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Orangutan population density, forest structure and fruit availability in hand-logged and unlogged peat swamp forests in West Kalimantan, Indonesia

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Abstract

We investigated the population density of Bornean orangutans *Pongo pygmaeus pygmaeus* and aspects of habitat quality in a selectively hand-logged peat swamp forest in West Kalimantan, Indonesia, and in a comparable unlogged forest nearby. We conducted orangutan nest surveys, measured different parameters of forest structure, recorded monthly changes in fruit availability, and noted the sex and the stage of maturity of orangutans encountered. Nest density, an index of orangutan population density, was 21% lower in the logged area. The forest, logged 2 years previously, had fewer large food trees and a greater number of canopy gaps. We discuss these differences in relation to the lower orangutan nest density in the logged forest. Significantly fewer adult orangutans were observed in the logged study area. We hypothesize that fully adult orangutans, particularly females, are the most severely affected by hand-logging.

Keywords: *Pongo pygmaeus pygmaeus*; Population density; Nest survey; Demographics; Phenology

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1. Introduction

The Bornean orangutan *Pongo pygmaeus pygmaeus* Linnaeus 1760 is an endangered subspecies of great ape that has, along with its Sumatran con-specific, declined in the wild by 30–50% since the middle of the 1980s (Soemarna et al., 1995; Sugardjito, 1995). A cause of their decline over this period is the loss of an estimated 80% of their forest habitat (Soemarna et al., 1995). One of the most important of these forest types is peat swamp forest (Rijksen and Meijaard, 1999; Yeager, 1999).

Peat swamp forests support the highest observed orangutan population densities of any forest type (van Schaik et al., 1995; Russon et al., 2001). Because these forests also contain high densities of valuable timber (Whitmore, 1984), they are often commercially logged (Cannon et al., 1994; Whitmore, 1995). Due to restricted access for heavy machinery, peat swamp forests are commonly harvested using selective hand-logging (Cannon et al., 1994). This technique normally targets only a few commercial tree species and involves the use of hand-held chainsaws and human-powered removal of timber to water-courses (Whitmore, 1984). Because of the lack of heavy machinery, hand-logging is considered less destructive to forest structure than mechanized logging (Ayres and Johns, 1987; Cannon et al., 1994; Grieser Johns, 1997; Putz et al., 2001). However, when carried out illegally by unsupervised and untrained workers, unnecessary damage is likely to result. To the authors' knowledge, no quantitative research has been conducted to assess the level of this impact on wildlife or vegetation.

Previous studies of impacts of selective logging on orangutans have been limited to mechanically logged lowland rainforests. The majority of these studies suggest that declines in orangutan population densities can

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range from 30% to localised extinction (Rijksen, 1978; Aveling and Aveling, 1979, cited in Aveling, 1982; Davies, 1986; Payne, 1987; Rao and van Schaik, 1997). The specific aspects of selective logging that cause these population declines are not fully understood (Rao and van Schaik, 1997). It is generally accepted, however, that selective logging changes the structure of the forest by increasing the abundance and size of canopy gaps and by reducing the proportion of larger trees (Grieser Johns, 1997). Knowledge of orangutan behavioral ecology suggests that such changes to forest structure could have negative effects on their population densities.

Orangutans travel almost exclusively through the canopy (MacKinnon, 1974; Rijksen, 1978; Sugardjito, 1995). Because of this, a significant loss of continuous arboreal pathways could decrease their traveling efficiency (Rao and van Schaik, 1997). Trees also provide the vast majority of food for orangutans (Galdikas, 1988). Orangutans are generalist frugivores that prefer to feed in trees with large patches of mature fleshy fruits belonging to several hundred tree species (MacKinnon, 1974; Rodman, 1977, 1988; Rijksen, 1978; Sugardjito et al., 1987; Galdikas, 1988; Djojosudharmo and van Schaik, 1992; Leighton, 1993; Knott, 1998). Although orangutans also feed on seeds, bark, leaves, shoots, insects and other miscellaneous items (Rijksen, 1978; Galdikas, 1988; Hamilton and Galdikas, 1994; Knott, 1998), the abundance of fleshy fruits and figs provides the most useful indicator of how dense an orangutan population the forest is able to support (te Boekhorst et al., 1990; Djojosudharmo and van Schaik, 1992; van Schaik et al., 1995; Blouch, 1997). The orangutans' preference for large fruit trees (Leighton, 1993) reflects the need of these large-bodied animals to maximise caloric intake relative to energy expenditure while traveling between patches of food (Wheatley, 1982; Knott, 1999a). Reduced fruit availability and canopy continuity (here: continuity of inter-crown pathways) are therefore likely to reduce the density of orangutan populations.

Hand-logging is considered the main threat to orangutans in the Gunung Palung region, West Kalimantan, Indonesia (Meijaard and Nijman, 2000; Knott, personal observation). The orangutan population in this region is estimated to be the largest in Borneo (Yeager, 1999) with densities ranging from 1.5 to 3 individuals/km^2 (Tilson et al., 1993). In this study we compare habitat quality and population density of orangutans between an unlogged and a selectively hand-logged peat swamp forest in the region of Gunung Palung. We also investigate impacts on orangutan demographics and discuss the importance of combining nest counts with demographic surveys.

