual were calculated. In this analysis too, nest size differed significantly between age–sex classes (Kruskal–Wallis test: $\chi^2 = 23.63$, $P = 0.003$, $n = 31$).

Nest Location

Generally, nests in stable locations were more common than those in unstable locations (73.9%, 68/92 stable, 26.1%, 24/92 unstable). Proportions of stable and unstable locations differed significantly across age–sex classes (Fisher exact test: $P = 0.019$)

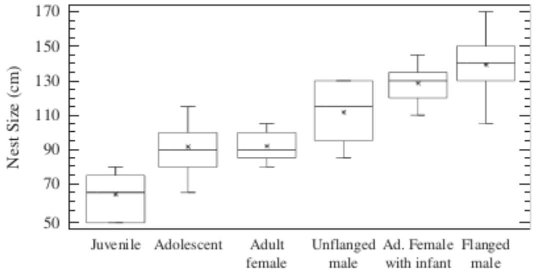

Fig. 2. Box and whisker plot of the means and distribution of nest size between different age–sex classes.

(Fig. 3a). The proportion of stable locations was high in flanged males (86.7%, 26/30) and adult females with an infant (87.0%, 20/23), and low in juveniles (45.5%, 5/11) and adolescents (53.3%, 8/15). To minimize effects of sample size variation among individuals, we focused on individuals for which two to four nests were observed ($n_o = 25$ and $n_b = 74$) and compared matured (flanged male, adult female with an infant, unflanged male, and adult female) with immatured (juvenile and adolescent) individuals. Proportions of stable and unstable locations also differed significantly between these two groups (Fisher exact test: $P = 0.012$). Correspondingly, there was also a significant relationship between nest size and nest site location. Nest sizes in stable locations were significantly larger than those in unstable locations (mean = 121.6, SD = 26.3, $n = 68$ for stable locations; mean = 94.2 cm, SD = 29.3, $n = 24$ for unstable locations; Wilcoxon test: $Z = 4.03$, $P < 0.0001$).

Reuse of Nests

The observed orangutans generally made new nests every day (70.7%, 65/92), but sometimes reused nests (29.3%, 27/92). We identified the original nest builder and the reuser of that nest in 5 of 27 cases of nest reuse. One adult male and one adult female with an infant each reused their own nest twice, and one adult female with an infant reused a nest originally made by an adult male. Although it has been suggested that rehabilitants reuse nests at higher frequencies than wild orangutans [Russon et al., 2007], we found no differences in the proportion of reused nests across the three study populations (Fisher exact test: $P = 0.958$) (KNP: 25.0%, 5/20 for wild individuals; Birawa: 31.9%, 15/47 for wild individuals; Meratus: 28.0%, 7/25 for wild and rehabilitants). Thus, we carried out the following analyses using data pooled from all three populations.

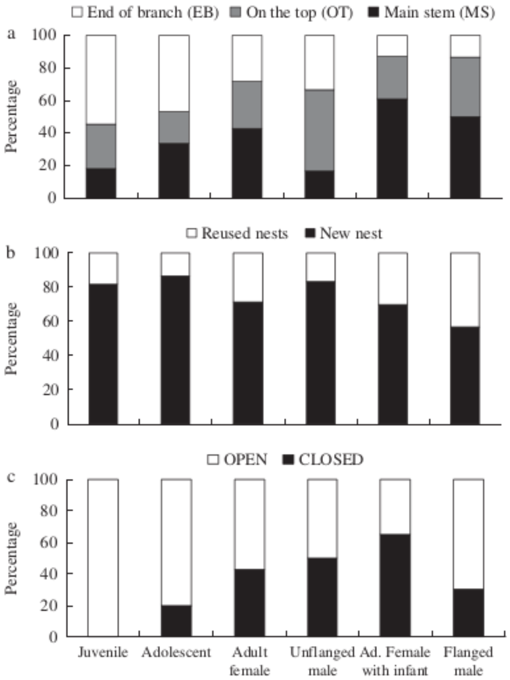

Fig. 3. Proportion of nests in each age–sex class represented by site location (**a**), new and reused nests (**b**), and open and closed position (**c**).

The proportion of reused nests was highest in flanged males (43.3%, 13/30; Fig. 3b) and lowest in adolescents (13.3%, 2/15), but differences between age–sex classes were not statistically significant (extended Fisher exact test: $P = 0.323$). Reused nests were larger than new nests in general (mean = 123.9 cm, SD = 22.3, $n = 27$ for reused nests; mean = 110.5 cm, SD = 31.4, $n = 65$ for new), although the statistical significance was marginal (Wilcoxon test: $Z = 1.92$, $P = 0.055$; Fig. 3c). When comparing nest size between new and reused nests within each age–sex class, no significant differences were detected.

