Orangutan Nesting Behavior in Disturbed Forest of Sabah, Malaysia: Implications for Nest Census

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High concentrations of orangutans remain in the multiple-use forests of the Lower Kinabatangan, Sabah, Malaysia. Compared to primary forest, the habitat is highly fragmented, characterized by a low tree density (332 stems/ha), small tree size (83.6% of trees are <20 m high), low basal area (18 m^2/ha), abundance of canopy gaps and high level of soil disturbance. The forest structure and composition influence orangutan nesting patterns, and thus directly influence the results of nest surveys used to determine orangutan population size. In logged forests, tall and large trees are the preferred nesting sites of orangutans. The scarcity of suitable nesting sites in the logged-over forests of Kinabatangan, could partly explain the lower daily rate of nest construction (r = 1.00) versus those of other orangutan populations. The nest decay rate t recorded at the study site (average ± SD = 202 ± 151 days) strongly depends on the species of tree in which a nest is built. Our results illustrate that the nest-related parameters used for orangutan censuses fluctuate among habitat types and emphasize the need to determine specific values of r for specific orangutan populations and of t for different tree species in order to achieve accurate analysis of census data.

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INTRODUCTION

The majority of orangutans (*Pongo pygmaeus*) in the State of Sabah (Malaysia, Borneo) live outside protected areas, in forests that are subject to human exploitation (Payne, 1988). In eastern Sabah, the forests of the Kinabatangan floodplain are composed of a mosaic of seasonally flooded freshwater swamp and lowland dipterocarp forests. They have been subject to human exploitation for the past two centuries but still harbor a significant orangutan population (Lackman-Ancrenaz *et al.*, 2001). In early 2001, a corridor of 27,000 ha of over-exploited forests along the Kinabatangan River was gazetted as the Kinabatangan Wildlife Sanctuary by the Malaysian government. It links together several other small protected forest reserves totaling 15,000 ha.

Forests worldwide continue to be exploited, and we can assume that the remaining habitat islands and multiple-use forests will greatly gain in importance for conservation (Phillips, 1997). There is a need to investigate the potential role of these fragmented and degraded forests for orangutan long-term survival. It is commonly believed that orangutans are particularly sensitive to habitat disturbance and may generally fare extremely poorly in forest fragments over the long run (Rijksen and Meijaard, 1999). However, except for a few short-term studies (Felton *et al.*, 2003; Rao and van Schaik, 1997), there has been a dearth of in-depth field studies on the impact of forest exploitation on orangutan ecology, so our knowledge of possible orangutan adaptation to habitat disturbance is still poor. The Kinabatangan Orangutan Conservation Project (KOCP) was created to rectify this situation, and KOCP scientists have studied orangutan adaptation to disturbed habitat since the end of 1998.

We investigated orangutan nesting behavior in the multiple-use forests of the lower Kinabatangan floodplain and compared the values of the specific nest-related parameters in exploited forest that are required for census operations (r, daily rate of nest construction; t, nest decay rate; p, proportion of nest builders in the population) with the values originating from other studies carried out in primary forests.

STUDY AREA AND METHODS

Study Site

The $4 \, \text{km}^2$ KOCP (E 118°17′ to 118°18′40″ - N 5°32′20″ to 5°33′30″) study site is established in Sabah (Malaysia) along the Kinabatangan River, 3 km
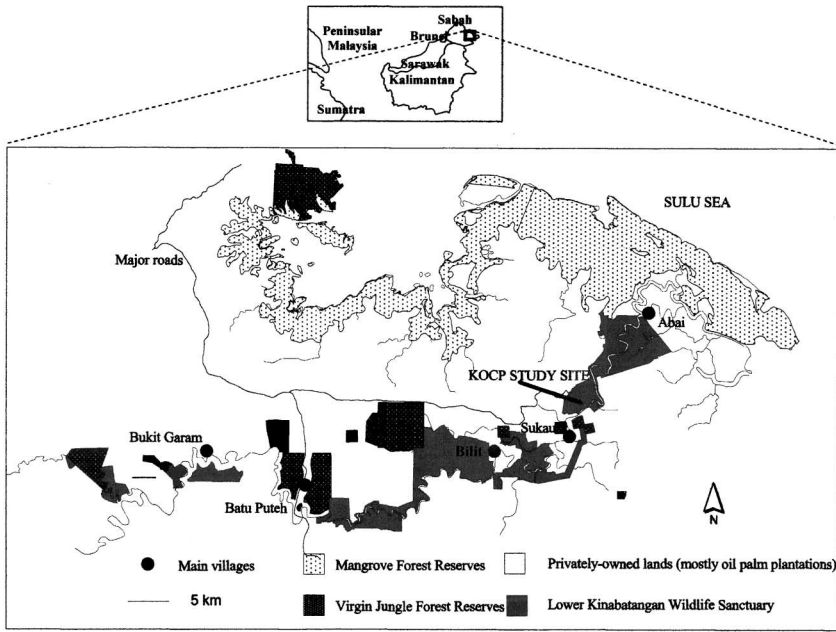
Fig. 1. Map of the Lower Kinabatangan Wildlife Sanctuary.

from the village of Sukau, and 20 km in a straight line from the sea (Figure 1). A large portion of the KOCP study area is flat and low (10–20 m asl). Most of the area is poorly drained and subject to periodic flooding. Recent alluvium and finely textured deposits rich in nutrients and magnesium occur near the river while gleyic luvisols occur in the poorly drained places (Haile and Wong, 1965). A low mudstone hill peaks at *ca.* 50 m asl and covers 23% of the study site.

