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The blowgun is mightier than the chainsaw in determining population density of Bornean orangutans (*Pongo pygmaeus morio*) in the forests of East Kalimantan

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ABSTRACT

Due to its practical relevance to conservation, considerable efforts have been devoted to understanding the effects of logging on orangutan (*Pongo* spp.) population densities. Despite these efforts, consistent patterns have yet to emerge. We conducted orangutan nest surveys and measured forest quality and disturbance level at 108 independent locations in 22 distinct sites in the forests of the Berau and East Kutai regencies of East Kalimantan, Indonesia. Survey locations varied substantially in orangutan density, forest structure, distance to villages, and logging intensity. We incorporated site-specific nest tree composition into our estimates of nest decay rates to reduce errors associated with inter-site differences in nest tree selection. Orangutan nest densities were uncorrelated with altitude, fig density, or any other ecological measure. Multivariate analyses demonstrated that densities were not significantly affected by logging intensity (at the relatively light levels we report here) or the distance to the nearest village, but were positively correlated with the distance from the nearest village known to hunt orangutans. These results indicate that provided hunting is absent, lightly to moderately degraded forests retain high conservation value for orangutans. Widespread incorporation of degraded areas into management plans for orangutan populations would substantially increase the size of populations that could be protected, and thereby improve their changes for long-term survival.

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1. Introduction

Orangutans are endangered apes whose distribution is confined to the South-East Asian islands of Borneo and Sumatra. These large-bodied, slowly-reproducing primates live at low population densities (Delgado and van Schaik, 2000; Galdikas

and Wood, 1990; Rijksen and Meijaard, 1999; Wich et al., 2004) and therefore need large contiguous areas of suitable habitat in order to maintain viable populations. As the remaining patches of undisturbed lowland forest on both islands are rapidly shrinking and becoming increasingly fragmented (Curran et al., 2004; Fuller et al., 2004; Linkie et al., 2004; Wich

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et al., 2003), sole reliance on pristine forest is unlikely to be a viable strategy for the prevention of orangutan extinction. If orangutans can survive and reproduce in lightly to moderately disturbed forests, the incorporation of these areas into orangutan management plans could substantially improve our chances of protecting the independent replicates of viable populations necessary to ensure long-term persistence of the species. Although this logic has prompted several of our colleagues to successfully argue for the incorporation of degraded forests into orangutan management plans (e.g., Ancrenaz et al., 2004a,b, 2005; Morrogh-Bernard et al., 2003), the conservation value of disturbed forests has yet to be widely accepted by politicians and natural resource managers. Additional information on how well orangutan populations can survive in degraded forests, and the effects of different types of degradation, is therefore urgently needed.

A substantial body of research has assessed the effects of logging on South-East Asian wildlife (e.g., Johns, 1986; Lammertink, 2004; Meijaard et al., 2005; Wilson and Wilson, 1975), and several studies have explicitly addressed orangutans (e.g., Felton et al., 2003; Knop et al., 2004; Morrogh-Bernard et al., 2003; Rao and van Schaik, 1997). Despite this attention, no clear picture has emerged regarding the effects of logging on orangutan population density. Published studies have reported density increases (Russon et al., 2001), decreases (Felton et al., 2003; Johnson et al., 2005) and no effects (Knop et al., 2004) associated with logging under different conditions. Interpretation of these results is confounded by variation in habitat type, habitat quality and population density prior to logging, the number of times a site has been logged, how long ago logging occurred, and possible life history differences between orangutan species and subspecies. In addition, the effects of other types of human-induced disturbance, such as hunting and the proximity to villages, have yet to be systematically addressed.

While historical hunting, possibly in combination with soil fertility (see Payne, 1990; Meijaard et al., 2005), is widely acknowledged to be the most likely explanation of why large areas of apparently suitable habitat on Borneo are currently devoid of orangutans (Rijksen and Meijaard, 1999; Yeager, 1999), relatively little attention has been paid to the effects of poaching on extant orangutan populations. In many parts of their current range orangutans are hunted, for food, to obtain infants for the pet trade, in response to crop raiding, or for traditional medicine (Rijksen and Meijaard, 1999). In most locations on Borneo hunting rates are reported as low, and thus the effects of hunting are normally ignored in studies addressing the effects of human disturbance on orangutans. However since orangutan populations have low intrinsic rates of increase, even low hunting rates (~1% annually) can have strong negative effects on populations (Leighton et al., 1995; Singleton et al., 2004). It is therefore important to assess whether orangutan populations are affected by hunting (or other forms of disturbance) before conclusions about the effects of logging can be drawn.

We here report the results of an extensive set of orangutan surveys conducted in forests in which habitat quality, logging intensity, distance to human habitation, and inferred hunting pressure differ widely. We use these data to test specific hypotheses about the effects of various types of

disturbance on orangutan densities, and consider how our findings can be practically applied to aid orangutan conservation efforts.

2. Hypotheses to be tested

2.1. H1: Orangutan densities are negatively correlated with logging intensity

Although there is substantial variation between studies, the majority have shown that logging has negative effects on orangutans. Logging removes large trees on which key food lianas and figs reside (Leighton and Leighton, 1983), disturbs canopy connectivity and therefore increases orangutan locomotor costs (Rao and van Schaik, 1997), and increases the accessibility of forest areas, thereby rendering them more susceptible to other forms of disturbance (e.g., fire, hunting).

2.2. H2: Orangutan densities are positively correlated with distance to human villages

Orangutans living in proximity to human habitations may experience elevated mortality and morbidity. Individuals living closer to humans are more likely to contract diseases from humans or domestic livestock (Deem et al., 2000; Wolfe et al., 1998), and if they enter gardens seeking food they are likely to be injured or killed (Rijksen and Meijaard, 1999).

2.3. H3: Orangutan densities are positively correlated with the distance to the nearest village known to hunt orangutans

Because orangutans reproduce so slowly even modest hunting pressure will force populations into serious decline. Thus in areas in which hunting is common, orangutan densities are predicted to be low. Direct assessment of hunting rates on orangutans at our study locations was unfeasible and would have been prone to substantial sampling error and bias. Therefore, we used the straight-line distance to the nearest village known to hunt orangutans as a simple proxy for hunting intensity (see below). Orangutans living near hunting villages are more likely to encounter hunters, and discussions with hunters suggested that they were more likely to kill orangutans if they encountered them closer to their own villages than if they encountered them further away from their village.

