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A survey of the orangutan (*Pongo pygmaeus wurmbii*) population in and around Gunung Palung National Park, West Kalimantan, Indonesia based on nest counts

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Abstract

We conducted the first orangutan population census of Gunung Palung National Park, West Kalimantan, Indonesia, between April and September 2001. We used a refined line-transect nest-count methodology utilizing transect recounts to survey 69 km at 14 sites within the park and 14.2 km in the buffer zone. We present the first Bornean orangutan density estimate using complete site-specific parameters and long term monitoring of nest decay rates. Average orangutan density was 3.0 individuals/km^2, with densities ranging from 2.4 ind/km^2 in montane forest to 4.1 ind/km^2 in primary peat swamp. In addition, we tested alternative approaches to calculation of the nest-duration parameter. The second count of each transect resulted in 30% higher density estimates overall. We conclude that recounts should be incorporated into standard line-transect methodology. We estimate there to be ≈2500 individual orangutans in Gunung Palung, indicating the importance of this site in plans to conserve a network of viable orangutan populations. While logging may reduce densities, disturbed forest both inside and adjacent to the park has high conservation value as orangutan habitat. Further research into long-term orangutan population persistence in disturbed forest is needed.

Keywords: Orangutan; Population density; Census methodology; Borneo; Nest counts

1. Introduction

Orangutans (*Pongo* spp.), the only great ape species outside Africa, are found solely on the islands of Borneo and Sumatra. The vast majority are within Indonesia's borders, where orangutan populations are in dramatic decline due to hunting and habitat loss, degradation, and fragmentation. Less than 16% of forest in the Bornean orangutan range is officially protected under Indonesian law, and even that which is nominally "protected", such as Gunung Palung National Park, is subject to rampant illegal logging (EIA, 1998, 1999; Jepson et al., 2001). Rijksen and Meijaard (1999) estimated that when compared to population levels at the beginning of the 20th century, no more than 14% of the Sumatran orangutan population, and a mere 7% of the Bornean population remain today – less than 27,000 individuals, and by some estimates half that, remain in the wild (Rijksen and Meijaard, 1999). If threats to orangutans are not addressed in the immediate future, some researchers estimate that the orangutan will be extinct from its native forests within the first part of the 21st century (Yeager, 1999).

Prior to systematic censusing, opportunistic observations indicated that the forests in Gunung Palung National Park contained one of Borneo's few remaining large orangutan populations. While orangutans have been the subject of an ongoing study at Cabang Panti Research Station since 1994 (Knott, 1996, 1998, 1999, 2001), the actual size of the orangutan population throughout the park has not been previously assessed

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through a field survey. Rijksen and Meijaard's (1999) published estimate of 143 orangutans relied solely on the interpretation of satellite imagery and topographic information. Our census represents the first comprehensive assessment of population size in Gunung Palung National Park based on nest surveys and other data collected on the ground. Furthermore, density calculations using both demographic and nest duration parameters calculated from site-specific data have yet to be done for any site on Borneo, largely because the data needed to generate site-specific parameters were not available. Existing estimates have often used parameters based on the dynamics of Sumatran populations, which ongoing studies indicate to be substantially different in several key areas (Delgado and van Schaik, 2000).

Line transect surveys of nests represent the best available technique for efficiently assessing the density of cryptic and widely-ranging animals such as the orangutan (see van Schaik et al., 1995; Buij et al., 2003) and have recently been applied with some variations at a number of sites (e.g., Gunung Leuser National Park, Aceh: van Schaik et al., 1995; Singleton, 2000; Danau Sentarum, West Kalimantan: Russon et al., 2001; Lanjak Entimau, Sarawak, Malaysia: Blouch, 1997; Berau, East Kalimantan: Marshall et al., in review; Sebangau, Central Kalimantan: Morrogh-Bernard et al., 2003). Refinement and standardization of this methodology to provide directly comparable population estimates, an important tool for conservation management, have been ongoing. This study tested the use of transect recounts to avoid violating a central assumption of the technique.

2. Methods

2.1. Study site

2.1.1. Census location

Gunung Palung National Park, West Kalimantan, Indonesia, encompasses 90,000 ha of coastal forest and mountains (maximum elevation 1119 m), including one of the largest remaining remnants of primary lowland mixed Dipterocarp forest on Borneo. Cabang Panti Research Station (1°13′S, 110°7′E) is a 2100 ha site at the western base of the mountains, with average rainfall 4275 ± 484 mm (Paoli et al., 2001). Logging has occurred periodically in the Gunung Palung region since the 1960s. Although all adjacent legal concessions have been closed for at least 10 years, illegal hand-logging with chainsaws continues to provide primary income to at least 40% of households in the surrounding areas, and supplemental income to many others (Hiller et al., 2004). In the past decade illegal logging activity has increased, intensified in impact, and moved further upriver into the core of the national park. Sixty percent of logging sites found in a recent survey of 20% of Gunung Palung's watersheds were less than three years old. There are at least nine sawmills operating in the immediate vicinity of Gunung Palung, despite the absence of any current legal timber concession in the area (Hiller et al., 2004).

It was estimated in 2001 that only 27% of Gunung Palung's forest remained undisturbed, though intensity of disturbance varies widely (Ridarso, 2002). The vast majority of logging has occurred in peat and lowland forest which comprise ≈74% of the Park's area. Three recent fires (1991, 1994, 1997) burned thousands of hectares in the park and buffer zone (Hiller et al., 2004).

2.1.2. Transect sites

Fourteen sites were selected to represent seven broad habitat types: primary and disturbed peat swamp, primary and disturbed lowland forest, lowland hill forest, mid-elevation forest, and montane forest. Sampling efforts were distributed in rough proportion to the prevalence of each habitat type within the park. All six sites surveyed outside the park boundary, representing 14.2 km of transect, were in disturbed peat or freshwater swamp. Efforts were focused on forested areas adjacent to the Park's northern border, a buffer-zone region deemed likely to still harbor a sizable orangutan population. Global Positioning System (GPS) points were taken at each site using a Garmin 12cx to facilitate recensusing efforts. Altitude measurements were recorded using a Suunto Vector watch with built-in altimeter, accurate to ±5 m. See Fig. 1 for census sites.