Climate

The Kinabatangan floodplain is characterized by a warm, wet and humid tropical climate. Temperature variation is diurnal rather than seasonal, and mean monthly temperatures range between 21°C and 34°C (Figure 2). Floods mainly occur between November and March during the west monsoon (Sooryanarayama, 1995). Over 5 yr (1996–2000) annual precipitations in Sukau averaged 2990 ± 342 mm (Figure 3). The longest droughts were in 1983 (81 consecutive days with no rain: Payne, 1989), and in 1998 (85 days: pers obs.).
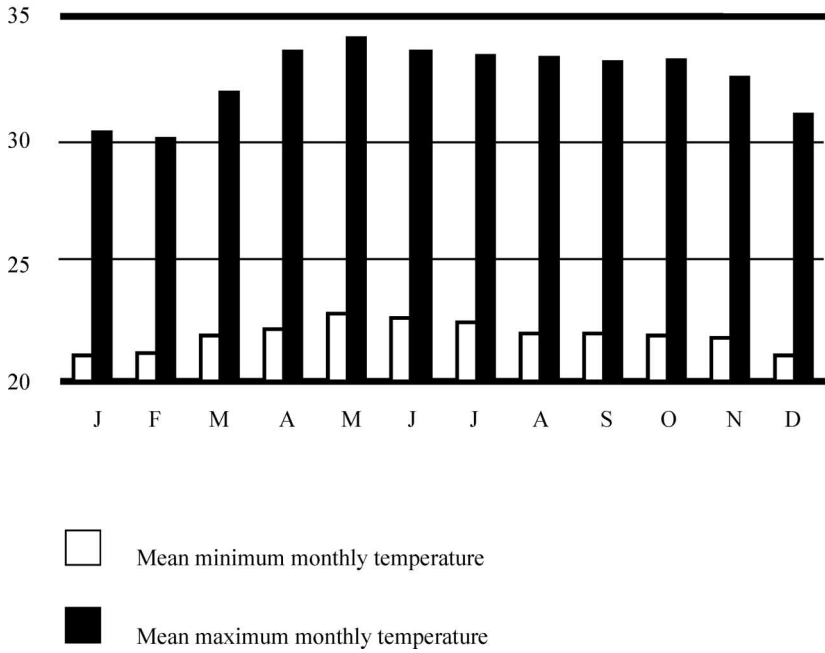
Fig. 2. Mean minimum and maximum monthly temperatures (°C) at Sukau over a 5-year period, 1996–2000 (Source: Malaysian Meteorological Services Department).
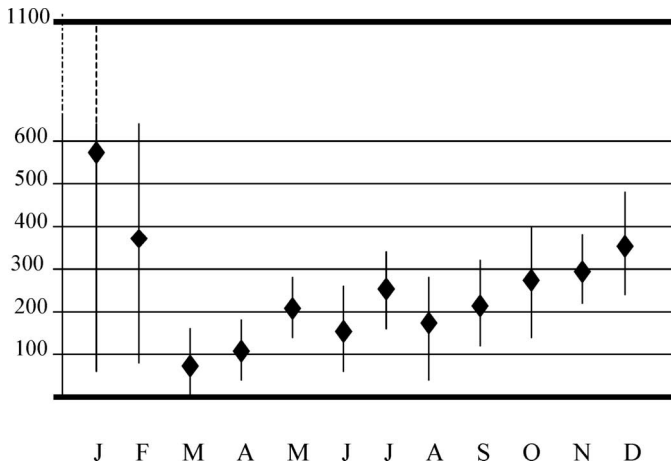

Fig. 3. Average (±SD) monthly rainfall (mm) in Lower Kinabatangan over a 5 years period, 1996–2000 (Source: Malaysian Meteorological Services Department).

Botanical Survey of the Study Site

Before extensive human disturbance of the area, the main climax formation in the Kinabatangan floodplain were lowland dipterocarp forests in better drained areas, seasonal fresh water swamp and swamp forests in poorly drained areas, riparian forests in flood-free terraces along the rivers, mangrove forests, limestone forests, and heath forests (Fox, 1978). Today, they are at various stages of degradation and successional regeneration. They are also highly fragmented and surrounded by industrial oil-palm plantations.