3. Methods

We collected data at 22 sites located in the Berau and East Kutai regencies in East Kalimantan, Indonesia between December 2001 and August 2004 (Fig. 1). At each site we erected a small campsite and used this as a base for all data collection at that site. Sites were separated from each other by at least 5 km, often much more. At each site we randomly placed a variable number of midlines ($n_{\text{total}} = 108$ midlines, mean 4.9, range 1–10 midlines/site) of 1 km in length, with the stipulation that each midline was at least 1 km from any other midline. Perpendicular to each midline we placed several transects by cutting a narrow trail of 500 m in length (slope

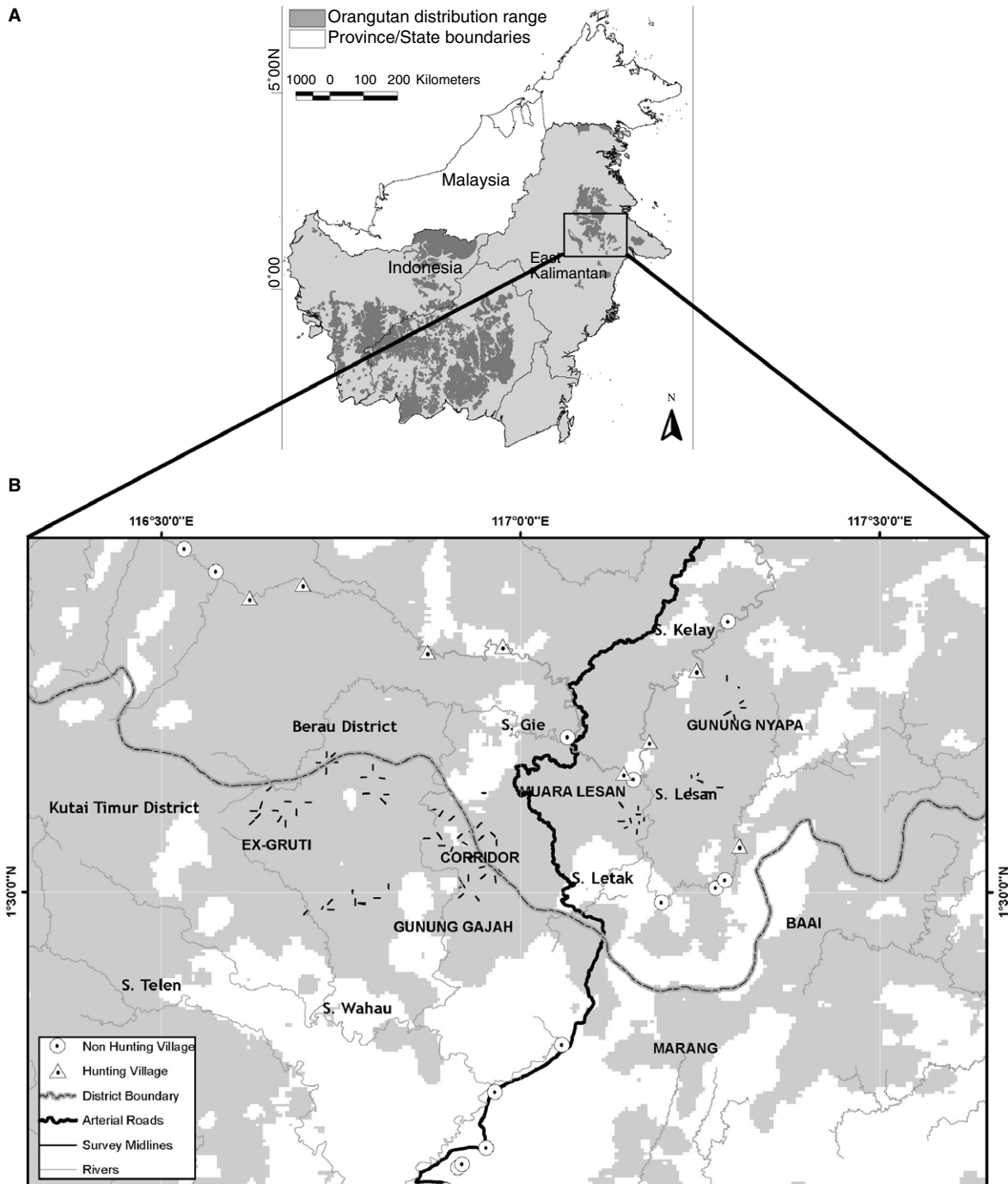


Fig. 1 – Location of all survey locations. (A) Map of Borneo showing country, province and district boundaries and orangutan distribution range (after Singleton et al., 2004). **(B)** Survey area showing degraded forest (canopy cover <70%) and non-forest areas (light grey), and forest areas (dark grey) (source MODIS imagery 2003 – D. Fuller, unpublished data). The locations of villages that are known to hunt and not to hunt orangutans are indicated.

corrected). At most midlines we placed eight transects, resulting in 4 km of transect at each midline, although at some midlines fewer transects were cut ($n_{\text{total}} = 762$ transects, 381 km surveyed) for logistical reasons (amount of available time, availability of trained, reliable field staff). The starting point and bearing of each transect were randomly selected, with the stipulation that all transects on the same side of the midline were at least 100 m apart.

3.1. Site descriptions

Data were collected at the following 8 locations. All locations were in timber concessions (except Marang, which had been illegally logged), although not all had been logged when we collected data. After each location we list the number of sites (S), midlines (M), and transects (T), and provide a brief description of each.

Baai (BAAI, $n = 1S, 1M, 2T$) site was located in limestone karst forest between 400 and 460 m elevation. The forests in this site were logged in 1975, and have been logged illegally since 1987. Few large trees remain at this site, and much of the ground is covered in dense secondary undergrowth.

Corridor (CDR, $n = 2S, 8M, 32T$) sites were located in a corridor of lowland forest between two larger blocks on intact forest (Fig. 1). Areas to the north and south of this location were a patchwork of cleared land and forest being actively logged at the time data were collected. The majority of the forest was logged secondary forest, interspersed with patches of primary forest and logging roads. CDR1 was logged in 1995–1996 and 2000–2001 and the areas directly adjacent to CDR2 were being actively logged while data were being collected.

Gunung Gajah (GG, $n = 7S, 40M, 312T$) sites were predominantly hill Dipterocarp forests, but incorporated a range of elevations, terrain, and disturbance intensities. Logging disturbance was moderate at GG1 and GG5, light at GG3, GG6, and GG7, and absent at GG2 and GG4. Small patches of freshwater and peat swamp habitats were present at GG2 and GG3. For sites for which we could obtain information (GG2, GG5, GG7), logging at these sites was carried out between 1999 and 2001.

Gunung Nyapa (GN, $n = 2S, 12M, 92T$) sites were in a mixture of hill Dipterocarp and limestone karst forest. A few of the transects at GN1 showed evidence of light logging by the timber concessionaire in 1973. Some transects on GN2 were more heavily logged, although we were unable to gain information on when this site had been logged.

Ex Gruti (GR, $n = 1S, 7M, 52T$) site was in a mixture of logged and primary hill Dipterocarp forests, mostly on steep terrain. Areas near rivers and on relatively gentle slopes were logged, while the steeper sites remained untouched, presumably due to the difficult terrain. Trees at the logged sites were cut between 1989 and 1995.