2.2. Study design

2.2.1. Line transect survey assumptions

The accuracy of line transect methodology estimates depends on several critical assumptions, namely: (1) transect placement is random with respect to distribution of objects to be sampled; (2) objects directly on the transect line are always detected; (3) distances are measured accurately; (4) objects are not counted twice (Buckland et al., 1993, 2001).

2.2.2. Transect placement

At each of the 14 sites, we placed 10 transects of 500 m in length in a stratified random manner on either side of and perpendicular to a 1 km straight midline. At sites within the research station trail system, we placed midlines along existing trails to minimize disturbance. When possible in logged forest, we used a previously-constructed main logging rail as the midline. To avoid overlap in nest observations, we maintained a minimum distance of 100 m between parallel transects.

This design was intended to optimize the tradeoff between having a large number of independent samples and making transects sufficiently long to avoid the po-

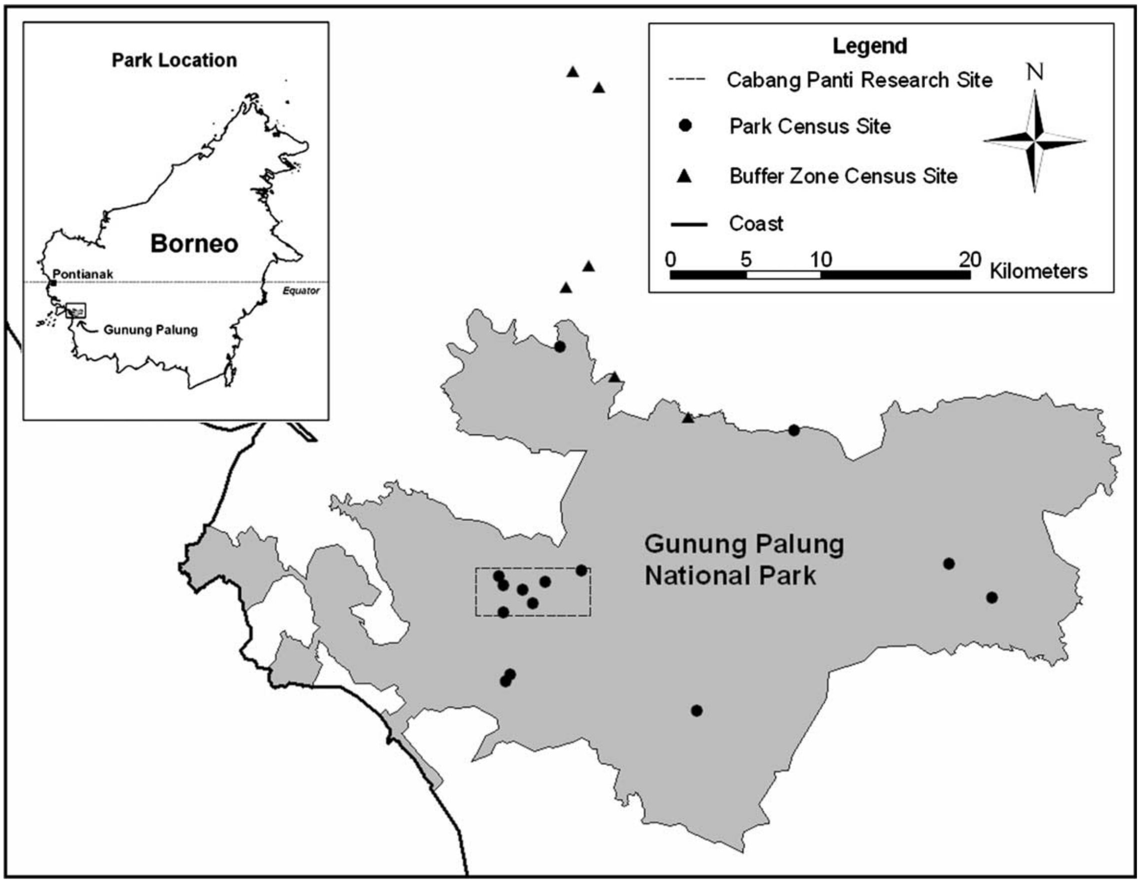

Fig. 1. Map of Borneo and Gunung Palung National Park showing census locations.

tential biases due to spatial heterogeneity associated with micro-habitat variation or the clumping of orangutan nests. Based on the cumulative mean number of nests encountered with increasing distance, Singleton (2000) suggested that 2 km of total transect may be enough to give a representative sample in forests with high orangutan density, and 3 km enough in habitats of lower density. Our design of 10 transects resulted in 5 km walked at all but one site (montane, where eight transects, or 4 km, were completed). In the buffer zone, where sites were located within an irregular patchwork of rivers, roads, settlements, agricultural lands, and burnt areas, we used irregular transect lengths fit to the forest patches in which surveys were conducted. All buffer zone sites were in disturbed peat or lowland forest.

2.2.3. Field procedure

Each transect was walked twice, on consecutive days in opposite directions, by different teams of two observers walking at even pace and stopping approximately every 10 m to look in all directions for nests. We hypothesized that the double count would: (1) minimize the chance that nests were missed, especially directly above the transect, in violation of a key assumption; (2) minimize error due to inter-observer variation.

All nests visible from the transect line were recorded. We measured perpendicular distance from directly below the nest to the transect. Although exact measurement is more time-consuming than estimation by pacing, it is important to the assumptions of line transect methodology. Singleton (2000) suggested that overestimation of nest distances in a study at Gunung Leuser, Sumatra, may have resulted in serious underestimates of density. Pilot data from Cabang Panti Research Station showed consistent differences of 2 m or more (generally overestimates increasing with distance from the transect) when estimates by experienced observers were compared to precise measurements.

We recorded the estimated height of each nest and its direction from the transect, and measured the diameter at breast height of each host tree. We affixed a uniquely-numbered aluminum tree tag to each nest tree to eliminate the risk of counting nests twice. Finally, each nest was assigned a decay class, A–E, defined as follows:

A = Nest is new, still entirely green,

B = Nest is relatively new, mixture of green and dried leaves,

C = Nest is brown, but shape remains intact,
D = Nest has begun to fall apart; there are holes or chunks of leaves missing,
E = Nest is old; leaves are gone and only the skeletal branch and twig structure remains.