2. Methods

2.1. Study sites and logging procedure

We collected data in Gunung Palung National Park, West Kalimantan, and in a selectively hand-logged peat swamp forest adjacent to this park (Fig. 1). The unlogged study area was within the trail system of the Cabang Panti Research Station, a site of on-going orangutan research (see Knott, 1998, for a description of the study site). We chose these study areas because both occurred

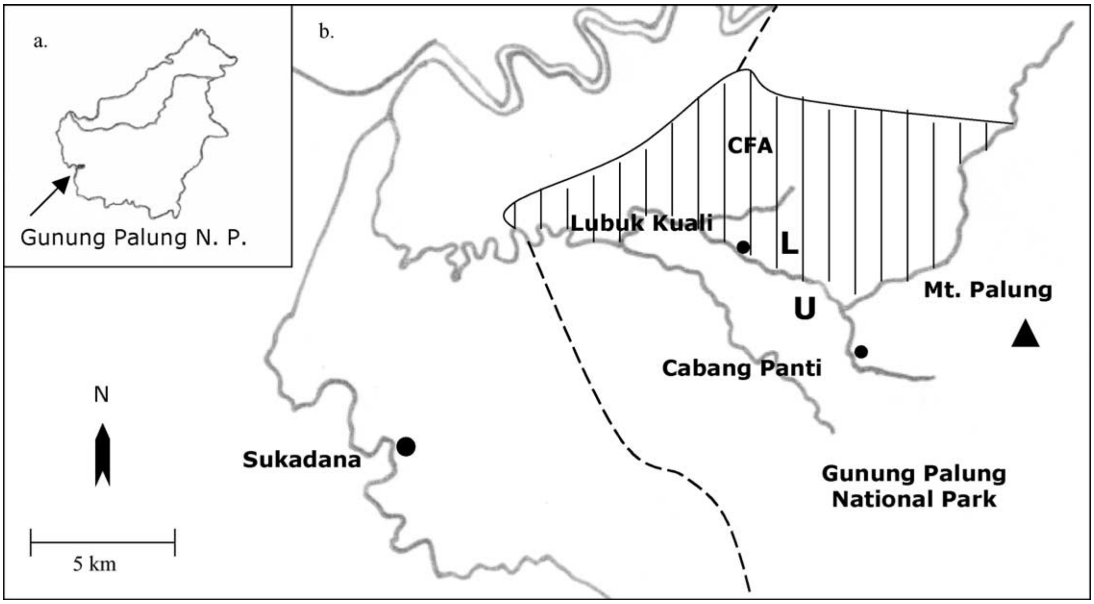

Fig. 1. (a) Map of Borneo and the location of Gunung Palung National Park (GPNP); (b) map of the Community Forestry Area (CFA, 6000ha, currently leased by the Proyek Hutan Kemasyarakatan Gunung Palung) and the location of our logged (L) and unlogged (U) study sites. Research stations Lubuk Kuali and Cabang Panti are also indicated.

within the same drainage area, had similar peat depth and forest composition, and the logging history was well documented by Proyek Hutan Kemasyarakatan Gunung Palung (PHKMGP). The two study areas were separated by a river and were located approximately 2.5–3 km away from each other (Fig. 1).

Illegal loggers extracted on average seven trees/ha (range 0–30 trees/ha; PHKMGP, personal communication) 1.5–2 years prior to the onset of this study. The most frequently harvested species were *Gonystylus bancanus* and *Dyera lowii*, and most harvested trees had diameters of 30–70 cm (PHKMGP, personal communication). Illegal logging camps active during the study were located at similar distances (several kilometers) from both the logged and unlogged study areas. There is no indication that primates were being hunted in any of the study areas (personal observation; PHKMGP, personal communication).

2.2. Study design

Within both the logged and the unlogged study areas, three sites were randomly placed approximately 500–700 m apart from each other. In each site we cut six parallel 300 m transects, placed 50 m apart. Along transects 100 m×10 m plots were placed at 100 m intervals (six plots per site).

2.3. Nest surveys

We counted orangutan nests along transects, using the distance sampling method (Buckland et al., 1993). This method is reliable for estimating relative abundances of orangutans (van Schaik et al., 1995; Blouch, 1997; Russon et al., 2001), as they normally build a new nest every night (Sugardjito, 1983) generally within 20 m of their last feeding site (Setiawan et al., 1996). Orangutan nest density corresponds to the time orangutans spend in an area regardless of whether it is disturbed or undisturbed (Rao and van Schaik, 1997). During surveys we stopped every 5 m and searched 360° for nests occurring within 30 m of either side of the transect. Nest trees were tagged to prevent double-counting. Small nests built within 3 m of larger nests, and constructed at the same time, were determined to be juvenile nests. As these nests are not statistically independent, they were excluded from analysis. We collected nest data in October and November 1999 and January 2000.