Muara Lesan (ML, $n = 4S, 13M, 89T$) sites were in lowland Dipterocarp forest. ML 1 was lightly logged and in close proximity to areas burned during fires in 1997–1998. ML2 was logged in 1980, but is now protected by the local community as a wildlife preserve. ML3 was comprised of pristine lowland forest, with high floristic diversity and excellent forest structure. ML4 was the most heavily logged of all sites, the result of logging in 1998–1999. As with the CDR sites, some areas immediately to the north and south were being actively logged prior to and during the surveys, and others had been clear-cut.

Marang (MRG, $n = 1S, 2M, 8T$) site was located in karst forest that was disturbed by illegal logging and fires in 1982 and 1987. Few large trees remained and dense undergrowth and secondary vegetation dominated most areas.

Sungai Gie (SG, $n = 4S, 25M, 175T$) sites were all located in pristine, well-structured lowland Dipterocarp forest. Although none of these sites had been logged (except the occasional hand extraction of gaharu, *Aquilaria malaccensis*, which occurred at most locations), some transects at SG3 were close to active logging operations. At SG we made frequent sightings of birds and mammals rarely seen at other sites.

3.2. Nest survey protocol

Data were collected by teams of two trained assistants who closely followed the protocol used by Johnson et al. (2005). Most transects were walked twice, by a different team and in opposite directions each time, and all orangutan nests along the transect were recorded. Following Johnson et al. (2005), for the transects that were not walked twice ($n = 81$, or 10.6%), we scaled up nest counts by the mean percentage of additional nests seen on the second count of transects that were walked twice. For each nest detected, we recorded the perpendicular distance between the point below the middle of the nest and the transect line (measured to the nearest 0.1 m, slope corrected), nest tree diameter at breast height, dbh (measured to nearest 0.5 cm), the local name of the tree, if known, and the nest age class (named by the letters A–E, see Johnson et al. (2005) for definitions of nest age classes used). We fixed a small aluminium tag bearing a unique sequential number to each nest tree.

3.3. Ecological assessment

We gathered data on forest structure and disturbance level along each transect. We measured the density of trees in three broad size classes and the density of figs and lianas in two size classes. Abundance and local names of trees with boles ≥ 80 cm dbh within 10 m on each side of the transect were recorded (resulting in a 500 m \times 20 m belt, or 1.0 ha per transect). The number and names of trees of 40–59.5 cm dbh and of 60–79.5 cm dbh, and lianas with stems 5–9.5 cm dbh and ≥ 10 cm dbh, that occurred within 5 m on either side of the transect were recorded (resulting in a 500 m \times 10 m belt, or 0.5 ha). Checks by A.J.M. and team leaders confirmed that local tree names were consistent between teams and reflected distinct taxa. We also recorded the number of tree stumps resulting from chainsaw cuts in each of the three size categories listed above, using the same belt widths. When discernable from the stump, the local name of these felled trees was also recorded. These data provided an estimate of logging intensity along each transect. Finally, at predetermined locations on each midline and transect we recorded altitude and location using Garmin III and 12 GPS units. At some sites we measured soil pH using an analog soil moisture pH meter to test the model provided by Buij et al. (2003) relating nest decay rates to soil pH.

3.4. Data analysis

Following van Schaik et al. (1995), we calculated the density of orangutan nests (D_N) using the following formula:

$$D_N = \frac{n}{l \times 2w}, \quad (1)$$

where w is the effective census width (km), l the length of the transect (km), and n the number of orangutan nests counted. We examined 'w' independently at each site and used the computer program Distance 4.1 Release 2 (Thomas et al., 2004) for all analyses. We stratified the nest sample by site ($n = 22$) to reduce size bias (see Buckland et al., 2001). In addition, we excluded nests which had perpendicular sighting

distances in the highest 5% of all observations to reduce potential bias introduced by extreme outliers. Following Buckland et al. (1993, 2001), we modeled our distribution of perpendicular line-to-nest distances at each midline using five different models and selected the best model based on the lowest value for Akaike's Information Criterion (AIC).

We calculated orangutan density by using the following equation:

$$D_{OU} = \frac{D_N}{p \times r \times t}, \quad (2)$$

where D_{OU} is the density of orangutans/km², p the proportion of the population that make nests, r the rate of nest building (nests/day/individual), and t the amount of time a nest is recognizable before decay (days).

3.5. Parameter selection

Since no long-term research has been conducted on the orangutan populations that we surveyed, we used the most appropriate published values for 'p' and 'r'. The proportion of nest builders in a population appears to be consistent at $p = 0.9$ across sites (Ancrenaz et al., 2004a; Johnson et al., 2005; van Schaik et al., 1995). The only two published nest production rate values for Borneo are $r = 1.01$ (range 0.94–1.03) at Kinabatangan (Ancrenaz et al., 2004a) and $r = 1.16$ (range 1.13–1.20) at Gunung Palung (Johnson et al., 2005). Following Ancrenaz et al. (2005), we used the average of these two values, resulting in $p = 1.08$ (SE = 0.06). For nest decay rates, we used an average of nest decay rates found at Gunung Palung in dry forest between 100 and 300 m elevation (272 days, Johnson et al., 2005), and values reported for Kinabatangan (mean 202 days, Ancrenaz et al., 2004). This resulted in an estimated nest decay rate of 237 days (SE = 0.21), which we used as a default nest decay rate at all sites.

We calculated site-specific estimates of nest decay rate that incorporated tree taxa-specific nest decay rates and altitude. Ancrenaz et al. (2004a) demonstrated that the type of tree in which a nest is made strongly affects nest decay rates. Specifically, nests in trees of the family Dipterocarpaceae and the genera *Dimocarpus* and *Eusideroxylon* had unusually slow rates of decay, and nests in Myrtaceae and Sterculiaceae decayed relatively rapidly (Ancrenaz et al., 2004a). In our sites, *Dimocarpus* and Sterculiaceae trees were uncommon and rarely used as nest trees, however Dipterocarpaceae, *Eusideroxylon*, and Myrtaceae were common and ignoring variation between sites in the use of these trees for nesting may have introduced substantial errors. Therefore, for each site we calculated the following nest decay parameter:

$$t_{tree} = ((N_{DIPT}/N_{tot}) * 205) + ((N_{MYRTA}/N_{tot}) * 128) + ((N_{EUSID}/N_{tot}) * 476) + ((N_{OTHER}/N_{tot}) * 151), \quad (3)$$

where t_{tree} is the nest decay rate corrected for tree species composition (in days), N_{DIPT} the number of nests in Dipterocarpaceae trees, N_{MYRTA} the number of nests in Myrtaceae trees, N_{EUSID} the number of nests in *Eusideroxylon* trees, N_{OTHER} the nests in all other tree taxa, and N_{tot} the total nests at that site. All values for taxa-specific nest decay rates were

taken from Ancrenaz et al. (2004a). To control for the fact that nest decay rates are positively correlated with altitude, we followed Johnson et al. (2005) by using the following formula:

$$t_{cor} = t_{tree} + 0.07 \times X, \quad (4)$$

where t_{cor} is the nest decay rate corrected for altitude (in days), t_{tree} the nest decay rate corrected for tree species composition (in days), and X the altitude (in m above sea level).