2.3. Data analysis

Following van Schaik et al. (1995) we used the following basic equation for calculating nest density (D_N) from line transect surveys

$$D_N = N/(L \times 2w),$$

where N is the number of nests observed, L, the length of transect covered (km), w, the effective width of strip of habitat censused.

Nest density was translated into orangutan density (D_{OH}) through addition of several parameters

$$D_{OH} = D_N \times 1/(p \times r \times t),$$

where p is the proportion of nest builders in the population, r, the number of nests produced per orangutan per day, t, the estimated length of time (total days) that nests are still detectable (decay rate).

We analyzed our data using DISTANCE 3.5 (Thomas et al., 1998). Following Buckland et al. (2001), we truncated the data to exclude nests seen at distances greater than 30 m from the transect line. We fit detection functions to the remaining data both by individual site and by habitat type. Due to small sample sizes and non-independent geographic locations, we pooled data from the 6 buffer zone sites for DISTANCE analysis.

We calculated density estimates separately for each of the 7 habitat types (Table 1). To calculate the overall population estimate, we multiplied the habitat-specific orangutan density value by an estimate of the total hectares of each habitat type in the National Park and summed this value across all habitats. Estimates of the total hectares of each habitat type in Gunung Palung National Park were obtained from a combination of existing maps and satellite photos analyzed using ArcView GIS software (Paoli et al., 2001; Ridarso, 2002). Figures for primary and disturbed forest within the peat and lowland habitat types were confirmed based on results from an extensive field survey of logging at Gunung Palung (Hiller et al., 2004) as well as personal knowledge of the region.

2.4. Parameter estimation

2.4.1. Demographic parameters p and r

All orangutans, except dependent offspring, make nests. We derived the parameter p, or proportion of nest builders in the population, using data from a set of 35 individuals followed for at least one day during 24 months of data collection in 1999–2000 (Knott, unpublished data). During this time, the sample of individuals followed were unbiased as no sex or age-class was prioritized for other research needs.

We calculated r, the rate of daily nest production, based on a subsample of eight years of long-term data at Cabang Panti, weighted for population composition observed in 1999–2000. Because unhabituated orangutans tend to make more nests as a defensive behavior (Knott, Johnson, pers. obs.), we only used data from fully habituated individuals that were followed for more than five full days. When possible for an individual, we analyzed data from at least two distinct time periods in order to minimize potential bias from changes in nest-making patterns due to variable fruit availability or rainfall. The total sample represented 437 follow days of 24 individuals (13 males, 11 females). Rebuilt or re-used nests were excluded from *calculations;* partial examination of our data suggests that reuse represents about 12% of all nesting activity (20 of 137 nests in 121 follow days).

2.4.2. Nest duration of visibility (t)

Studies in Sumatra (van Schaik et al., 1995; Singleton, 2000) suggest that nest duration varies substantially with respect to forest type; differences in tree species

Table 1
Habitat and density figures (for nests D_N and orangutans D_{OH}) used in the Gunung Palung population estimate. Approximate habitat area adapted from Paoli et al. (2001), updated based on Ridarso (2002)

Habitat	Area (ha)	Census sites	T (nest duration)	D_N/ha	D_{OH} /km^2	D_{lcl}	D_{ucl}
Primary peat swamp (0–100 m asl)	509	CP IP	399	17.056	4.09	3.00	5.50
Disturbed peat swamp	24,951	Rangkong, Sawak	399	13.347	3.20	2.75	3.67
Primary lowland (0–100 m asl)	2996	CP ST, CP Bayas, Selingsing	259	8.704	3.22	2.71	3.76
Disturbed lowland	34,453	Rangkong, Simpang Tiga, Jerungkung	259	8.100	3.00	2.26	3.89
Lowland hill (100–300 m asl)	11,410	CP GP, Riam Berasap	272	7.387	2.60	2.10	3.23
Mid-elevation (300–800 m asl)	5130	CP NB, CP MR	297	8.579	2.77	2.33	3.29
Montane (800+ m asl)	3420	Pondok Kelana (4 km)	321	8.150	2.43	1.81	3.27
Non-forested	7131	None	–	–	–	–	–
Buffer zone		6 sites (14.2 km total)	329	8.671	2.50	1.60	3.11

Two-letter codes denote sites located in research station trail system. Five kilometers were surveyed at each site unless otherwise noted. Lower and upper 95% confidence limits indicated by "lcl" and "ucl", respectively.

composition, rainfall, temperature, humidity and wind exposure may all influence the rates at which nests decay. Differences in nesting behavior, such as construction patterns, re-use, or frequency of day-nest building, may also influence the mean time nests are visible. For example, orangutans at Tanjung Puting National Park have been seen to make "bunk bed" nests, one atop the other (van Schaik et al., 2003); were this observation common enough, it might lengthen the mean period of time a nest is visible, as the bottom nest is effectively shielded from the elements. Our data suggest that Bornean orangutans build fewer day-nests than do their Sumatran counterparts. Day nests are generally of flimsier construction and disappear more rapidly than night nests (Singleton, 2000). Therefore we predict higher median t values for Bornean populations.

Given these factors, use of a generalized t value for all habitats or elevations is undesirable even within a single contiguous area, much less between large islands. It is difficult and time-consuming, however, to derive accurate site- and habitat-specific t values. Therefore, a variety of alternate methods have been used by researchers (see Buij et al., 2003). Long-term monitoring of a large sample of nests from creation until disappearance may be the method least prone to error. We had sufficient monitoring data for two habitat types; several alternate methods were tried and evaluated for other habitats.