In order to determine the botanical composition of the KOCP study area, we randomly selected and permanently marked 12 permanent quarter-ha plots (50 × 50 m). We assigned each plot to one of the following vegetation sub-types: riverine forest (RF), mixed semi-inundated lowland dipterocarp forest (MSILDF), and dry lowland dipterocarp forest (DLDF). From May to September 2000, we counted, tagged, and identified all living trees ≥10 cm dbh (diameter at breast height). We assessed forest structure by recording tree height, dbh and basal area, evidence of past-logging activities, structure of the climbing community, and occurrence of canopy gaps.

Tree Selection for Nesting

In September 1998, we initiated an eco-ethological study of KOCP orangutans. When encountered, team members followed the focal orangutan from nest to nest for several days or until it was lost. We recorded nest construction by direct behavioral observations and the sounds of an orangutan cracking branches to make a platform. For each nest, we noted dbh, height and species of the nesting tree; height of the nest from the ground; whether the nest was above or below the canopy; size of branches and leaves used for nest construction; and identity of the nest builder. We collected additional information on orangutan nesting tree species during several censuses along line-transects inside KOCP.

Estimation of *p, r* and *t*

Orangutan density estimates are generally produced via the formula: $\hat{D}_{ou} = \frac{\hat{D}_n}{p \times r \times t}$, with $\hat{D}_{ou}$ and $\hat{D}_n$ the estimated orangutan and nest densities respectively, p the proportion of nest builders in a population, r the daily production rate of nests, and t the nest decay rate or the number of days a nest stays visible in the forest (Tutin and Fernandez, 1984).

We determined p from our detailed knowledge of the Kinabatangan orangutan population structure, r via data from the eco-ethological study

from habituated subjects and for complete follows of 24-h periods, and *t* via direct monitoring of 115 night nests from the day they were built until the day they were no longer visible (March 1999 to July 2001). We monitored nests that were re-used by orangutans until their complete decay. The day following construction, we recorded the date; weather conditions; nesting site location; height of the canopy (≤ 10 m); species, height and dbh of the nesting tree; height of the nest; location of the nest in the tree; approximate size of the nest, leaves and branches used for construction; presence of other orangutan nests in the same tree; and identity of the nest builder (if known). We checked nests every 3 weeks until they were no longer visible. We classified nest age according to 5 successional stages: I—new: presence of green leaves; II—recent: all leaves dry and brown; III—old: some leaves already gone, the others still attached, nest still firm and solid; IV—very old: holes visible in the nest structure; or V—almost gone: a few twigs and branches, original nest shape no longer evident.

RESULTS

Botanical Survey

The last major logging operations occurred in the study site in 1992. Within the 12 botanical plots, $\leq 35\%$ of the forest floor showed old signs of disruption by tractor tracks, skidder trails, and log-landing areas. Gaps associated with past logging activities ranged in size from 0.01 to several ha. Our direct observations suggested that $\geq 80\%$ of the original canopy has been destroyed and showed that creepers (*Spatholobus sp.*, *Merremia sp.*, *Uncaria sp.*) were common on the edges of the forest fragments, and inside the forest.

In the 12 botanical plots, we identified a total of 995 trees (dbh >10 cm), belonging to ≥ 224 different taxa from 56 families and 139 genera, which yielded a mean ($\pm$SD) of 331.7 ± 57.2 trees/ha. Most of these trees were small, as shown by the low mean basal area (17.96 m^2/ha: Table I), dbh distribution (Figure 4), and height (Figure 5a).

Choice of Nesting Sites in Degraded Habitat

During orangutan follows and censuses, we recorded 1546 trees with orangutan nests, representing a minimum of 89 different genera and 125 species from 37 different families. However, because nest decay rate varied with tree species, we use only data collected during the orangutan follows in the analysis of the nest parameters to avoid bias.

From 1999 to 2002, we completed 602 full observation days of 25 (13 males: 12 females) orangutans and observed 744 nesting events, involving 614 separate nesting trees. Nest trees harbored a single nest in 86% of cases,

Table I. Tree composition (in percentage of total number of trees), density and basal area of the most common families in 12 50-m × 50-m botanical plots at the KOCP study site and at several other sites located in Borneo