We calculated site-specific nest decay rates based on average nest tree composition from nests recorded along all transects at each midline within a site. This t value and site-specific estimated strip width (w) was used to calculate an estimate of orangutan density at each of the 22 sites. In order to calculate an estimate of orangutan density for each midline, w and t_{tree} were assumed to be the same for all midlines at a site, but midline-specific altitude was used to calculate t_{cor} .

3.6. Identification of hunting villages

Although hunting is known to have strong effects on the abundance of vertebrates across the tropics (e.g., Cullen et al., 2000; Meijaard and Nijman, 2000; Jerozolinski and Peres, 2003), estimation of true hunting rates is difficult, especially for rare species. We therefore opted for a simple index of hunting intensity (distance to the nearest hunting village) that we expected to be well correlated with true hunting rates and that was easily replicable across sites. Information used to classify villages as hunting or non-hunting villages was collected at a series of participatory conservation planning workshops carried out in each of the villages, and was augmented and cross-checked by in depth follow-up socio-economic interviews with more than half of all households in each village. In order to be classified as a hunting village, at least two respondents in a village had to have positively indicated that hunting occurred in their village. However, whether or not orangutans were hunted was strongly linked with tribal and village identity, so this arbitrary cut-off was not necessary to classify villages. Villages in which orangutans were hunted had been ape hunters for at least three generations, and there were no reports of orangutan hunting within the last three generations in villages classified as non-hunting villages. Therefore, the characterization of villages as hunting or non-hunting was robust and reflected long-practiced behaviours. Due to incomplete knowledge of the hunting practices of all villages, these data were available for only a subset of midlines.

3.7. GIS analysis

We obtained Landsat ETM 7 maps of the survey areas in August 2000 and used ArcGis 8.3 to calculate the straight-line distance from each midline to the nearest human village and to the nearest hunting village. For analyses that compared data between sites, we calculated the mean distance to the nearest village and hunting village for all midlines at a site.

3.8. Statistical tests

We used standard non-parametric tests to assess the relationship between most variables. When the assumptions associated with regression were met, we used ordinary least squares and stepwise regression. Where appropriate, variables were logarithmically transformed to reduce non-normality and heteroscedasticity. Significance was set at $\alpha = 0.05$. We tested all hypotheses using both data from all midlines and means of all midlines at each site. We also conducted all analyses (results not presented) using means of all data for given location ($n = 8$), to confirm that patterns held across various sampling scales. As the independent variables were likely to be correlated with each other, and since multiple factors may simultaneously have affected orangutan density, we conducted multivariate analyses to determine the relative importance of each factor.

4. Results

4.1. Nest tree selection

We recorded a total of 9464 orangutan nests. Mean nest tree diameter across all sites was 26.5 cm dbh and site-specific means varied from 19.9 cm dbh (CDR2) to 38 cm dbh (BAAI; Table 1). Orangutans rarely made nests in large trees; only 4% of nests were made in trees of greater than 60 cm dbh

diameter, and 75% of nests were made in trees smaller than 33.2 cm dbh. Nest tree diameter was unrelated to availability of trees of different size classes across sites.

For the majority (95%, $n = 9028$) of nests we recorded the local name of the tree in which it was built. Orangutans built nests in 199 types of trees (i.e., those with distinct local names). The most common nest trees used were *jambu* trees (*Eugenia* spp., Myrtaceae), which comprised 18% ($n = 1713$) of all nest trees. There was substantial variation between sites in the usage of specific trees for nests (Table 1).

4.2. Site-specific nest decay rates

Incorporation of tree composition dramatically affected estimated nest decay rates at some sites (Table 2). In order to determine whether pH could be used as a reliable indicator of nest decay rate at our sites, we compared estimates of t produced by the equation provided in Buij et al. (2003) against our estimates of t based on altitude and nest tree composition for the midlines along which we collected pH data ($n = 24$ midlines from 5 sites, Table 2). Estimates produced by the pH equation were significantly lower than (paired t test, $t = 6.30$, $p < 0.0001$, $n = 24$) and uncorrelated with ($r^2 = 0.05$, $p = 0.26$, $n = 24$) estimates based on nest tree composition. Therefore for all density calculations we used the nest decay estimates based on Eqs. (3) and (4).

Table 1 – Nest tree use at each site

Site	Dipterocarps		<i>Eusideroxylon</i>		Myrtaceae		Other		Dbh		# Nests
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	Mean	SD	
BAAI	6	42.9	0	0.0	0	0.0	8	57.1	39.8	14.6	14
CDR1	106	19.7	40	7.4	90	16.8	301	56.1	24.2	13.0	537
CDR2	34	12.5	0	0.0	97	35.7	141	51.8	19.9	10.3	272
GG1	55	13.4	18	4.4	36	8.8	300	73.3	25.8	14.3	409
GG2	39	15.9	3	1.2	32	13.0	172	69.9	28.0	14.9	246
GG3	103	20.3	12	2.4	70	13.8	323	63.6	22.8	12.5	508
GG4	77	15.8	1	0.2	105	21.5	305	62.5	23.8	13.1	488
GG5	146	11.4	150	11.7	135	10.5	854	66.5	28.8	15.4	1285
GG6	24	7.5	39	12.2	14	4.4	243	75.9	34.4	18.4	320
GG7	188	15.2	1	0.1	223	18.1	823	66.6	25.5	15.3	1235
GN1	16	13.1	0	0.0	14	11.5	92	75.4	34.1	21.6	122
GN2	26	21.3	6	4.9	13	10.7	77	63.1	28.4	18.4	122
GR1	84	13.7	7	1.1	71	11.6	452	73.6	28.4	16.5	614
ML1	27	8.2	27	8.2	56	17.0	219	66.6	26.2	14.4	329
ML2	202	15.6	2	0.2	464	35.9	623	48.3	25.1	13.3	1291
ML3	7	5.0	6	4.3	54	38.6	73	52.1	34.5	24.3	140
ML4	103	11.1	60	6.5	176	19.0	586	63.4	24.2	12.1	925
MRG	0	0.0	8	80.0	1	10.0	1	10.0	35.8	27.1	10
SG1	13	31.0	0	0.0	2	4.8	27	64.3	28.3	11.4	42
SG2	17	16.8	6	5.9	15	14.9	63	62.4	30.1	13.2	101
SG3	26	11.8	3	1.4	24	10.9	167	75.9	28.7	13.2	220
SG4	23	9.8	10	4.3	21	9.0	180	76.9	33.7	19.0	234
Total	1322	14.0	399	4.2	1713	18.1	6030	63.7	26.5	15.1	9464

Table lists the number (n) and percentage (%) of nests that are made in trees in the families Dipterocarpaceae and Myrtaceae and the genus *Eusideroxylon*, the mean (and standard deviation, SD) diameter at breast height (Dbh) of nest trees at each site, and the total number of nests at each site. Site name abbreviations indicate Baai (BAAI), Corridor (CDR), Gunung Gajah (GG), Gunung Nyapa (GN), Ex Gruti (GR), Muara Lisan (ML), Marang (MRG), and Sungai Gie (SG).