2.4.2.1. Long-term monitoring. We calculated nest duration t for lowland forest and peat forest by using long-term data collected from February 1997 through January 2002 (Knott, unpublished data). Approximately 21 km of trail were monitored for nests on a monthly basis by researchers or field assistants. Each month the observer marked new nests visible from the trail and noted decay status (as per definitions above) for all previously identified nests. We monitored nests until they were no longer visible. The complete data set represents 1568 nests. For purposes of the current study, however, only nests monitored from "A" or "B" state until disappearance were used to calculate t. Nests of "B" state were assumed to have been built since the previous month's survey, and assigned a mean creation date of 15 days prior to the first survey in which they appeared. For the few clearly rebuilt nests in the sample, we used the month of rebuilding as the creation date. To avoid bias by exclusion of long-lasting nests, only nests built before January 2001 were used. Of the 286 nests included under these criteria, 35 were in what can clearly be classified peat swamp habitat, and 251 were in non-peat lowland forest under 100 m elevation.

2.4.2.2. pH equation. Buij et al. (2003) found a linear relationship between soil pH and nest visibility duration at Gunung Leuser according to the following equation:

$$t = -38.682x + 397.67, \text{ where } x = \text{pH}.$$

We calculated t values for lowland and peat forest by this formula, and compared results to t values calculated by long-term nest monitoring. Alluvial lowland soils yielded a mean soil-moisture pH of 4.2, while the CaCl pH value was 3.54 (Paoli, unpublished data). Mean peat swamp pH was 3.4 (Harting and Knott, unpublished data).

2.4.2.3. Altitude–duration regression. Nest visibility duration has been found to correlate positively with altitude (e.g., van Schaik et al., 1995, Gunung Leuser National Park). While this relationship may be influenced by a variety of meteorological or vegetative factors, van Schaik et al. (1995) suggest the most significant to be a decrease in air temperature and humidity which produce correspondingly slower decomposition rates. We therefore modified the altitude–duration regression from van Schaik et al. (1995), adjusting the slope of the linear equation to fit the altitude–temperature relationship at Gunung Palung. Temperature data were collected along a gradient between 10 and 1000 m altitude during a 13-month period from November 2000 to November 2001 (Marshall and Paoli, unpublished data). The intercept was determined based on our long-term monitoring data in lowland forest. The final equation is

$$t = 0.07002x + 258.3,$$

where x = altitude (in meters).

This relationship was used to calculate nest duration rate t for higher elevations at Gunung Palung.

2.4.2.4. Markov analysis. Several previous studies (e.g., van Schaik et al., 1995; Russon et al., 2001; Buij et al., 2003; Morrogh-Bernard et al., 2003) have estimated decay rates using Markov chain analysis (Kemeny et al., 1956). This technique uses matrix mathematics to estimate nest duration based on transition rates between stages of decay (as enumerated in Section 2.2.3). This method enables use of a larger subset of the long-term monitoring nest data, because censored nests (nests that were not found in stage "A", or did not disappear during the time period in question) can be included in the data. Accuracy of results is heavily dependent, however, on whether a sufficient number of nests enter the absorption state, i.e., disappear within the resurvey period. (See e.g., Buij et al., 2003 for a more detailed explanation of the Markov methodology.)

We created transition matrices from a 12 month subsample of the monthly nest route data (January 2000–January 2001), collection of which is described in Section 2.4.2.1. Buij et al. (2003) found that transition matrices can be summed to reduce the biases likely to arise from small sample size and large variation. Routes in lowland habitat were therefore pooled.

2.5. Slope correction factor

All five sites above 100 m encompassed significantly hilly terrain. In the field, transect length was measured along the ground (rather than horizontally), and subsequently multiplied by a correction factor for slope based on degree measurements along midlines and/or transects. The correction factor at CP GP was 1.17 (based on average slope of 34°), and at CP UB the factor was 1.09 (average slope of 25°). For the three sites where slope measurements were not taken directly, a conservative 1.05 correction factor was applied.

3. Results

3.1. Parameter estimation

3.1.1. Demographic parameters (p, r)

Our analysis of long-term data indicated that 4 of 35 individuals (0.11) were offspring who did not regularly make nests for sleep or for play. Therefore the proportion of nest builders in the population (*p*) is 0.89, or at one significant figure, 0.9. This is comparable to Sumatran data (van Schaik et al., 1995; Singleton, 2000). We calculated a nest production rate (*r*) of 1.16 nests/individual/day (see Table 2).

Table 2

Nest (*N*) production rates (*r*) by age–sex class (N_{OH} = total orangutan individuals), weighted for population structure

Age–sex class	N_{OH}	N_{DAYS}	Nests/day	Weighted
Adult females	7	178	1.09	
Adolescent females	4	74	1.18	
All females	11	252	1.135	1.126
Adult males	6	142	1.22	
Adolescent males	7	43	1.19	
All males	13	185	1.205	1.200
Overall	24	437	1.17	**1.163**

Overall weighted mean (in bold) is *r*.

3.1.2. Calculation of nest duration parameter (t)

Table 3 shows a comparison of *t* values calculated by long-term monitoring, pH, Markov matrices, and the altitude–duration equation. The lowland nest visibility duration figure derived from soil-moisture pH data, 236.7 days, is 0.91 of that derived from the long-term monitoring data for lowland habitat. The peat swamp figure based on pH, 256.5 days, is 0.64 of that derived from the long-term monitoring data. Using CaCl pH instead of soil-moisture pH proved more comparable for lowland forest, producing a nest visibility duration of 257.6 days, which is almost identical to the figure derived from long-term nest monitoring (259 days). CaCl pH values were not available for peat swamp.

Using the Markov method, bi-monthly summed matrix results produced a *t* value of 291.5 days in lowland forest. When compared to lowland monitoring data, the habitat for which we had the largest sample size, this suggests a correction factor of 0.89 for results calculated with this method.

3.1.2.1. Nest duration parameter choice for density calculations. Table 1 shows density calculations made with the *t* values that we considered most reliable. Long-term monitoring data were used for lowland forest and peat swamp, the two habitats for which sufficient data were available to produce a reliable figure. Peat swamp *t* was derived from a relatively small sample of nests ($n = 35$) monitored from beginning to completion. The Markov matrix technique utilized a much larger subset of data to derive an estimate of 377.7 days, taking into account the correction factor noted above (0.89). This estimate differs by only 5% from the value calculated by monitoring data ($t = 399$); given this confirmation, we chose to use the monitoring result. Lowland hill, mid-elevation and montane densities were calculated using the altitude–duration *t*. Due to small sample size and the experimental nature of the pH approach, no *t* values derived from pH calculations were used in density estimates. Disturbed forest was assigned the *t* of its corresponding intact habitat type, as previous work at Gunung Palung suggests no significant difference in nest decay rate between primary and disturbed forest (Felton et al., 2003).