	KOCP				Sepilok[a]	Danum[b]		Mulu[c]		Gunung Palung[d]			
	All plots 12 plots 995 trees		RF 2 plots 119 trees	Dry LDF 4 plots 393 trees	Mixed SILDF 6 plots 483 trees	Mixed SILDF	Dry LDF 939 trees		AF	Dry LDF	Primary Mixed SILDF Dry LDF		Logged Mixed SILDF Dry LDF	
	%	BA	%	%	%	%	%	BA	%	%	%	BA	%	BA
Euphorbiaceae	14	2.1	11.9	10.1	17.4	10.2	20.6	1.8	15.8	9	6.3	1.5	6.6	0.8
Dipterocarpaceae	9.8	2.1	0	20.1	3.7	27.1	16.2	13	5.4	14.7	22.6	14.3	21.8	5.7
Lauraceae	7.5	1.3	0	10.1	7.4	2.5	6.8	1.5	4.5	2.6	0	0	1.8	0.3
Rubiaceae	7.3	1.2	16.1	1.3	10.1	n.a	0.01	n.a	n.a	n.a	n.a	n.a	n.a	n.a
Annonaceae	4.5	1.0	11.9	2.3	4.5	n.a	6.1	0.6	2.9	0.5				
Sterculiaceae	4.1	1.2	16.1	1.8	3.1	n.a	n.a	n.a	1.6	0.5				
Tiliaceae	3.5	0.3	22.9	1.3	0.6	4.1	4.4	0.6	0.3	0.5				
Myrtaceae	3.2	0.4	0	0.8	6.0	6.9	5.7	1.2	7.1	8.3	1.6	0.4	1.4	0.1
Anacardiaceae	3.1	0.5	0.8	3.8	3.1	5.3	n.a	n.a	1.9	2.6	5.9	0.9	0.7	0.1
Verbenaceae	3.0	0.9	3.4	0.5	5.0		n.a	0.3	n.a		n.a	0.9	n.a	n.a
Leguminosae	2.8	0.5	0.8	3.3	2.9		0.01	0.7			3.2	0.9	0	0
Moraceae	2.7	0.8	2.5	5.1	0.8	n.a	n.a	n.a	n.a	n.a	n.a	n.a	n.a	n.a
Flacourtiaceae	2.6	0.5	0	1.0	4.6		0.01							
Dilleniaceae	2.5	0.2	5.9	0	4.1									
Ebenaceae	2.5	0.4	0.8	0.3	4.8		n.a							
Melastomataceae	2.4	0.2	0	4.3	1.4			0.1						
Other families	24.3	3.9	12.0	46.7	49.1	n.a		n.a						
Tot. families	56		17	46	50		59							
Tot. genera	139		21	96	102		164							
Density	332		238	393	322	608	470		615	778	221		158	
Basal area	18		n.a	n.a	n.a	37.8	26.6		28	57	32.3		16.4	

Note. RF: riparian forest; Dry LDF: dry lowland dipterocarp forest; Mixed SILDF: mixed seasonally inundated lowland dipterocarp forest; AF: alluvial forest; BA: basal area in m²/ha; Tot. total; na: not available.
[a]Nicholson, 1965.
[b]Newberry et al., 1992.
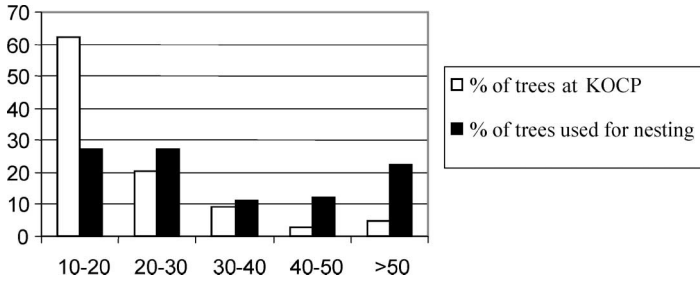[c]Proctor et al., 1983.
[d]Cannon et al., 1994.

Fig. 4. Percentages of dbh (cm) distribution of trees at KOCP ($n = 995$) and orangutan nesting trees ($n = 614$).

2 nests in 9.5%, 3 nests in 3%, and >3 nests (maximum of 8 nests in a single tree) in 1.5%. Mapping of all the nests built by orangutans showed that they were unevenly distributed and clustered throughout the study site. In 58% of nesting events, feeding bouts—fruits from the tree or young leaves
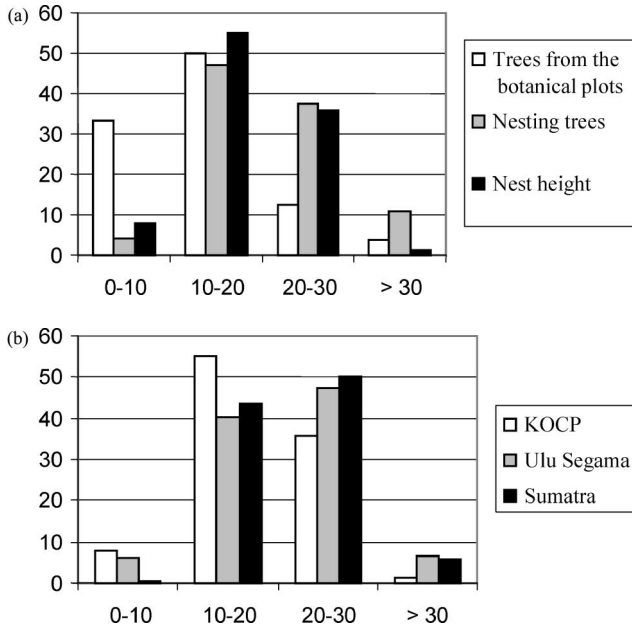

Fig. 5. (a) Percentages of height of trees ($n = 995$) in 12 50-m × 50-m botanical plots, of nesting trees used by orangutans ($n = 614$) and of orangutan nests ($n = 744$) at the KOCP study site (1999–2002). (b) Percentages of height distribution of nests at KOCP, Ulu Segama (MacKinnon, 1972) and Sumatra (Sugardjito, 1983).