Open and Closed Nests

Nests were mostly constructed in open locations (64.1%, 59/92) (Fig. 3c). A Fisher exact test showed significant differences in this proportion between age–sex classes ($P = 0.002$). The majority of nests made by juveniles (100%, 11/11), adolescents (80.0%, 12/15), and flanged males (70.0%, 21/30) were in open locations, whereas the majority of nests made by adult females with an infant were in closed locations (65.2%, 15/23). To minimize effects of sample size variation among individuals, we focused on individuals for which two to four nests were observed ($n_o = 25$ and $n_b = 74$). Proportions of open and closed nests also differed significantly between age–sex classes in this data set (Fisher exact test: $P = 0.024$). Nest size did not differ between the two location types (Wilcoxon test: $n_b = 92$, $Z = 1.34$, $P = 0.179$).

DISCUSSION

The main purpose of this study was to identify nest and nest site features that reflect age–sex class differences. The patterns found in nest size, nest reuse, and nest location corresponded well with age–sex classes. In this discussion we focus mainly on nest size differences between age–sex classes. Our observations for other nest site features may not be insignificant, but owing to the limited sample size our results cannot be conclusive. Further studies on nest features might reveal more and should be encouraged.

This study shows that mature orangutans with larger body size make larger nests than immature individuals. Juveniles (with the smallest body size) made the smallest nests and flanged males (with the largest body size) made the largest nests. A similar pattern has been reported in gorillas, where nest size was smaller for juveniles (0.75 m) than for adult females (1.15 m) and adult males (1.32 m) [Groves & Sabater Pi, 1985]. As nests may improve comfort and thermoregulation [Anderson, 2000; Fruth & Hohman, 1996], it is reasonable to expect that the nest size required corresponds to the body size of the user.

Immature orangutans with smaller nests tended to make their nests at higher sites than adults, although differences between age–sex classes were not statistically significant. A similar pattern was reported by Sugardjito [1983] and Setiawan et al. [1996] where adult males made their nests at lower sites than orangutans in other age–sex classes. These patterns may be related to nest size and location: in our study, larger orangutans tend to make larger nests at stable locations, which are more likely to be found at lower sites.

The proportion of stable nest locations was higher in flanged males and adult females with an infant than in juveniles and adolescents, and the nest size in stable locations was significantly larger than in unstable locations. This may reflect a need for larger orangutans to make larger nests in locations that support heavy body weight well; larger nests need more stable locations, whereas smaller nests may be enough for smaller orangutans and can be made on the end of a branch.

It may also be safer for juveniles to make a nest at the end of the branch because they are more vulnerable to predators. This location may facilitate observation of the surroundings and reduce accessibility to mammalian predators. A potential predator, the clouded leopard (*Neofelis diardi*), which weighs 11–25 kg and is arboreal and terrestrial [Wilting et al., 2006], usually takes prey with weight lower than its own. Clouded leopard predation on proboscis monkeys (*Nasalis larvatus*) has been reported in Kinabatangan Borneo [Matsuda et al., 2008]. Juvenile orangutans having similar body size to adult proboscis monkeys may be at risk of predation by the clouded leopard.

The finding that reused nests were larger than new nests may reflect the observation that adult males with larger nest size reused nests more often. A similar pattern has been found for orangutans in Kinabatangan, where nest reuse was higher for adult males (22.4% for unflanged males; 17.9% for flanged males) than for females (13.7%) [Ancrenaz et al., 2004]. Adult males require larger nests that need more material and stable locations. These resources may be limited in comparison with those needed for smaller nests; therefore, flanged males may more frequently reuse nests. They may also save time and energy by not constructing new large nests.

Reusing old nests is relatively common in orangutans [17.5%, Ancrenaz et al., 2004; 29.3% in this study] compared with chimpanzees [13.8%, Plumptre & Reynolds, 1997], gorillas [4.1%, Iwata & Ando, 2007], and bonobos [0.2%, Fruth & Hohman, 1996]. The findings in gorillas and chimpanzees suggest that ecological conditions, including the availability of nesting materials, fruit tree season, and suitable places for nests, may have an influence on the frequency of reuse [Iwata & Ando, 2007]. Orangutans generally make larger nests than chimpanzees [Groves & Sabater Pi, 1985] and use higher sites than gorillas [Fruth & Hohman, 1996]; thus, resource limitations may lead to a higher proportion of nest reuse in orangutans.

Most nests were made in open locations, but adult females with an infant usually made their nests in closed locations. This may be explained by correlation with other nest features. Females with infants frequently made nests near the main stem, which were likely to be covered by the tree crown. However, they also made nests at the ends of branches in places covered by the tree crown or a taller tree. Closed nests may help infants to avoid getting too cold at night and reduce exposure to heavy rain and strong wind.

We have demonstrated that nest size variation is clearly related to age–sex class, reflecting body size variation, and thus it may be possible to infer the age–sex composition of a population from the nest size variation. A large nest size variation should imply a broader age–sex composition, for instance, whereas a small variation should imply a narrower age–sex composition. By combining data on nest size with data on the number of nests, we should be able to discuss not only population size but also the population structure of orangutans.

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