Table 3

Nest duration parameters for each habitat calculated using four methods

Habitat	Monitoring (median)[a]	pH	Altitude–duration curve	Markov chains[b]
Peat	**399** ($n = 35$, standard deviation = 194.6)	256.48 (H_2O)		424.4/377.7
Lowland	**259** ($n = 258$, standard deviation = 203.9)	236.7 (H_2O), 257.6 (CaCl)	259 (assumed, see 2)	291.5/259
Lowland hills		240.6 (H_2O), 254.2 (CaCl)	**272.3** (mean of 100–300 m)	
Mid-elevation	–	–	**296.8** (mean of 300–800 m)	–
Montane	–	–	**321.3** (mean of 800–1000 m)	–

Values in bold were used for density calculations. Empty cells indicate that data were unavailable.

[a] Nest durations were significantly different between habitats (one-way ANOVA, $p < 0.005$).

[b] The second Markov chain estimates represent calculated values adjusted by a correction factor of 0.89 derived from lowland data (calculated Markov value/long-term monitoring value).

3.2. Densities

3.2.1. Density and population estimates

Table 1 shows the relative nest and orangutan densities in the seven habitats or sub-habitats surveyed, based on habitat-specific strip width (w) estimates. Peat forest is by far the most densely populated habitat, exhibiting a 49% higher density of nests or, taking nest visibility duration into account, a 31% higher density of individuals than primary lowland forest. Disturbed peat is 21% lower in density than corresponding primary peat forest, while there is only a 7% difference between orangutan densities in lowland primary and disturbed habitat. Density decreases somewhat above 100 m asl.

The overall density figure for Gunung Palung National Park, based on habitat-specific densities and total habitat hectarage, is 3.00 orangutans/km^2. The population within the park is estimated to be ≈2470 orangutans (CI 95% 1984–3046). This estimate does not include buffer zone forested areas adjacent to the park. It is therefore a conservative estimate of the total orangutan population in the Gunung Palung region.

3.2.2. Density in the buffer zone

Orangutan density in the buffer zone area was found to be 2.5 individuals/km^2. Nest density was calculated to be 7.59 nests/ha (CI 95% 5.54–10.8). Because no second count was done for 5 of the 6 sites, which together represent 195 of 308 observations (63.3%), we applied a correction calculation to make these data comparable with sites inside the park. Our second counts increased density figures by a mean of 22.5% (see below). Therefore, 0.663 was multiplied by 0.225, giving a correction factor of 0.142. We then multiplied the nest density derived by DISTANCE by 1.142 to arrive at a corrected nest density of 8.67 nests/ha (CI 95% 6.33–12.34). We averaged t values for peat and lowland forest ($t = 329$ days) to calculate the nest duration visibility parameter for the buffer zone.

3.3. Variance

Between transect variance (measured as nests per 0.5 km transect) was fairly consistent for a given census site, with the notable exception of five sites (see Table 4). Variance between sites within a given habitat classification was also large in the primary and disturbed lowland forest habitats. Both the Simpang Tiga and CP ST sites had significantly lower densities than the other two sites in their habitat class (two-sample equal variance t-test, ST $p < 0.01$, Simpang Tiga $p < 0.05$).

Table 4
Variance (nests per 0.5 km transect) and standard deviation by site, using data truncated at 30 m

Habitat	Site	Nests (N)/transect	Variance (standard deviation)
Primary lowland	Bayas	18.1	22.77 (4.77)
	ST	9.8	17.96 (4.24)
	Selingsing[a]	19.1	103.88 (10.19)
Disturbed lowland	Jerungkung[a]	17.6	96.27 (9.81)
	Rangkong	14.2	21.96 (4.69)
	Simpang Tiga[a]	9.5	48.94 (7.00)
Primary peat	IF[a]	32.2	177.07 (13.31)
Disturbed peat	Rangkong	22.2	29.07 (5.39)
	Sawak[a]	20.8	103.07 (10.15)
Lowland hills	GP	12.5	28.50 (5.34)
	Riam Berasap	12.0	26.89 (5.18)
Mid-elevation	MR	14.7	24.46 (4.95)
	NB	13.7	21.57 (4.64)
Montane	AS	13.4	21.12 (4.60)

[a] Denotes sites with high variance and/or standard deviation of at least 50% of average nests per transect.

Table 5
First and second counts, by site

Site	First count	Second count	Second count as percentage of total nests (N) (%)
AS Montane	93	18	16.2
CP Bayas	151	35	18.8
Sawak	171	41	19.3
Rangkong	187	45	19.4
CP MR	120	33	21.6
Jerungkung	140	39	21.8
CP GP	101	29	22.3
Riam Berasap	93	29	23.8
Selingsing	149	57	27.7
Rangkong	100	43	30.1
CP NB	102	44	30.1
CP ST	68	32	32.0
Simpang Tiga	64	34	34.7
Total	1539	479	23.7

3.4. Transect recounts

Over all sites, the resurvey of each transect resulted in an increase of 23.7% in total nests encountered, varying by site from 16.2% to 34.7% (standard deviation 5.6%, $n = 2018$). Due to methodological discrepancies between counts, the primary peat site is not included in this calculation (see Table 5).

The lower nest-encounter rate resulting from a single count method does not necessarily render density calculations inaccurate, provided that almost 100% of nests directly above the transect are sighted. When first count data alone were modeled using DISTANCE, however, effective strip width only decreased 1.3% on average, and for lowland hills habitat even increased. Orangutan density estimates (D_{OH}) derived by first-count data alone increased by a mean of 30.0% across habitats when data from the second count were included (minimum 16.5%, maximum 45.7%). This indicated that the second count indeed found additional nests directly above the transect. The percentage of total nests 0–2 m from the transect found by the second count was 30.3% ($n = 245$). The proportion of total nests found 0–2 m from the transect was 12% in both the first and the second count, refuting the conclusion that the distance distribution of nests encountered changed between counts.