Table II. Number and percentage of nesting trees according to tree families and genera at KOCP ($n = 614$ trees)

Tree family	Number of trees	Percentage	Tree genera the most commonly used for nesting
Euphorbiaceae	73	11.9	Mallotus sp.: 65 (10.6%)
Dipterocarpaceae	55	9.0	Shorea sp.: 30 (4.9%)
Anacardiaceae	47	7.6	
Sterculiaceae	45	7.3	Pterospermum sp.: 35 (5.7%)
Rubiaceae	42	6.8	
Moraceae	37	6.0	Ficus sp.: 34 (5.5%)
Lauraceae	37	6.0	Eusideroxylon: 36 (5.9%)
Myrtaceae	31	5.0	Syzygium sp.: 31 (5%)
Ebenaceae	14	2.3	
Tiliaceae	14	2.3	
Fagaceae	12	1.9	
Total	407	66.3	231 (37.6%)

from woody climbers in the tree—occurred in the nesting tree shortly before or following nest construction and/or the next morning following the orangutan's exit from the nest. In <10% of nesting events the nest was >20 m away from the last food source utilized during the afternoon.

Five tree families and 5 genera accounted for 42.7% and 32.7%, respectively, of all nesting sites (Table II). Choice of tree species for nesting is related to family abundance in the forest when we considered the 13 tree families most often used for nesting (chi-square = 53.9, df = 12, $p < 0.001$). However, many trees producing large crops of fruits consumed by orangutans were utilized for nesting at a higher frequency than expected, especially during fructification: Moraceae (6.2% of the total nesting trees), Anacardiaceae (7.6%) and Sterculiaceae (7.3%).

At KOCP, there is a significant trend for orangutans to select trees with the largest diameters in which they build their nests (chi-square = 232.2, df = 4, $p < 0.001$): Figure 4, and to choose the tallest trees available (chi-square = 397, df = 3, $p < 0.001$): Figure 5a. Nests are generally in the upper part of the tree (Figure 5b).

Determination of Nest Parameters Used for Census Operations

From a set of 92 different individuals encountered during a general survey in Kinabatangan, we identified 14 dependent offspring that were not nest-builders, giving a p value of 0.85.

During 602 dawn-to-dusk follows, we observed the use of 744 nests by focal orangutans. They used 127 day nests (21.1% of observation days: Table III), but 41.2% ($n = 53$ nests) of them were reused (frequently the

Table III. Number and type of nests, population structure ($n = 92$ individuals) and corresponding relative and absolute values of nest building rates for the Kinabatangan orangutan population, compared with data from literature

		N	Days	Night Nests			Day Nests		Nesting events	Relative "r"	Population structure	Absolute "r"
				Old	New	Not visible	Old	New				
KOCP (Borneo)	Fl.M	5	107	13	94	1	11	15	134	1.02	20.5%	0.2091
	Un. M.	6	197	31	167	2	23	18	241	0.94	29.5%	0.2773
	Ad.F.	10	267	29	238	8	16	38	329	1.03	37.2%	0.3832
	Adol/Juv	4	31	4	29	1	3	3	40	1.03	12.8%	0.1318
	Total	25	602	77	528	12	53	74	744	1.00	100%	1.001
Gunung Palung[a] (Borneo)	Fl/Un. M	6	142			n.a			n.a	1.22	n.a	n.a
	Ad.F.	7	178			n.a			n.a	1.09	n.a	n.a
	Adol/Juv	11	117			n.a			n.a	1.18	n.a	n.a
	Total	24	437			n.a			n.a	1.17	n.a	1.163
Suaq[b] (Sumatra)	Fl. M	12	126			208/5[c]			208	1.65	n.a	n.a
	Un. M.	11	73			180/2[c]			180	2.47	n.a	n.a
	Ad. F.	18	410			757/54[c]			757	1.85	n.a	n.a
	Adol/Juv	11	51			110/7[c]			110	2.15	n.a	n.a
	Total	52	660			1255/68[c]			1255	2.03	n.a	1.902

Note. Fl.M.: Flanged males; Un.M.: Unflanged males; Ad.F.: Adult females (reproductively mature and usually accompanied by young animals); Adol.: Adolescent (7–10 years); Juv.: Juvenile (4–7 years: still with their mother); n.a: not available; *N*: number of individuals.
[a]Johnson *et al.*, in press.
[b]Singleton, 2000.
[c]Pooled data: new nests (day and night)/old nests (day and night).

nest built for the previous night). When resting during daytime, orangutans preferred the abundant tangles and mats of leafy vines and woody climbers in the crowns of trees. These resting sites did not present the classic structure of a nest and were not visible from the ground. Overall 617 night nests were used by focal orangutans but only 85.6% ($n = 528$) of them were new. The same nest could be used ≤4 different nights by the same orangutan. A nest could also be used by 2 different orangutans over intervals of several days or weeks. On 3 occasions, a consorting pair entered the same nest and spent the night together inside.