Table 2 – Estimates of nest duration at each site

Site	n pH	Mean pH	pH range	t_{tree}	Mean altitude	Minimum altitude	Maximum altitude	Alt cor	t_{cor}
BALI				174	435	400	460	30	205
CDR1				182	233	126	419	16	198
CDR2				150	456	315	625	32	181
GG1	4 (86)	6.07	5.51–6.82	171	416	180	682	29	200
GG2	3 (44)	6.14	5.23–6.77	161	406	270	491	28	189
GG3	6 (73)	5.88	5.11–6.80	166	329	123	510	23	189
GG4	5 (65)	5.95	5.09–6.82	155	257	174	408	18	173
GG5				193	257	189	330	18	211
GG6				194	198	154	269	14	208
GG7				155	525	321	635	37	192
GN1				155	332	168	405	23	179
GN2				176	186	157	221	13	189
GR1				159	296	250	415	21	180
ML1				178	43	42	45	3	181
ML2				152	213	114	301	15	167
ML3				159	94	94	94	7	165
ML4				174	291	247	366	20	194
MRG				409	125	120	130	0	418
SG1	6	6.08	5.80–6.40	167	278	208	340	19	186
SG2				176	229	170	288	16	192
SG3				159	385	300	490	27	186
SG4				168	358	298	454	25	193

Table lists the sample size for soil pH measurements ($n = \#$ midlines (total measurements)), mean estimated pH, pH range, the estimated nest decay rates corrected for site-specific nest tree composition (t_{tree} , calculated using Eq. (3)), mean altitude (m asl) for all midlines at the site, minimum and maximum altitude recorded on midlines at that site (m asl), the number of days added as an altitude correction factor (Alt cor) and the site-specific estimate for nest decay rate (t_{cor} from Eq. (4)), which incorporates corrections for both nest tree taxa and altitude. Soil pH data were only available from 5 sites and 24 midlines. Site name abbreviations are listed in the legend of Table 1.

4.3. Nest transect recounts

On the transects that were walked a second time, an average of 22.3% additional nests were spotted. The number of additional nests seen on the second walking of a transect was only weakly correlated with the number of nests seen on the first walking ($r^2 = 0.09$, $p < 0.0001$, $n = 681$ transects), and was not significantly different between sites or locations. In order to scale up the nest counts on transects that were walked only once, we multiplied the density estimate for transects walked only once by 1.22.

4.4. Orangutan density estimates

At one site, MRG, there were too few data to model the distribution of perpendicular sighting distances. We therefore used the distance (12.5 m) beyond which sighting frequency dropped markedly as the estimated strip width (w) at this site. Estimates of orangutan density varied widely among the 22 sites that we surveyed (Table 3, mean 3.66, range 0.27–13.43 orangutans/km²). Orangutan density estimates calculated for each midline were similarly variable (mean 3.54, range 0.04–21.08 orangutans/km²).

4.5. Ecology data

We found considerable variation between sites in various ecological measures of interest (Table 4). Many sites ($n = 11$) were undisturbed and logging intensity at disturbed sites was generally low ($n = 11$, mean 2.45, range 0.31–6.63 stumps/ha). Log-

ging intensity was weakly related to the number of trees ≥ 80 cm dbh ($n = 22$, $\rho = 0.43$, $p = 0.04$), and unrelated to any other measured environmental parameter. The mean distance from each site to the nearest village and hunting village was 30.1 km ($n = 19$, range 4.3–69.5 km) and 31.2 km ($n = 15$, range 7.15–105.2 km), respectively. Logging intensity was unrelated to the distance to the nearest village ($n = 19$, $\rho = 0.06$, $p = 0.80$) or hunting village ($n = 15$, $\rho = -0.04$, $p = 0.87$).

4.6. Hypothesis tests

Orangutan densities at the six sites at Muara Lesan and Corridor were the highest we recorded (minimum 5.2 orangutans/km², mean 7.6 orangutans/km², Table 3), and well above the norms recorded for lowland Dipterocarp forest in Borneo. Both locations were in close proximity (<1 km) to an area that was actively being logged prior to and during the time when data were collected (whereas all other sites were >10 km from active logging operations), and it is reasonable to assume that orangutan densities in these sites had increased well above carrying capacity due to an influx of individuals from the area that was actively being logged. No obvious ecological factor (such as presence of an unusually large number of fruiting trees or atypically slow nest decay rates) can explain the high density in these areas. Since including sites with density estimates that were artificially inflated would obscure true relationships between ecological factors and orangutan density, we removed these sites from our analyses prior to conducting any hypothesis tests. As the karst sites (i.e., MRG, BALI, and GN) that we surveyed were