4. Discussion

4.1. Sources of error

4.1.1. Potential violations of assumptions

Violations of line transect survey's four main assumptions can result in inaccurate density figures; of these, two are of particular concern. It is difficult to ascertain whether the assumption that *transect placement is random with respect to distribution of objects to be sampled was met*. Midlines were often situated along existing trails or logging rails, which may be features that orangutans tend to avoid for nesting purposes. Research suggests that situating transects along existing trails or ridge tops does not seem to affect randomness (van Schaik et al., 1995). Main logging rails are lined by a relatively narrow cleared swath that precludes orangutan nesting, but we felt that the adjacent forest through which perpendicular transects passed was representative of exactly the disturbance we wished to sample. Midlines themselves were not sampled. If site placement was biased in any direction, it seems probable that it would lead to conservative density estimates, because sites were closer to areas of relatively frequent human presence.

The assumption that *objects directly on the transect line are always detected* was also of concern. Our second count methodology reduced this potential source of error (see below). However, examination of nest distance histograms for each site shows that at both mid-elevation sites and the Sawak disturbed peat site, the curve's peak is not at 0 m. This results in an underestimation of density at these three sites which were perhaps the most difficult to survey in the field, due to steep slopes or deep flooded swamp. It is possible that practical difficulties in moving along transects caused observers to bias searches outwards, rather than upwards. Sawak was also a heavily logged site with a low canopy and more understory growth, vines, and rattan than the relatively open primary forests, potentially blocking the view directly above. This supports Singleton's (2000) suggestion that there may be an optimal angle of observation (and thus distance) at which nests of all heights, sizes, and decay classes are most likely to be seen. However, our other 11 sites showed regular histograms peaking at 0 m, indicating that this is not universally true.

4.1.2. Parameters

The largest potential for error in this type of study lies in the parameters used to convert nest densities into orangutan densities.

4.1.2.1. Demographic parameters. The two demographic parameters, p (population fraction building nests) and r (nest production rate, per day per individual), are unlikely to introduce substantial error. Both were based on a wide cross-section of long-term data, and are comparable to the values found at other orangutan research sites where sufficient data have been collected (Orangutans Compared Workshop, San Francisco, CA, 2002).

The figure derived for nest production rate r at Gunung Palung, 1.16 nests/individual/day, is comparable to unpublished data from other sites on Borneo, but substantially lower than that calculated for Sumatran orangutans, ranging from 1.7 (van Schaik et al., 1995) to 1.9 (Singleton, 2000). Sumatran orangutans clearly make more day nests than their Bornean counterparts. This highlights the fact that Sumatran values are inappropriate for use in surveying Bornean populations.

4.1.2.2. Nest visibility duration parameter. Nest visibility duration (t) is both difficult to derive, for reasons discussed in Methods above, and highly influential in calculations. For example, if t increases only 10 days, from 283 to 293 days, lowland density figures in this study decrease by 3.4%.

Singleton's (2000) study at Gunung Leuser, Sumatra, represents the only other data available on long-term nest monitoring. His findings roughly corroborate our conclusions that nests are more long-lasting than previously estimated by means other than monitoring (e.g., van Schaik et al., 1995). At Gunung Leuser, mean duration of visibility for nests in swamp habitat was found to be $\approx$228 days, and for hill habitat 319 days. Many of the nests in swamp habitat were day nests that disappeared within one month, substantially reducing the mean visibility duration. Just as at Gunung Palung, Singleton found some nests visible up to two years after construction. One important question is whether long-term monitoring durations should be truncated to account for the likelihood that census observers will not find nests in the final stages of decay. Here we decided not to truncate after deliberations with field observers. Shortening mean durations by two months would have increased density figures in various habitats 18–30%.

Estimation of t by the Markov matrix technique resulted in values that appeared to overestimate nest duration and required a correction factor of 0.89. This factor is similar to the 0.85 correction factor derived by Buij et al. (2003). This technique is certainly useful for rapid assessment, allowing nest visibility to be derived from as little as two surveys of a new site, as long as sample size is sufficiently large and the interval sufficiently long that nests disappear between surveys. Further validation is needed to establish correction factors for Bornean sites.

Efficacy of using soil pH to determine the *t* parameter on Borneo remains an open question. While the relationship described by Buij et al. (2003) fits Sumatran data well, preliminary attempts to use this method at Gunung Palung and in Berau, East Kalimantan (Marshall et al., in review) suggest that this relationship does not hold on Borneo, at least not without a site-specific correction factor. It is intriguing that use of the CaCl pH value in lowland forest resulted in a figure identical to that derived by long-term monitoring. Further investigation is merited, but in the interim we do not advocate use of this proposed method without confirmation of *t* by another method.

For the lowland hill, mid-elevation and montane habitats, in which we had neither pH nor decay rate data, we used the altitude–duration relationship modified from van Schaik et al. (1995). As the relationship between altitude and duration is probably not solely based on temperature, but on a suite of factors as discussed above, these figures are potentially problematic.

4.2. Densities

4.2.1. Comparison between primary and disturbed forest

Our results show that in disturbed peat swamp orangutan density was 22% less than it was in primary peat swamp. This finding corresponds well with a previous study at Gunung Palung indicating a difference of 21% in nest density between 2 logged and unlogged sites in peat swamp (Felton et al., 2003). In contrast, orangutan density in disturbed lowland forest was only 7% less than it was in primary lowland forest. It is important to note that this census was not designed to test differences between logged and unlogged forest in a statistically robust manner.

While logging has a negative impact, disturbed forest appears to remains a valuable resource for orangutan populations. This fact has important implications for conservation. However, in interpreting this finding, there are two possibilities that merit exploration. First, the impact of selective logging over an extended time period may not destroy canopy structure or feeding tree composition to the extent that the habitat becomes inhospitable, as long as the disturbance is not too intense and/or orangutans retain access to adjacent less-disturbed areas. Logging impacts are a partial function of effects on key food sources; this may occur either by direct extraction of food trees, or felling of large canopy trees that host important liana or *Ficus* species (Felton et al., 2003) An animal's dietary diversity and resilience when faced with shifting relative abundance of food types is important in assessing impact (Johns, 1986). Orangutans are known to eat several hundred plant species and show dramatic shifts in their dietary composition based on the availability of preferred foods (Knott, 1998). It has further been suggested that in the shorter term, logging's negative effects on food availability may be mitigated by the rapid growth and fruit production of colonizing tree species (Chivers, 1974).