There is no statistical difference (Kruskal-Wallis; $p = 0.607$) in the relative rates of nest construction according to sex and age classes (Table III). However, nest reutilization was higher for males (22.4% for unflanged males; 17.9% for flanged males) than for females (13.7%). The weighted absolute daily rate of new nest construction for the population in Kinabatangan is thus 1.0 (Table III).

Our cohort of 115 nests includes 15 nests (or 13.0%) that were used ≥2 times by orangutans, which is close to the rate of nest re-use documented during our ecological study (14.6%). We thus directly monitored the impact of nest reutilization by the subjects on the decay rate. The average nest decay value t is 202.5 ± 151 days ($n = 115$ nests, median: 146 days, range: 10–730 days: Table IV). There is no statistically significant influence of season of nest construction (dry [March/October] vs humid [November/February]: Mann and Whitney, $U = 688$, $p = 0.14$); of protection of the nest by the canopy (protected vs. unprotected: $U = 651.5$, $p = 0.523$); of size of the leaves (> vs. <10 cm: $U = 682.5$, $p = 0.34$); of size of the branches (big vs. small: $U = 824$, $p = 0.51$); of size of the nest (big vs. small: $U = 859$, $p = 0.66$); or of height of the nest from the ground (4 classes: 0–15 m, 15–20 m, 20–25 m, >25 m: one way analysis of variance, df $= 79$, $F = 1.58$, $p = 0.2$).

We grouped together 7 families of nesting trees (Table IV), and a one-way ANOVA showed a statistical difference between them (df $= 114$, $F = 19.12$, $p < 0.0001$). Via the pairwise Tukey method, we identified 2 distinct subgroups: Group 1 (*Eusideroxylon* and *Dimocarpus*, $p = 0.182$), and Group 2 (other families, $p = 0.593$). The mean $\pm$ SD of nest visibility for Group 1 and 2 are 431 ± 170 days and 153 ± 93 days, respectively (Table IV).

DISCUSSION

The forest canopies of the lower Kinabatangan are low stature, which is common in seasonally flooded forests (Proctor *et al.*, 1983; Whitmore, 1974). However, they lack a clearly recognizable division of canopy layers, have an overall low stem-density (332 trees/ha), very few large trees with small

Table IV. Nest decay rate (in days) according to tree families at KOCP and comparison with rates originating from other locations below 500 m asl

| Site | Habitat type | | N | Methodology | | Nest decay rate (days) | | | |
	Forest	Exploitation				Mean	SD	Min.	Max.
KOCP	MSILF	heavy	115	direct monitoring	Total	202	151	10	520
			20		Group 1	431	170	92	730
			95		Group 2	153	93	10	520
			13		*Dipterocarpaceae*	205	119	61	400
			10		*Eusideroxylon*	476	140	294	730
			7		*Myrtaceae*	128	99	33	287
			10		*Dinocarpus*	385	193	92	641
			13		*Sterculiaceae*	135	44	45	193
			17		*Rubiaceae*	143	60	52	319
			45		*Other*	151	102	10	520
Ketambe[a]	AH	none	83	Markov		92	n.a	n.a	n.a
Suaq Balimbing[b]	MSILF	none	55	Markov		228	172	n.a	n.a
Danau Sentarum[d]	MSILF	none	264	Markov		145	n.a	n.a	n.a
Gunung Palung[e]	MSILF	none/medium	621	Markov		72	n.a	62	84
Sebangau[f]	MSILF	none/medium	86	Markov (correction factor)		217	0.2	n.a	n.a
Ketambe[g]	MSILF	none	n.a	Markov (correction factor)		234	0.2	n.a	n.a
	HDF		n.a	Markov (correction factor)		250	0.3	n.a	n.a
Suaq Balimbing[b]	HDF	none	45	direct monitoring		319	181	n.a	n.a
Ketambe[c]	AH	none	30	direct monitoring		81	n.a	n.a	n.a
Ketambe[g]	MSILF	none	n.a	direct monitoring		193	0.2	n.a	n.a
	HDF		n.a	direct monitoring		228	0.3	n.a	n.a
Gunung Palung[g]	MSILF	none	35	direct monitoring		399	195	n.a	n.a
	LDF	none	258	direct monitoring		258	204	n.a	n.a