Calculating population densities from nest counts is potentially unreliable as it involves numerous assumptions (van Schaik et al., 1995). Alternatively, nest density (nests/km^2) may be used as an index of population density (as per Plumptre and Reynolds, 1997) if decay rates of nests are the same in the two forests (van Schaik et al., 1995). To determine decay rates of nest material, we classified nests into five sequential states: (A) fresh; (B) recent; (C) old; (D) rotting but recognizable; and (E) nest gone/not recognizable (as per Hashimoto, 1995). Using Markov chain analysis (Kemeny et al., 1956) we estimated the rates at which nests change from one state to another in each study area (as per van Schaik et al., 1995).

To be able to calculate nest density we measured perpendicular distance to each nest from the transect. We used the computer package DISTANCE™ to model the probability of sighting nests at a given distance (Buckland et al., 1993). We used the program's Akaike information criterias (Buckland et al., 1993) in conjunction with comparisons of variance estimates and goodness-of-fit tests to select the best model (Quinn and Gallucci, 1980). The hazard rate model was chosen and provided values for effective strip width of the transects sampled. To obtain nest density estimates (d) for the logged and unlogged forests, the formula $d = N/(L \times 2w)$ was used (Buckland et al., 1993), where N is the number of nests found in the final survey, L is total length of transects (km), and w is the effective strip width (km). We do not compare our survey results with those of other researchers due to variations in survey methodology.

During surveys we also estimated the height of each nest above ground to get an indication of the demographic structure of the orangutan population.

2.4. Habitat analysis

We quantified canopy cover, vegetation height and gaps along four transects in each site. We recorded canopy cover and vegetation height at 10 m intervals along transects using the point-intercept method (Brockelman, 1998). Canopy cover was defined as vegetation taller than 2.0 m. Using a horizontally held mirror subdivided into four squares, we categorized the percentage canopy cover above each point. We used midpoints of the recorded interval classes for analyzing height and canopy cover. Height of vegetation was estimated to the closest 5 m.

To assess the impact of logging on canopy continuity we measured the number and length of gaps. We defined a gap as a canopy opening of at least five meters length along transects. The gap boundary was defined either as the canopy edge belonging to a tree $\geqslant 15$ m in height (its position determined by using a Suunto clinometer), or a canopy cover reading of $\geqslant 51\%$.

Within each of the 0.1 ha plots we measured the diameter of every tree at breast height (DBH: 1.4 m above ground) or immediately above buttresses. We recorded all trees $\geqslant 10$ cm DBH that had at least part of their main trunk within the plot boundary. Using the DBH measurements we calculated basal area for the total stand (cross-sectional area of trunks, m^2/ha).

Of those trees present in plots we tagged individuals belonging to 26 species regarded as the principal orangutan food trees in the peat swamp habitat of Gunung Palung National Park (Knott, 1999a; Yeager, 1999; T. Laman, personal communication). We identified trees with the help of local field assistants and a floral key (Andersson, 1972). We also recorded, tagged and measured strangling figs (*Ficus* subg. *Urostigma*) within plots. The diameter of the main root above the point of cleavage was recorded in four size classes: <5 cm; 5–9.9 cm; 10–19.9 cm; and $\geqslant 20$ cm. Strangling figs were not identified to species.

To quantify fruit availability, we monitored the presence of fruit on the tagged food trees every month (as per Leighton, 1993; and Knott, 1998). We classified fruits into three stages of maturation: immature, mature, and ripe. We noted the percentage of each tree canopy that was visible and excluded from analysis trees with $\leqslant 50\%$ visible canopy.

2.5. *Orangutan encounters*

We recorded three stages of maturity of orangutans encountered in logged and unlogged peat swamp habitat: dependent offspring, undeveloped males/ adolescent females, and adults. Dependent offspring are small individuals accompanied by an adult female. Undeveloped males may be sexually immature or mature but lack secondary sexual characteristics (Knott, 1999b; Rodman, 1988). Adolescent females, although independent of their mother, do not have offspring (Knott, 1999b). Undeveloped males and adolescent females are defined for the purpose of discussion but could not be distinguished from each other in the field. We refer to females with offspring and fully developed males as adults.

2.6. *Statistical analysis*

All statistical analyses were conducted using the program STATISTICA^{TM} (alpha level set at $P=0.05$). To test for differences in total nest densities between the two areas for the 3 months surveyed we used one-way repeated measures nested analysis of variance. This design was also used to compare densities of newly built nests (decay states A and B) between the two areas. A Kolmogorov–Smirnov test was used to compare the distribution of nest detection distances. Two-tailed *t*-test was used to compare nest heights in the two areas.

To investigate overall differences in food tree abundance and vegetation structure (stem density, basal area, gap characteristics and vegetation height and cover) between the areas, we performed a stepwise forward discriminate function analysis (DFA; StatSoft^{TM}, 1995). A significant result between study areas indicates that it is appropriate to assess the relative contribution of each vegetation parameter without correcting to preserve experiment-wise error rates (Sokal and Rohlf, 1995). Mann–Whitney *U*-tests were used to test differences in these vegetation parameters between logged and unlogged plots.