Second, it is likely that the full effects of disturbance have yet to emerge in recently logged areas. Comparison of our sites points to such a conclusion. Logging history and intensity, as well as tree species composition, varied widely among lowland and peat sites. At Gunung Palung, peat swamp forest has historically been the most accessible and economically viable forest for logging. The disturbed peat sites had been logged more intensively, and in all but one case, for a longer period of time, than the disturbed lowland sites; this could account, in part, for the greater impact logging appeared to have on peat forest. Moreover, Simpang Tiga, the one lowland non-peat site where logging had been occurring for at least two decades according to local sources, showed the lowest nest density of all sites in the study. These data suggest that the impact of disturbance in reducing orangutan density takes years to become fully apparent.

Explanations for orangutan declines in logged forest suggest that logging renders habitat less energetically favorable, forcing animals to travel further and/or feed less selectively, and disturbs arboreal travel pathways by increasing gap size and frequency (Rao and van Schaik, 1997; Felton et al., 2003). Orangutans also have large ranges of at least 2500 ha in males and 850 ha in females (Singleton and van Schaik, 2001). Data is somewhat lacking on range flexibility, but a study from Sumatra (van Schaik et al., 2001) suggests that they may well remain in their home range after significant disturbance, although the habitat is no longer capable of sustaining the same number of individuals. Compression effects may potentially play a role in elevating density in the short-term, as land-clearing, active logging, or fire force populations to vacate areas. Elevated densities in logged areas have been noted elsewhere and attributed to such displacement effects (Rijksen and Meijaard, 1999; Russon et al., 2001). However, this does not appear to be the case in Sumatra (van Schaik et al., 2001).

During periods of low food availability orangutans have been demonstrated to alter their activity budgets by spending more time resting, and less time feeding and traveling (Knott, 1998, 1999). They also utilize their stored fat reserves and often lose weight (Knott, 1998, 1999). This appears to be a viable strategy over the relatively short-term, but is dependent on periods of increased food abundance. Further research is needed to learn if orangutans use this strategy in degraded habitats and if so to assess how this affects long-term survival. Another question of critical importance is whether such habitats allow female orangutans to gain sufficient energetic reserves to support successful reproduction (see Knott, 1998, 2001, for a full discussion). During periods of low fruit availability ovarian hormones, and successful conception, are suppressed in orangutans (Knott, 2001). Thus, the lower availability of preferred foods in logged forests (documented at Gunung Palung by Felton et al., 2003) leads us to predict that orangutans living in degraded habitat will (1) be more energetically stressed overall, (2) experience fewer periods of high food availability, and thus (3) have longer inter-birth intervals than orangutans living in undisturbed habitats. Such further lengthening of the already long (8 years) inter-birth interval in orangutans (Galdikas and Wood, 1990) could have serious repercussions for species viability. In summary, the effects of habitat degradation on long-term orangutan persistence remain poorly understood.

4.2.2. Elevational gradient

It has been suggested that orangutans favor habitat below an altitude of 500 m (Rijksen and Meijaard, 1999), while existing Sumatran studies indicate that orangutan density only drops off drastically above 1000 m (Djojosudharmo and van Schaik, 1992; van Schaik et al., 1995). Although our density figures did decrease with increasing elevation, this decrease was not dramatic; further, 95% confidence intervals for all habitats above 100 m were mutually inclusive.

Our findings indicate that while carrying capacity in upland forest is lower than that at sea level, mountain habitats are also an important resource for orangutans. Analysis of long-term census data from Gunung Palung demonstrates that montane forests occasionally hold over 40% of the total orangutan population within the study area (Leighton and Marshall, unpublished data). While home range data collected during focal follows indicates that many individuals range regularly into the hills and mid-elevation forests (Knott, unpublished data), it remains unclear whether there are individuals whose ranges lie entirely or mostly in mid- and upper elevation forest. It is possible that this habitat is not productive enough to sustain orangutans without access to the rich lowland forests below. The abundance of soft-pulp fruit, in particular figs, has been postulated as a critical constraint on orangutan density; availability of such food species declines with altitude, while seasonality appears to increase (Djojosudharmo and van Schaik, 1992).

Further data on orangutan ranging and feeding patterns at mid- to upper elevations are increasingly important as undisturbed lowland forests across Kalimantan have mostly disappeared. Not only are populations being restricted to hill and upland forest, but it is likely that if and when reintroduction of orangutans occurs in West Kalimantan, it will occur in this forest type. Such is the case with reintroduction efforts in East Kalimantan.

4.2.3. Buffer zone

The disparity between density in the buffer zone and density found in the corresponding habitat type within the park indicates that habitat quality in these buffer zones is more substantially reduced than in disturbed areas within park boundaries. This is particularly clear when we consider the possibility that density in these border areas is elevated by compression into remaining forest fragments.

The land to the north of Gunung Palung's border has been subjected to a variety of intense human use for decades. Indigenous Dayak communities in this region hunt orangutans. There are villages, roads, abandoned and active rice fields, oil palm plantations, and logging on both commercial and local scales. These activities have resulted in a deeply fragmented matrix in which the remaining patches of forest grow. The negative effects of fragmentation on wildlife have been well-documented, especially when fragments become isolated from larger reserves (MacArthur and Wilson, 1976). Although orangutan movement in this area has not been studied, it seems likely that the fragmented forest on Gunung Palung's borders must remain connected to the intact forest in the national park to provide viable orangutan habitat over the long term.