Table 3 – Density estimates at each site

Site	# Nests	Survey effort (km)	ESW (m)	Nests/km ²	Lower 95% CI nests/km ²	Upper 95% CI nests/km ²	D _{OU} default	D _{OU} t _{cor}	Prop not checked	D _{OU}
BAII	14	1.0	17.4	401.6	195.8	823.6	1.74	2.02	1.00	2.46
CDR1	537	8.0	19.2	1624.1	1133.0	2328.2	7.05	8.42	0.00	8.42
CDR2	272	8.0	17.2	981.4	547.8	1758.3	4.26	5.56	0.00	5.56
GG1	409	16.0	17.5	675.1	389.1	1171.3	2.93	3.48	0.00	3.48
GG2	246	12.0	20.5	472.9	156.6	1427.9	2.05	2.57	0.00	2.57
GG3	508	24.0	13.8	746.0	532.0	1047.0	3.24	4.05	0.00	4.05
GG4	488	20.0	16.0	726.4	561.4	939.9	3.15	4.31	0.00	4.31
GG5	1285	32.0	23.7	805.9	601.7	1079.0	3.50	3.94	0.06	3.99
GG6	320	24.0	24.2	245.8	105.2	574.3	1.07	1.22	0.00	1.22
GG7	1235	28.0	22.4	952.2	753.0	1204.0	4.13	5.10	0.00	5.10
GN1	122	24.0	14.6	165.4	73.9	370.2	0.72	0.95	0.00	0.95
GN2	122	22.0	21.4	123.0	64.3	235.2	0.53	0.67	0.00	0.67
GR1	614	26.0	21.5	521.0	382.3	708.0	2.26	2.98	0.00	2.98
ML1	329	7.0	17.6	1236.0	1015.7	1503.9	5.37	7.02	0.00	7.02
ML2	1291	17.5	16.6	2122.0	1297.9	3472.2	9.21	13.10	0.11	13.43
ML3	140	4.0	17.4	970.0	806.4	1166.8	4.21	6.04	0.00	6.04
ML4	925	16.0	28.2	971.5	653.8	1443.5	4.22	5.15	0.00	5.15
MRG	10	4.0	12.5	90.0			0.39	0.23	1.00	0.28
SG1	42	22.5	21.5	43.5	20.7	91.4	0.19	0.24	0.51	0.27
SG2	101	24.0	22.6	88.3	30.9	252.6	0.38	0.47	0.67	0.54
SG3	220	21.0	28.4	179.3	101.5	316.7	0.78	0.99	0.00	0.99
SG4	234	20.0	28.4	188.9	129.9	274.8	0.82	1.01	0.05	1.02
Mean	430	17.3	20.1	651.4	454.9	1056.6	2.83	3.61	0.15	3.66

The estimates of orangutan density at each site using various parameters are listed. “ESW” represents the estimated strip width (m) and “nests/km²” represents the nest density point estimate and the lower and upper 95% confidence intervals calculated by Distance 4.0 Release 2. “D_{OU} default” is the point estimate of orangutan density (orangutans/km²) using the default parameters $p = 0.9$, $r = 1.08$, and $t = 237$ days, D_{OU} t_{cor} is the point density estimate using t values corrected for tree species composition and altitude (Table 2). D_{OU} scales the D_{OU} t_{cor} density estimate by the proportion of transects that were not rechecked. CDR and ML sites are considered to be above carrying capacity. Site name abbreviations are listed in the legend of Table 1. See text for details.

substantially different from the other sites in tree species composition, soil acidity, and structure, we reran all analyses with these sites removed to ensure that the relationships that we found between variables were not due to strong effects from these karst sites.

Contrary to our prediction (H1), orangutan density was weakly positively correlated with logging intensity across sites ($n = 16$, $\rho = 0.41$, $p = 0.11$). When the karst sites were removed, the positive relationship between orangutan density and logging intensity became stronger ($n = 12$, $\rho = 0.53$, $p = 0.07$). This relationship also held when all of the midline data were used ($n = 76$ midlines, $\rho = 0.23$, $p = 0.04$), and when only the non-karst midlines were analyzed ($n = 62$, $\rho = 0.38$, $p = 0.002$).

As predicted (H2), orangutan density was positively correlated with distance from the nearest village across sites ($n = 13$, $\rho = 0.79$, $p = 0.002$). When the karst sites were removed, the relationship between orangutan density and the distance to the nearest the nearest village remained ($n = 11$, $\rho = 0.73$, $p = 0.01$). These relationships held when data for all midlines ($n = 79$, $\rho = 0.67$, $p < 0.0001$) and all non-karst midlines ($n = 67$, $\rho = 0.63$, $p < 0.0001$) were analyzed.

Also, as predicted (H3) orangutan density was positively correlated with distance from nearest hunting village across sites ($n = 9$, $\rho = 0.70$, $p = 0.03$). When the karst sites were removed, the relationships between orangutan density and the distance to the nearest hunting village was similar but

less significant, due to the small sample size ($n = 7$, $\rho = 0.68$, $p = 0.09$). When all midlines for which data were available were used, orangutan density was well correlated with distance to the nearest hunting village ($n = 51$ midlines, $\rho = 0.51$, $p = 0.0001$, Fig. 2). This correlation became stronger when data for midlines in karst habitat were removed ($n = 39$ midlines, $\rho = 0.61$, $p < 0.0001$).

4.7. Multivariate analyses

As several factors were correlated with orangutan density, and since two of these factors (the distance to the nearest village and the nearest hunting village) were highly correlated with each other ($n = 9$ sites, $\rho = 0.90$, $p < 0.001$), we conducted multivariate analysis to determine the relative importance of each factor. Using the site data (i.e., the mean of all midlines at a site as a single datum) resulted in sample sizes that were too small to permit multivariate analyses, so we conducted these analyses using data from individual midlines. In order to determine the independent effects of distance from the nearest village (VILL) and the distance from the nearest hunting village (HUNT) once the covariation between these variables was controlled, we calculated partial correlation coefficients between orangutan density and these two variables. Both data for all midlines ($n = 51$, $r_{\text{OU,HUNT} \cdot \text{VILL}} = +0.38$, $r_{\text{OU,VILL} \cdot \text{HUNT}} = -0.26$) and only non-karst midlines ($n = 39$, $r_{\text{OU,HUNT} \cdot \text{VILL}} = +0.32$, $r_{\text{OU,VILL} \cdot \text{HUNT}} = -0.01$) showed