To test whether differences in tree size distribution between study areas were due to logging activity and not to inherent site differences, we compared the proportion of medium and large trees in our unlogged sites with data from an undisturbed section within the logged forest concession (PHKMGP, unpublished data) using a Pearson's chi-square test. A Pearson's chi-square test was also used to compare the proportion of small, medium and large food trees between the two study areas.

To assess the relationship between vegetation parameters and nest density we performed multiple regression analysis. We used mean nest densities from the three surveys as the dependent variable. For the independent variables we used parameters from the DFA that explained the overall difference in vegetation structure. We included nest density data only from transects where we collected vegetation data.

Multiple correlation analysis was conducted to test the relationship between the number of gaps and other vegetation parameters. Correlation analysis was also used to assess how the density of newly built nests related to the density of trees with mature or ripe fruit, and to test the relationships between the DBH of fruiting trees, the DBH of food trees, and the DBH of all trees. Tree circumference is a reliable index of the potential size of a tree's fruit crop (e.g. Peters et al., 1988; Chapman et al., 1992). We used Mann–Whitney *U*-tests to compare the number of fruiting trees in logged and unlogged plots. To assess differences in the demographic make up of the two orangutan populations we used Fisher Exact test.

3. Results

3.1. *Nest density and its relation to vegetation structure*

We recorded 626 nests, including five juvenile nests that were removed from analysis. The time taken for nests to decay was similar for logged and unlogged sites [Markov chain results: mean logged = 71 days (range: 67.5–75 days); mean unlogged = 73 days (range: 62–84 days)]. The distribution of perpendicular nest distances from transects did not differ significantly between study areas (Kolmogorov–Smirnov: $n_1=290$, $n_2=331$, $P>0.10$), implying that detectability was similar in the two areas. This allowed us to use nest density for comparison between study areas and as a measure of orangutan population density. Using the estimated means for strip width (logged = 17.5 m; unlogged = 17.4 m) the

Table 1
Results from discriminate function analysis of vegetation structure [parameters in table explain the overall difference between logged (L) and unlogged (U) study areas]

Vegetation variable	Partial Wilk's Lambda	P	Relative contribution
No. of gaps	0.477	***	L > U
Stem density	0.528	**	L > U
No. of food trees	0.725	*	L > U

* $P<0.05$.
** $P<0.01$.
*** $P<0.001$.

number of nests per km^2 was calculated for each transect. There were significantly fewer nests per km^2 in the logged area than in the unlogged area (repeated measures ANOVA: $F=4.62$, d.f. = 1, $P<0.05$). The logged area had 21% fewer orangutan nests per km^2 (mean = 43.4 nests/km^2 ± 1 S.E. 4.26) than the unlogged area (mean = 54.7 nests/km^2 ± 1 S.E. 3.48).

Nests were built closer to the ground in the logged area than in the unlogged area ($t=-2.03$, d.f. = 619, $P<0.05$). Nests built lower than 10 m from the ground represented 26% of all nests in the logged area, but only 17% in the unlogged area.

There was a significant difference in vegetation structure between the two areas (DFA: Wilk's lambda = 0.091, $F_{(6,16)}=26.53$, $P<0.001$). Of vegetation variables included in the DFA, three were found to significantly contribute to the discrimination between the study areas: number of gaps, stem density, and abundance of food trees (Table 1). Of these variables, only number of gaps was significantly (negatively) related to nest density (Table 2).

3.2. Vegetation parameters

Vegetation height was not significantly different between study areas (Mann–Whitney U-test: $U=68$, $P>0.05$). There was less canopy cover in the logged area (74% vs. 85%; Mann–Whitney U-test: $U=18.5$, $P<0.05$). Total gap length per kilometer was significantly different between the study areas (Mann–Whitney U-test: $U=37$, $P<0.05$). We found 38 gaps in the logged area and 18 gaps in the unlogged. Gaps > 35 m in length were found only in the logged area (Fig. 2). The number of gaps was significantly correlated with gap length, vegetation height and canopy cover (Table 3). Total stem density, food tree density and basal area of large trees were not significantly correlated with number of gaps (Table 3).

Table 2
Results from regression analysis performed on nest density and vegetation parameters that explain difference in vegetation structure between logged and unlogged areas (Table 1)

	Nest density (b)	S.E. of b	P
No. of gaps	−0.66	0.18	**
Stem density	−0.66	1.17	n.s.[a]
No. of food trees	0.68	1.60	n.s.

[a] n.s. = not significant.
** $P<0.01$.