Note. N: Number of nests; SD: Standard Deviation; Min.: Minimum Value; Max.: Maximum Value; MSILF: mixed semi-inundated lowland forest; HDF: hill dipterocarp forest; LA: lowland alluvium; AH: alluvial hill; LDF: lowland dipterocarp forest; n.a: not available.
[a]van Schaik et al., 1995.
[b]Singleton, 2000.
[c]Rijksen, 1978.
[d]Russon et al., 2001.
[e]Felton et al., 2003.
[f]Morrogh-Bernard et al., 2003.
[g]Buij et al., 2003.
[h]Johnson et al., in press.

basal areas, large canopy gaps, and a high rate of soil disruption, which are characteristic of disturbed forest (Johns, 1997): Table I. At KOCP, emergent trees are mostly Dipterocarpaceae, Leguminosae and Moraceae, which is comparable to most primary forests. They are never taller than 40 m, though they usually reach 50 m or more in primary forest (Whitmore, 1974). Saplings that survive well in disturbed habitats, species that produce sprouts easily, and pioneer species that can respond quickly to the high light environments resulting from canopy disturbance are overrepresented at KOCP (Table I). Nevertheless, recruits of climax tree species are also widespread, but they are small. Today, the forest composition and structure of KOCP is a mosaic of different types of habitats, all at different stages of degradation and early regeneration. They greatly differ from the mature lowland forests that were the natural habitat for orangutans in Sabah, which is likely to affect general orangutan behavior and forest use.

We identified a minimum of 89 tree genera and 125 species that orangutans used for nest construction in a total data set of 1546 nesting trees. In Sabah, MacKinnon (1972) noted that orangutans rarely used some tree species for nesting, viz. several species of Dipterocarpaceae, *Dillenia sp*., *Garcinia sp*., and *Eusideroxylon zwagerii*. In contrast, Horr (1977) found that orangutans extensively used *Eusideroxylon* for nesting at Lokan, as we observed in lower Kinabatangan. At KOCP, 5 tree families and 6 tree genera accounted for 42.6% and 37.6%, respectively, of all nesting sites (Table II). Frequency of nest use was related to family abundance except for several genera that produce large crops of fruits consumed by orangutans: *Ficus sp*., *Lithocarpus sp*., and *Dracontomelon sp*. Nests were concentrated inside these trees mainly during fructification, which was similar to primary forests (Felton *et al.*, 2003; Singleton, 2000). In African apes, feeding nests serve to better defend food access against other frugivorous animals (Fruth and Hohman, 1996), and they may have a similar function at KOCP.

Overall, orangutans in Kinabatangan appear to be less selective in their choice of nesting trees than most populations of African apes are (Fruth and Hohman, 1996). In Uganda, chimpanzees used 33 tree species in the Kalinzu Forest, with 5 genera accounting for 78% of 437 nests (Hashimoto, 1995), and 5 species accounting for 50.1% of all nests at Budongo Forest (Brownlow *et al.*, 2001; but see Goodall, 1967). Bonobos in Lomako used only 24 different trees species (Fruth and Hohman, 1993), while they used slightly >100 tree species for nesting in Wamba (Kano, 1992). In Gabon, the 5 most common tree genera accounted for 32.9% of 373 gorilla nests (Tutin *et al.*, 1995), which is comparable to the values for KOCP orangutans.

Most of the nests at KOCP were 10–20 m above the ground, which is slightly lower than those at Ulu Segama (MacKinnon, 1974) and Ketambe (Sugardjito, 1983; Figure 4b). The lower canopy of the degraded habitat at

KOCP may be the most likely underlying cause, as it is in Gunung Palung (Felton *et al.*, 2003). Most of the nests were in the upper parts of tree crowns at sites that provided a clear view of the surroundings, where more leaves were available, and where the apes were not directly exposed to sunlight or rain, as in primary forest (Horr, 1977; MacKinnon, 1974; Sugardjito, 1983). On average, orangutan nests are higher than those of gorillas and similar to those of most chimpanzee and bonobo populations (averages 5–20 m for chimpanzees and bonobos; 0–10 m for gorillas: Fruth and Hohmann, 1996).

KOCP orangutans favor the largest and tallest trees available (Figure 4 and 5). The preference for larger stems is unlikely to be a response to the presence of nocturnal predators, as has been described for other ape populations: chimpanzees (Baldwin *et al.*, 1981); gorillas (Yamagiwa, 2001); Sumatran orangutans (Sugardjito, 1983). In Borneo, the only natural nocturnal predators of orangutans are big pythons that can climb all trees irrespective of their size or diameter and clouded leopards that could prey only on younger individuals (Rijksen, 1978). However, tree falls are common in the fragmented and degraded forest of KOCP because of abiotic (wind; Phillips, 1997) or biotic factors (elephants; obs. pers.). The choice of the tallest and largest trees in overexploited forests as nesting sites may be a means to minimize risks of tree fall and to provide more relaxed sleeping opportunities during the night, which is a time of reduced alertness. One might expect that a decrease in available large trees due to logging activities will result in the reuse of the same suitable nest sites and trees over the years. This action could in turn alter the shape and features of the crown structure of favored nesting trees in such a way that the rate of tree reutilization increases through time (Fruth and Hohmann, 1994). Several trees (*Acantocephalus chinensis*, *Nauclea sp.*, *Neonauclea sp.*) at KOCP exhibit signs of past use—broken branches, bent and healed branches creating forks and other deformities—and we have observed them to be repeatedly used as nesting sites by the same or different individuals, resulting in the creation of ≪villages≫ (Kurt, 1971; in MacKinnon, 1972, pp. 69).