Table 4 – Summary of key ecological data collected at each site

Site	Trees/ha			Lianas/ha		Figs/ha		Stumps/ha			Mean distance to nearest village (km)	Mean distance to nearest hunting village (km)
	40–59.5 cm dbh	60–79.5 cm dbh	>80 cm dbh	5–9.5 cm dbh	>10 cm dbh	5–9.5 cm dbh	>10 cm dbh	40–59.5 cm dbh	60–79.5 cm dbh	>80 cm dbh		
BAII	2.5	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	NA	NA
CDR1	24.6	15.5	5.0	9.8	3.3	1.3	0.1	0.5	2.1	2.8	19.0	22.1
CDR2	22.3	5.0	0.6	8.8	2.1	0.0	0.0	0.0	0.0	0.0	21.5	28.3
GG1	30.8	15.4	5.5	20.4	7.0	1.1	1.5	0.4	0.6	1.2	31.0	81.0
GG2	46.3	27.8	10.3	23.4	13.0	2.3	2.9	0.0	0.0	0.0	41.2	55.2
GG3	32.7	24.1	6.1	13.7	7.8	0.7	0.5	0.0	0.1	0.2	37.1	51.1
GG4	33.1	19.1	2.6	16.6	7.0	0.4	0.8	0.0	0.0	0.0	66.8	NA
GG5	28.8	12.6	5.5	17.5	5.6	0.7	0.5	0.1	1.7	1.2	53.3	NA
GG6	23.6	12.3	6.2	20.1	9.4	1.7	1.9	0.5	0.5	0.5	55.2	105.2
GG7	25.5	14.1	5.8	17.3	7.3	1.9	0.5	0.1	0.8	0.6	69.5	NA
GN1	28.1	15.9	5.5	18.8	12.6	0.9	1.1	0.0	0.2	0.3	7.1	7.1
GN2	23.5	10.9	3.7	16.8	6.5	1.1	1.0	0.3	0.8	0.6	9.1	9.1
GR1	21.7	11.8	4.8	16.7	6.8	0.8	0.9	0.2	1.1	1.6	62.9	NA
ML1	19.0	8.7	2.7	11.9	3.6	0.6	0.3	0.7	0.4	0.4	5.4	8.4
ML2	26.9	8.8	2.2	12.4	1.9	0.5	0.1	0.0	0.0	0.0	7.6	10.2
ML3	25.5	16.8	3.4	18.5	9.3	1.8	1.5	0.0	0.0	0.0	4.3	7.7
ML4	22.9	13.0	3.6	11.9	4.1	0.8	0.7	0.0	4.7	1.9	9.1	12.1
MRG	10.0	1.0	1.0	2.5	0.0	0.0	0.0	0.0	0.0	0.0	NA	NA
SG1	30.0	20.5	4.0	21.7	9.6	0.2	0.5	0.0	0.0	0.0	14.9	14.9
SG2	23.8	15.1	3.6	18.4	6.9	1.5	1.6	0.0	0.0	0.0	23.3	23.3
SG3	35.1	15.3	4.0	21.6	5.8	1.2	0.3	0.0	0.0	0.0	32.8	32.8
SG4	31.6	14.4	4.4	20.7	8.4	0.4	0.8	0.0	0.0	0.0	NA	NA

Table provides mean values of various ecological parameters at each site. Site name abbreviations are listed in the legend of [Table 1](#). See text for details.

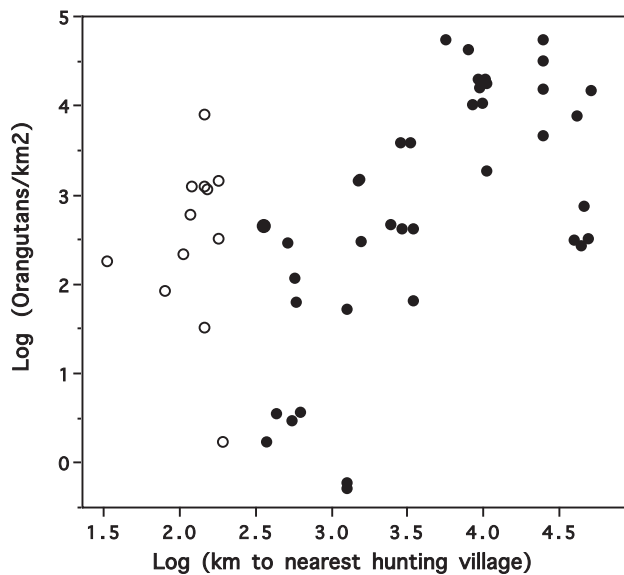


Fig. 2 – Orangutan density vs. distance from nearest hunting village. The relationship between orangutan density (individuals/km²) and the distance (km) from the nearest village known to hunt orangutans (all midlines: $n = 51$, $\rho = 0.51$, $p = 0.0001$; all non-karst midlines: $n = 39$, $\rho = 0.61$, $p < 0.0001$). Open circles indicate karst midlines, closed circles indicate all other midlines. See text for additional details.

that the distance to the nearest hunting village was the stronger positive predictor of orangutan density. Partial correlation coefficients between orangutan density and the distance to the nearest hunting village and logging intensity showed that once covariation between variables was controlled, only the distance to the nearest hunting village was a strong predictor of orangutan density (all midlines $n = 43$, $r_{OU, HUNT \cdot LOG} = +0.52$, $r_{OU, LOG \cdot HUNT} = -0.05$, non-karst midlines only $n = 31$, $r_{OU, HUNT \cdot LOG} = +0.54$, $r_{OU, LOG \cdot HUNT} = +0.01$). Stepwise regression models using all three variables showed that hunting was a significant predictor of orangutan density (all midlines: $n = 43$, $F = 13.7$, $p = 0.009$, $r^2 = 0.32$; non-karst midlines only: $n = 31$, $F = 15.7$, $p = 0.0003$, $r^2 = 0.28$) and that the addition of the other variables did not explain significantly more of the variance in orangutan density (both variables in models $F < 1.05$, $p > 0.33$). Addition of data on various ecological factors (e.g., altitude, fig density) to the stepwise model did not improve its explanatory power. Taken together, these analyses show that the key variable of interest is the distance from the nearest hunting village (H3) and that the apparent support of the hypotheses implicating logging intensity (H1) and distance from the nearest human habitation (H2) was due to spurious correlations.

5. Discussion

Our multivariate analysis of the ecological correlates of orangutan population density across a large number of independent sites showed that the only significant predictor of orangutan densities in this region was the distance to the

nearest hunting village. Contrary to results found at some other sites (Djojosedharmo and van Schaik, 1992; van Schaik et al., 1995; Wich et al., 2004b), orangutan density was not correlated with fig density or altitude (but note that we did not sample above 700 m asl). In addition, orangutan density was unrelated to both logging intensity and the distance from the nearest village once hunting was taken into account. Below we discuss relevant methodological issues, consider the effects of logging and hunting on orangutan densities, and discuss the management implications of our study.

5.1. Methodological issues

In addition to errors associated with failing to meet the central assumptions of line transect methodology (Anderson et al., 1979; Buckland et al., 2001), the inappropriate choice of multipliers, particularly nest decay rate (t), can seriously bias density estimates (Ancorenaz et al., 2004a; Laing et al., 2003). Although site-specific assessment of nest decay rate is ideal, this is time consuming and unfeasible for rapid surveys. Buij et al. (2003) showed that pH could be used as an indicator of nest decay rate on Sumatra, however, this relationship has produced implausibly short decay rates on Borneo (Johnson et al., 2005; this study). Therefore new methods are required to reliably determine nest decay rates on this island. Following Ancorenaz et al. (2004a), we scaled our estimates of nest decay rate to control for the fact that nests in trees with dense wood decay more slowly than nests in other trees. We agree with Ancorenaz et al. (2004a) that this methodological refinement may substantially enhance our ability to obtain orangutan density estimates that are comparable across sites. Furthermore, we note that it would be advisable to test decay rates in taxa not previously examined, particularly those with dense wood that may be used as nesting trees at other sites (e.g., *Aporosa*, *Tristaniaopsis*).

Our nest counts increased by an average of 22.3% after a recount of the transect by a second set of observers. This value is similar to that obtained at Gunung Palung in West Kalimantan (23.7%; Johnson et al., 2005), and validates the utility of transect recounts to more accurately determine true nest density.