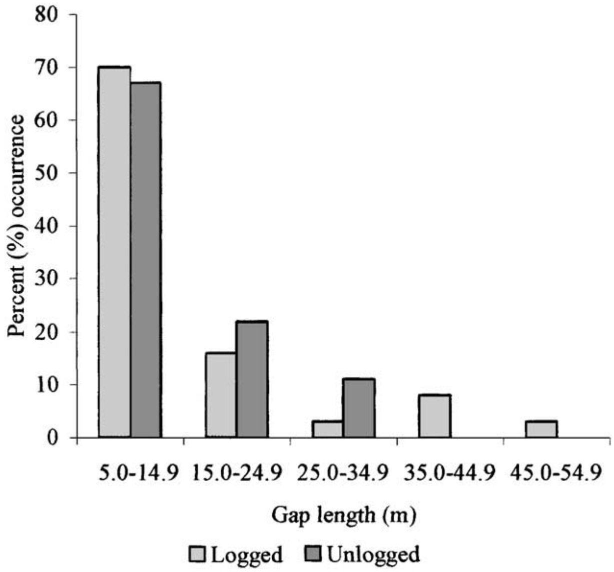

Fig. 2. Relative proportion of different sized gaps in the logged area ($n=38$), and the unlogged area ($n=18$).

Total stem density was significantly different between study areas, whereas total basal area was not (Table 4). Density and basal area of trees ⩾35 cm DBH was significantly lower in the logged area (Table 4). Tree diameter was significantly smaller in the logged area (Mann–Whitney U-test: $U=52$, $P<0.001$). Proportions of small, medium and large trees found within the two study areas are displayed in Fig. 3.

There was no significant difference in the proportions of medium and large trees between our unlogged study area and an undisturbed section within the logged forest concession (Pearson's chi-square test: $\chi^2=1.83$, d.f. = 1, $P>0.05$).

Table 3
Correlations between number of gaps and other structural parameters

	Number of gaps (r)	P
Length of gaps	0.90	*
Forest height	−0.64	*
Canopy cover	−0.64	*
Stem density	−0.21	n.s.[a]
No. food trees	−0.11	n.s.
No. large food trees	−0.10	n.s.
Basal area of large food trees	−0.28	n.s.
Total basal area of large trees	−0.36	n.s.

[a] n.s. = not significant.
* $P<0.05$.

Table 4
Mean stem density (trees/ha with 1 S.E.) and mean basal area (m^2/ha with 1 S.E.), for the stand in general and for trees $\geqslant$35 cm DBH in logged and unlogged areas (Mann–Whitney U-test, $n_1 = n_2 = 18$)

Size class	Parameter	Logged	Unlogged	P
>35 cm DBH	Stem density	44.4±4.0	74.4±7.4	**
	Basal area	6.4±0.59	14.2±1.44	**
Total	Stem density	915±58.1	625±15.6	***
	Basal area	29.2±1.6	28.1±1.36	n.s.[a]

[a] n.s. = not significant.
** $P < 0.01$.
*** $P < 0.001$.

Of the 26 food species targeted in our inventory, 25 species were found in the logged area and 23 species in the unlogged. In total, we tagged and measured 1002 food trees. Proportions of small, medium and large food trees were significantly different between study areas (Pearson's chi-square test: $\chi^2 = 20.96$, d.f. = 2, $P < 0.001$; Fig. 3). The unlogged area had a greater proportion of food trees in the large size class, although the number of food tree species per plot (Mann–Whitney U-test: $U = 31$, $P < 0.001$) and stem density of food trees (Mann–Whitney U-test: $U = 27.5$, $P < 0.001$) were significantly higher in the logged area.

Similar numbers of strangling figs were recorded in the two areas (logged = 11.7 ind./ha; unlogged = 9.4 ind./ha; Mann–Whitney U-test: $U = 149.0$, $P > 0.05$). There were five times as many strangling figs within the largest size class in the unlogged area than in the logged area (25% vs. 5%). In the logged area 62% of fig trees were in the smallest size class, compared to 18% in the unlogged area. Diameter of host trees was significantly smaller in the logged area (Mann–Whitney U-test: $U = 43$, $P < 0.01$). Host trees with a DBH less than legal minimum harvesting size (35 cm DBH) represented 88% of all host trees in the logged area, and 29% in the unlogged area.

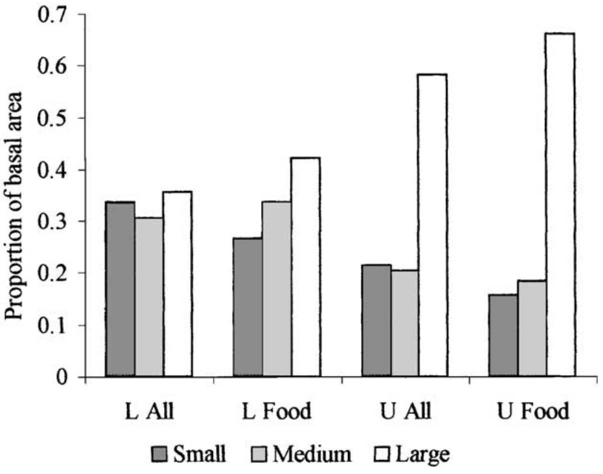

Fig. 3. Basal area of small (10–19.9 cm DBH), medium (20–29.9 cm DBH) and large ($\geqslant$30 cm DBH) trees presented as proportions of the entire tree population (All), and basal area of small, medium and large food trees presented as proportions of the food tree population (Food) in logged (L) and unlogged (U) sites.