The number of individuals of prenest building age is slightly lower in Sabah (0.86: Mac Kinnon, 1972; Payne, 1988—0.85: this study) than in Kalimantan (0.89: Johnson *et al.*, in press) and Sumatra (0.90: van Schaik *et al.*, 1995), and might reflect inter- and intraspecific differences in life-history parameters.

As noted by Johnson *et al.* (in press), the average daily rate of nest construction by orangutans is lower in Borneo than in Sumatra (Table III). Bornean orangutans build fewer day-nests (12.3% of days in this study) than Sumatran orang-utans do (Singleton, 2000). In the degraded forests of Kinabatangan, most of the day resting periods are spent on simple, unwoven mattresses of leaves, composed of the abundant leafy material of entangled vines and creepers inside the crown of most trees. The platforms are often

made in, or close to, a feeding tree and are poorly constructed, suggesting that they are used for rest stops between two consecutive feeding bouts, as documented for chimpanzees (Brownlow *et al.*, 2001). The high rate of nest reuse during the night at KOCP (12.8% of nights) also contributes to a lower *r* when compared to other study sites (5% in Suaq Balimbing, Sumatra; Singleton, 2000). This specific behavior in Kinabatangan might be explained by the shortage of potential nesting sites in degraded forests, as suggested by Kortlandt (1992) for chimpanzees in Guinea. Plumptre and Reynolds (1997) also documented fluctuations in the rate of nestreuse for different populations of chimpanzees in Africa.

The wide variation in the duration of nest visibility among sites (Table IV) probably will have a larger influence on overall density estimates than other nest parameters (Singleton, 2000), making precise estimate of the nest decay rate *t* a critical factor for accuracy of census results. On average, orangutan nest visibility is longer than it is for African ape species 46–120 days in most populations: Blom *et al.*, 2001; Tutin *et al.*, 1995). The difference in nest life span likely indicates that nests built by orangutans are more complex and more elaborate than those built by African apes (Bernstein, 1969).

The low height of the KOCP forest most likely makes nest detection easier from the ground (especially the older nests in their last stage of decay) than in tall primary forests, and could contribute to the higher *t* value at KOCP. The proportion of day-nests will also directly influence *t* because day-nests tend to have a weaker structure than night-nests, and their mean lifespan is most probably shorter (Johnson *et al.*, in press; Singleton, 2000). Since it is almost impossible to distinguish between day- and night-nests during field surveys, reliance on a decay rate based solely on night-nests will give a more conservative density estimate (Plumptre and Reynolds, 1997), especially in Sumatra where the proportion of day-nests is higher than that in Borneo (Singleton, 2000).

Discrepancies in results could also be a consequence of the various methodologies used for the calculation of the parameter. Abstract statistical models, such as transition matrices and Markov chains, can be useful techniques for rapid assessments but they tend to underestimate *t*, unless correction factors are introduced (Buij *et al.*, 2003; Johnson *et al.*, in press; Table IV). The correction factors are habitat dependent and must be estimated specifically for each study area (Johnson *et al.*, in press). Other models, validated in Sumatra, assume a relationship between nest decay rate and altitude (van Schaik *et al.*, 1995) or pH (Buij *et al.*, 2003). However their validity for Borneo still needs further investigation (Johnson *et al.*, in press).

The most reliable estimates of *t* are obtained with the direct monitoring of the survival of a sufficient number of nests (Buij *et al.*, 2003; Singleton, 2000). At KOCP, we found that the species of tree used for nest construction

was the only habitat-related parameter with a significant impact on nest decay rate. Since tree specific composition changes with study areas, the mean nest decay rate estimated at KOCP cannot simply be extrapolated to other sites. A possible way to overcome this shortcoming would be to directly determine the nest decay rate for the tree genera most frequently used by orangutans for nesting all over their range. The nest decay rate for a given tree genus probably will not change much among different study sites, and thus could be extrapolated to other parts of the orangutan range without necessarily introducing a correction factor. A weighted general $\hat{t}$ value could then be calculated for each site using: $\hat{t} = \Sigma_0^i q_i \times \hat{t}_i$, with $\hat{t}_i$ the estimated time of nest visibility for different groups of trees and q_i the proportion of nesting trees from each group recorded during the field surveys and supposed known without sampling error. This method might help to obtain more reliable t estimates and decrease the biases in density estimates from nest counts.

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