5.2. Effects of logging and hunting

Logging appeared to have little effect on orangutan densities at the sites we surveyed. Although this result agrees with some published findings (e.g., Russon et al., 2001), it is at odds with the findings of many others. The effects of several confounding factors may explain why results to date have been contradictory. First, the amount of time that has elapsed since logging occurred clearly affects how strongly orangutans will be affected (Morrogh-Bernard et al., 2003). Several studies have demonstrated that given sufficient time to regenerate forests can support pre-logging densities of some primate species (Johns and Skorupa, 1987; Knop et al., 2004). Unfortunately, we did not have sufficient information on the logging history of many of our sites to assess the impact of this factor. However, since most of the sites for which we have data were logged 3–4 years prior to our surveys, it seems unlikely that these sites had sufficient time to regenerate.

Second, it has been argued that there are life-history differences between orangutan species and subspecies that may affect their susceptibility to logging (Meijaard and van Schaik, unpublished data; Wich et al., 2004a). Specifically, it has been argued that the subspecies that we studied (*P.p. morio*) is the least effected by logging. Among the Bornean orangutans, *P.p. wurmbii* and *P.p. pygmaeus* of southern and western Borneo seem to be somewhat sensitive to logging, losing some 20% or less of their densities in logged areas (Felton et al., 2003; Russon et al., 2001), whereas *P.p. morio* (including Sabah's orangutans) displays a remarkable ability to cope with damage by logging and even fire (Ancrenaz et al., 2004b, 2005). The coastal areas of East Kalimantan and eastern Sabah are markedly drier than northern Sumatra and the rest of Borneo (MacKinnon et al., 1996; Whitten et al., 2000), an effect that was probably more pronounced during several Pleistocene glacial periods that *P.p. morio* experienced since it became separated from the other subspecies (Warren et al., 2001; Meijaard, 2003a,b; Bird et al., 2005). It is conceivable that *P.p. morio* is better adapted than the other taxa to dry, El Niño-induced conditions and concomitant effects on forest phenology, which increase from west to east in this region (Wich and van Schaik, 2000). *P.p. morio* may thus also be better adapted to coping with periods of lower availability of preferred food items. We should stress that these assessments are still preliminary, and that orangutan species and subspecies may differ more in the speed with which they respond to habitat damage rather than in the extent of their response. It is possible that the apparent improved ability of *P.p. morio* to deal with low-quality fibrous foods allows them to survive for longer after logging has reduced the abundance of fruits, but that even these populations will decline after years spent feeding on low quality diets. While the paucity of data preclude a rigorous assessment of this hypothesis, this possibility suggests that the wider application of our results to other subspecies should be done with caution.

Third, and probably most importantly, there may well be a level of logging intensity below which it has few deleterious effects (Wilson and Wilson, 1975). Ancrenaz et al. (2005) reported orangutans living at high densities in lightly logged forests, but showed that at relatively heavily logged sites orangutan density appeared to be inversely related to logging intensity. It is important to stress that the logging intensity at most of our sites was low (mean 2.45 stumps/ha); even the most heavily logged sites (6.6 stumps/ha) were logged less intensely than forests examined in some other Bornean studies (e.g., 18.3 stems/ha: Johns, 1986; 8 stems/ha: Wilson and Wilson, 1975). It is likely that all of our sites were logged at an intensity below which orangutan densities are not substantially affected, and that this explains why we failed to detect effects of logging. This result should not be interpreted as suggesting that logging has no effect on orangutan population density, rather that at relatively low levels the impacts are minimal.

As noted above, we used a simple measure, the distance from the nearest hunting village, as an indicator of hunting intensity. Although our index clearly does not encapsulate the complexity of hunters' behaviour, this relatively crude measure was the strongest predictor of orangutan density across our sites. A more sophisticated measure that incorpo-

rated details of actual distance traveled by hunters to access an area would presumably have explained more of the variance. However such a method would have been more prone to error and less replicable at other sites. Poaching of orangutans in these areas is primarily for local consumption or for the perceived spiritual or medicinal benefits of orangutan body parts. They are not killed for the pet trade or the commercial sale of bushmeat. Most hunters recalled that there were more orangutans near their villages when they were children than there are today. They claim to rarely hunt orangutans in recent years, but acknowledge that this is largely due to the fact that orangutans are rarely encountered nowadays. These stories, in conjunction with the empirical results of our surveys, support the conclusion that recent hunting was the primary factor reducing orangutan density at the sites in which few nests were seen.

5.3. Conclusions and management implications

1. Light to moderate logging (less than 5 stems/ha) appears to be compatible with the persistence of orangutan populations at densities comparable to unlogged forest on Borneo. While the preservation and protection of remaining tracts of undisturbed forest should remain a central conservation goal, the management of active and former timber concessions promises valuable benefits for the conservation of orangutans and many other types of wildlife (Ancrenaz et al., 2005; Meijaard et al., 2005). If conservation efforts are focused solely on the preservation of pristine wilderness areas important opportunities will be lost.
2. Proximity to human habitation does not have strong effects on orangutan density. Although agricultural encroachment and habitat conversion are clearly deleterious, simply allowing humans and orangutans to coexist near each other is unlikely to have a strong negative effect on orangutan populations. Thus allowing minimally-invasive human practices (e.g., collection of non-timber forest products) is unlikely to be a major threat to orangutan populations.
3. Hunting is a far more serious threat to orangutans than are light to moderate logging operations. Even low levels of hunting conducted solely for traditional uses can strongly reduce orangutan density. Therefore provided land is not threatened by clear cutting or heavy logging, efforts to protect orangutans should focus on eliminating hunting. This is a far more realistic goal in East Kalimantan than many other tropical areas, (e.g., central Africa) as orangutans are not important sources of meat or income for local communities in this area.
4. Our results support previous studies (e.g., Ancrenaz et al., 2005), indicating that lightly to moderately logged forest retains high value for the conservation of umbrella species such as orangutans. As conservation practitioners in Indonesia we frequently encounter the belief that degraded forests have little conservation value. This attitude is prevalent among politicians and natural resource managers, and allows areas with good potential for conservation to be neglected, resulting in repeated logging, burning, or

conversion to oil palm plantations. This suggests that efforts need to be made to protect lightly logged forests from further degradation, and to educate stakeholders about the potential conservation benefits of such action.

5. The addition of lightly to moderately degraded land to existing protected areas and management units would substantially increase the amount of suitable habitat available to orangutans. The addition of a lightly logged buffer zone around a protected area or the integrated management of a mosaic of degraded and undisturbed forest blocks may make the difference between an orangutan population that has long term viability and one that does not. With pristine forest rapidly disappearing, the widespread acknowledgement and explicit consideration of the conservation value of degraded forest is essential if we are to protect orangutans and the key ecological functions (e.g., seed dispersal) that they provide.

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