3.3. Fruit availability

Ten food tree species in the logged area and five species in the unlogged area bore fruit during the study. There was twice the percentage of fruiting trees in the unlogged area compared to the logged area in October (11.1% vs. 5.2%), with the extent of this difference decreasing over subsequent months (November: 7.1% vs. 5.1%; January: 0.9% vs. 1.0%). There was no significant difference between study areas in the total number of trees with mature fruit (logged = 54 trees; unlogged = 50 trees; Mann–Whitney U-test: $U = 1192$, $P > 0.05$). Four of 27 fig trees monitored bore fruit. All fruiting fig trees were >5 cm DBH.

Fifty-one trees (of the 666 sampled) in the logged area and six trees (of 336) in the unlogged area were excluded from fruit and flower analysis due to poor canopy visibility. Equal numbers of strangling figs were excluded in both areas. Excluded trees disproportionately represented the small and medium size classes. Therefore, a direct comparison of DBH of fruiting trees between the two areas could not be made.

3.4. Density of new nests in relation to fruit availability

There was a significant difference in the density of newly built nests between months (ANOVA: $F = 3.74$, d.f. = 2, $p < 0.05$). The density of new nests was significantly correlated with the number of fruiting trees ($r = 0.65$, $n = 13$, $P < 0.05$; Fig. 4). There was a significant correlation between DBH of fruiting trees and DBH of food trees ($r = 0.64$, $n = 13$, $P < 0.05$), and between DBH of food trees and DBH of all trees ($r = 0.86$, $n = 13$, $P < 0.05$). Hence, areas with larger mean tree size were likely to harbor larger orangutan food trees in fruit at any one time (Fig. 5).

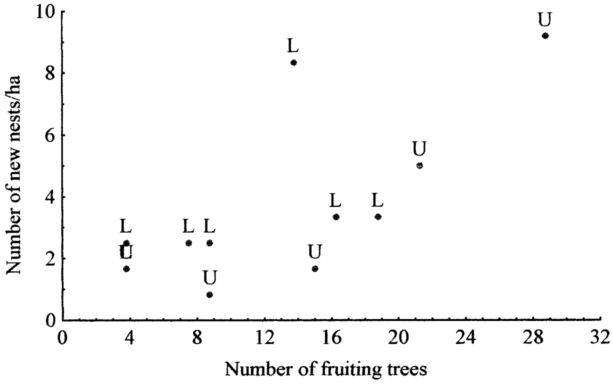

Fig. 4. Relationship between abundance of fruiting trees and density of newly built nests in logged (L) and unlogged (U) sites.

3.5. Orangutan demographics

Eight adult orangutan females were encountered in the unlogged area. In the logged area three adult females were encountered, in addition to one adult male and eight undeveloped males/adolescent females. We encountered significantly fewer adult individuals in the logged forest (Fisher Exact test two-tailed: $P<0.01$). Insufficient numbers of adults, males in particular, were encountered to statistically assess differences in male and female representation between study areas.

4. Discussion

Orangutan nest density was 21% lower in the hand-logged peat swamp forest than in the comparable undisturbed area. The orangutan populations in the logged and unlogged peat swamps also differed in their demographic composition. These differences are likely to have been caused by changes in habitat quality—altered tree size distribution, reduced availability of large fruit crops and increased extent of canopy gaps—associated with logging disturbance. There are several reasons why these structural changes can negatively impact on this endangered species.

The orangutan is the world's largest arboreal species (average weight for males: 86.3 kg, females: 38.5 kg; Markham and Groves, 1990) and individuals expend a considerable amount of energy traveling (Rodman, 1979; Wheatley, 1982; Knott, 1999a). To minimize this expense, orangutans move between the sparse fruit trees using a slow quadrupedal gait along inter-crown pathways (MacKinnon, 1974; Wheatley, 1982; Tuttle and Cortright, 1988). This technique may be compromised, though, when individuals are confronted by large gaps in the canopy, as caused by logging operations. Orangutans would then be forced either to travel a longer distance around the gap, or to descend from the canopy and cross the gap on the ground. Regardless of the strategy employed, orangutans must expend more energy when negotiating gaps than when traversing a continuous forest canopy (van Schaik et al., 2001). Although the above has not been empirically tested, some evidence of this cost is provided by a study of Sumatran orangutans in which individuals adopted more energetically expensive locomotor behaviour within logged versus unlogged forests (Rao and van Schaik, 1997). These orangutans also spent more time traveling while in the logged forest, consistent with the reduction in the continuity of the canopy (Rao and van Schaik, 1997). Other studies conducted in forests where canopy pathways have been reduced by timber extraction found that the energy demands of primates increased along with the risk of falling and the possibility of predation (Marsh et al., 1987; Gebo and Chapman, 1995).

In our study, orangutan nesting behaviour appeared to be negatively influenced by the presence of gaps. The number of gaps did not, however, correlate with vegetation parameters expected to influence the presence of orangutans directly such as the abundance of food trees and the availability of trees to nest in (here defined as trees >10 cm DBH; for more detailed assessment of nest tree preference, see Engström, 2000). In light of these findings, it is possible that gaps influenced orangutan presence through their impact on the orangutans' arboreal pathways.

The hand-logged area also had a different tree size distribution compared to the unlogged area. Our statistical comparison of vegetation structure between an undisturbed section of the forestry concession and our unlogged study area supports our assumption that the differences in tree size distribution are due to logging and not to inherent site differences. Whereas the high level of incidental damage associated with mechanized logging (e.g. construction of roads and log-loading areas) generally results in a reduction of all tree size classes evenly (Johns, 1988), hand-logging in this study appeared to have a disproportionate impact on large trees (Fig. 3). In addition to the smaller number of large timber trees in the logged forest, there were fewer large food trees, resulting in a forest with fewer large trees fruiting at any one time (Fig. 5). This situation should be costly for orangutans as their foraging strategy is dictated by the need to maximise calorie intake relative to travel costs (Wheatley, 1982; Knott, 1999a), achieved by seeking large patches of fruit (Leighton, 1993). Because large tropical trees generally produce large fruit patches (e.g. Peters et al., 1988; Chapman et al., 1992) and also constitute reliable sources of food (Rijksen, 1978; Leighton, 1993), their abundance should facilitate efficient foraging. The correlation between density of fruiting trees and orangutan nest density found in this and other studies (te Boekhorst et al., 1990; Djojo-

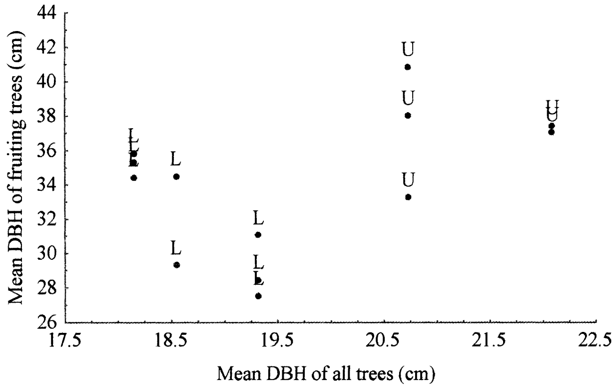

Fig. 5. Relationship between the size (DBH) of fruiting trees and the size of all trees in logged (L) and unlogged (U) sites.

sudharmo and van Schaik, 1992; Blouch, 1997) supports the importance of fruit availability to orangutan habitat preference. We believe that the importance of large fruit patches to orangutan habitat preference is a logical extension of this relationship. A recent study in Sumatra (Wich et al., 2002), comparing phenological measures of fruit availability with behavioral observations, add support to our hypothesis as they found orangutans to preferentially forage in fruit trees significantly larger than the mean size of available fruiting trees. Although orangutans occasionally fed in small trees, preference was exhibited for trees >50 cm DBH (Wich et al., 2002), the category of trees most frequently taken by loggers in our study area.

Logging not only removes large timber trees, but can also have an adverse effect on the abundance of large strangling figs (Leighton and Leighton, 1983; Lambert, 1991). Due to the asynchronous fruiting habits of these hemi-epiphytes (Corner, 1988; Laman and Weiblen, 1998; Kinnaird et al., 1999), they are an important and reliable food source for orangutans during periods when other fruits are scarce (Rodman, 1977; Leighton and Leighton, 1983; Djojosudharmo and van Schaik, 1992; Blouch, 1997; Knott, 1998). Strangling figs are known to disproportionately use large host trees, which in turn are preferred targets of loggers (Leighton and Leighton, 1983; Johns, 1987; Lambert, 1991; Laman, 1996; Patel, 1996). It is likely that many mature strangling figs were killed in this logging operation, as 88% of the remaining individuals were found in host trees smaller than those generally harvested. We also found a fifth as many large strangling figs in the logged area—a degree of impact similar to that recorded in forests mechanically logged (Rosenbaum et al., 1998). Because large strangling figs are more likely to produce large fruit crops (T. Laman, personal communication), their loss, in combination with the loss of other large fruit trees and the disruption of canopy continuity due to logging, should result in an environment of lower energetic return for orangutans. This may explain why the density of orangutan nests was 21% lower in the logged forest.

In addition to a lower nest density, the logged area also had a lower proportion of adults and appeared to have a lower proportion of reproductively mature females. This information gives us a greater insight into the impacts of logging than nest counts alone can provide. The demographic difference between the two populations may be explained if we assume that orangutans fled to undisturbed areas at the time of logging. Such behaviour and subsequent "crowding" has been suspected in other parts of Borneo where researchers have recorded unusually high orangutan densities in areas where surrounding forests were being actively disturbed by humans (Davies, 1986; Russon et al., 2001). A crowded population eventually experiences a relative shortage of food, with increased competition as a result (Rijksen and Meijaard, 1999). Because undeveloped and adolescent orangutans are subordinate and often transient members of the population (van Hooff, 1995; Rijksen and Meijaard, 1999), these individuals may be forced to search for resources in poorer habitats (Rijksen and Meijaard, 1999) such as our hand-logged study area.

An alternative scenario, favored by authors studying the impacts of logging on Sumatran orangutans (van Schaik et al., 2001), is that resident orangutans do not flee the disturbance but remain in their home range. The lower orangutan density observed after logging is therefore explained by the elimination of these individuals from the population due either to hunting, capture or stress-induced disease (van Schaik et al., 2001). Their evidence for this scenario is based on observations that nest densities within pockets of undisturbed forest do not increase despite the logging of surrounding areas. The authors suspect that transient orangutans still use the damaged forest that was previous home to a larger resident population, although to a lesser extent.

Regardless of the underlying cause of the observed demographic imbalance in this study, we suggest a number of reasons why undeveloped and adolescent orangutans may cope better than adults in forests with many gaps and few large food trees. One reason could be their ability to travel more rapidly and to cover a greater distance every day (Galdikas, 1995) resulting in a better chance of finding sufficient fruiting trees. In addition, undeveloped males have a much smaller body size than fully developed adult males and consequently have lower energy demands (Mitani et al., 1996). Adolescent females, similarly, do not have the added nutritional requirements associated with pregnancy and lactation (Galdikas, 1988).

Furthermore, there are several explanations why adult females may be more severely impacted by logging than adult males. Rao and van Schaik (1997) found that a female was less capable than a male at traveling efficiently through a logged forest. Females and their young are also more vulnerable to ground predators (Galdikas, 1988) and therefore are more likely to avoid forests with discontinuous canopies. This is supported by orangutan behavioral studies showing that females spend less time traveling and feeding on the ground than males (Galdikas, 1979, 1988; Rodman, 1979). These factors, in combination with the physiological requirements of reproduction, suggest that a selectively logged forest may be less favorable for adult female orangutans.

Evidence for a demographic imbalance was also provided by the distribution of nest heights. Male orangutans in the forests of Gunung Palung National Park are known to build their night nests closer to the ground than the more vigilant adult females, whether or not the females have offspring (Setiawan et al., 1996; also found in Sumatran orangutans by Sugardjito, 1983; and in bonobos by Fruth and Hohmann, 1993). In this study the mean nest height was significantly lower in the logged forest than in the unlogged forest, even though forest height was similar between the two areas.

Because of the demographic imbalance, the full impact of hand-logging on this orangutan population may not be seen for many years. Orangutans have the slowest reproductive rate of all mammals, with females giving birth on average every 7.9 years (Galdikas and Wood, 1990; Knott, 2001). The length of time between births appears to be influenced by peaks in fruit abundance, such as mast fruiting events (Knott, 1999a). Every 2–10 years, up to 88% of lowland rainforest trees flower and fruit in synchrony, led by the dominant dipterocarps (Medway, 1972; Appanah, 1985; Ashton et al., 1988; van Schaik, 1986). During mast fruitings orangutans eat large amounts of calorie-rich foods, such as dipterocarp seeds, which allows them to put on fat stores (Knott, 1998, 1999a). In combination with the general negative effect of logging on the extent and intensity of masts (Curran et al., 1999), preferential logging of large dipterocarps could compromise orangutans' ability to survive the long post-mast periods of low fruit availability. Any reduction in sufficient fat stores may lead to lengthened birth intervals (Knott, 2001). This can be disastrous because population simulations show that orangutan birth intervals lengthened by 2 years can cause a negative population growth (Tilson et al., 1993). The logged forest in this study contained a larger number of young food trees than the unlogged forest and there is a possibility that sufficient food resources will develop in the future if the forest is left to recover. Unfortunately, such recovery is unlikely given the fact that the rate of illegal logging has increased in this area since the time of our study and has now even affected large sections of Gunung Palung National Park. Although hand-logging is a type of disturbance commonly regarded as light (Ayres and Johns, 1987; Putz et al., 2001), from our own observations we can conclude that illegal logging crews often cause unnecessary wastage and damage to the residual stand despite the lack of heavy machinery, due to their haphazard construction of extraction trails and lack of any incentive or training to minimize impacts.

In conclusion, we hypothesize that a decrease in the abundance of large fruit trees and an increase in the extent of gaps caused the 21% difference in orangutan nest density between the hand-logged and unlogged sites. The combination of these two factors may have reduced the habitat quality for orangutans in the logged forest. Our observations in the logged and unlogged peat swamps revealed that fewer adult orangutans used the logged study area. We hypothesize that this results from a disproportionate impact of hand-logging on adults, particularly adult females.

In relation to studies comparing orangutan densities in unlogged and mechanically logged rainforests, which report declines ranging between 30% and localised extinction (Rijksen, 1978; Davies, 1986; Payne, 1987; Rao and van Schaik, 1997), the difference in nest density between our study areas is relatively low. Our demographic results suggest, however, that there were impacts that could not be revealed by population counts alone. We therefore recommend that if nest surveys are performed to assess the impacts of habitat disturbance on orangutans, they be carried out in combination with quantified observations of orangutan demographics.

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