4.3. Transect recounts

This study clearly shows that the transect recount substantially increases the accuracy of population estimates. While line-transect models do not depend on finding 100% of objects in a given area, they do depend on finding 100% of objects directly over the transect. According to our data, had we not done recounts this assumption would have been consistently violated, resulting in an underestimation by up to 30% of both nest and animal density. While observer skill clearly serves to reduce the need for a second count, we found that even our most experienced and highly-skilled observers regularly missed nests. Fatigue, weather conditions, and morale are among the factors that may lead to variability in nest encounter rates for any one individual.

The difference found in our work is comparable to results from at least one trial in Sumatra, which reported ≈20% additional nests added with subsequent walkings of a transect at Gunung Leuser National Park (R. Buij, personal communication). Based on analysis of results using line-transect methodology at a Sumatran site with known density, Buij et al. (2003) suggest the use of a correction factor that adjusts density calculations upwards. They suggest that this habitat-specific factor be derived by doing a second count of a single transect. We argue that incorporating recounts of all transects is the preferable alternative to creation of such a correction factor, and eliminates the need for one. In the few cases where a transect was walked three times during this census, new nests were rarely encountered.

4.4. Variance

High variance implies caution in interpreting any single survey's results. Variance among transects or sites is partly a byproduct of the constraints of using "rapid assessment" techniques to survey a large geographical area. "Lowland" habitat for our purposes was a broadly defined category encompassing forests of freshwater swamp, rich alluvial bench, and sandstone-substrate soil. Within the three "disturbed lowland forest habitat" sites, widely disparate levels of logging intensity and history were also present. Even within sites, variance in nests encountered on transects was quite high.

With most standard deviations close to or over 50% of the average N per transect, one potential conclusion is that even 5 km of sampling is not enough to capture density in a given site. However, as van Schaik et al. (1995) noted, small-scale ecological variation may cause high variability in nest duration and prevent densities from stabilizing with increasing transect length in what is termed, for expediency's sake, a "single" habitat type. For example, if within the Jerungkung site data we removed the two transects which traversed a riverside partially-inundated patch of forest, variance dropped by almost 30%. We may thus interpret high variance as a reflection of inherent microhabitat patchiness.

Furthermore, it is known that orangutans exhibit seasonal movements to fruit-abundant areas (Leighton and Leighton, 1983). While the effects of such movements on nest surveys are dampened by the long duration in nest visibility, they may still unduly influence density assessments gathered at a single point in time. Given greater financial and temporal resources, population estimates would clearly benefit from repeated surveys performed in different seasons.

4.5. The population estimate

We estimate that Gunung Palung National Park has a population of ≈2500 individuals. The values chosen for each of the parameters in the equation were based on long-term data and the most recent techniques available in the literature. Where a range of values were available, we used the most conservative ones (i.e., those resulting in the lowest density estimate). Therefore, any errors in our projection are likely to have underestimated population size, rather than inflating it.

This figure is dramatically higher than Rijksen and Meijaard's (1999) estimation, based on interpretation of satellite imagery and topographic information, that Gunung Palung contains little good orangutan habitat and less than 150 individuals. In fact, the densities we found here of 3.00 orangutans/km^2 overall with primary peat densities of over 4 ind/km^2, are among the highest reported for Borneo, although robust comparison among studies is hampered by methodological disparities. Marshall et al. (in review) found 2.00 ind/km^2 in the lowland forest of Gunung Gajah, Berau, East Kalimantan, using transect recounts. Morrogh-Bernard et al. (2003) in the vast peat catchment of Sebangau, Central Kalimantan, found densities ranging from 0.85 ind/km^2 in recently logged swamp to upwards of 3 ind/km^2 in areas of older disturbance. Russon et al. (2001) found from 0.43 to 4.09 ind/km^2 in disturbed swamp and peat forest of Danau Sentarum in northern West Kalimantan (recalculation using a Borneo-based r parameter revises these figures downwards somewhat). Application of a transect-recount correction factor to these latter studies would increase densities by 30% according to our findings.

The Gunung Palung population may represent up to 9% of the world's remaining wild orangutan population and 17% of the Bornean population, using the most recent available estimates of 27,000 and 15,000, respectively in Rijksen and Meijaard (1999). However, given that Rijksen and Meijaard's (1999) estimate is too low for Gunung Palung, their world totals may be underestimates as well.

The images from which our habitat area data were derived are from 2001, and were up-to-date at the time the census was done. The increase in illegal logging since 2001, as well as forest loss from several fires in the 1990s, leads us to conclude that the population trend is downward.

4.6. Conservation implications

The results of this study have implications for orangutan conservation at Gunung Palung and many other sites. At Gunung Palung, it is clear that orangutans make considerable use of forest disturbed by logging and fire on both sides of the park border. Disturbed regions within the park support fairly high orangutan densities and buffer zone areas outside the park provide additional food resources and may act as corridors to tracts of intact forest further inland. These areas should not be dismissed as worthless – a common underlying assumption in the Indonesian discourse over Gunung Palung's status – but protected from further disturbance and, ideally, rehabilitated. Formal protection of the expanses of disturbed forest on the northeast and southern borders of the park would help maximize the amount of contiguous forest habitat available to orangutans at Gunung Palung. In addition, conservation efforts at Gunung Palung should focus on opposing the conversion of large areas around the park to oil palm plantation. These commercial monocultures stretch for kilometers and provide a daunting barrier to animals that travel arboreally. Preventing such land conversion should be considered as high a conservation priority as stopping illegal logging in the Gunung Palung region.

More broadly, our study highlights the fact that degraded forests can retain conservation value. Our data agree with results from several previous studies indicating that orangutans can utilize degraded forest, albeit at lower densities and with possible behavioral shifts (e.g., Yoshiba, 1964; Wilson and Wilson, 1975; Lackman-Ancrenaz et al., 2001; Felton et al., 2003). Despite the fact that virtually all lowland forest remaining in both Indonesian and Malaysian Borneo has or soon will be disturbed, the conservation value of disturbed forest remains under-appreciated. Future conservation planning must acknowledge the increasing importance of these areas, and work to prevent these areas from becoming more seriously disturbed or converted to oil palm plantations. Investigations into the long-term effects of habitat disturbance on orangutan ranging, behavior, reproduction and carrying capacity should be given higher priority. Similarly, additional work is required to strengthen our understanding of the importance of higher elevation forests, which our survey suggests can be significant resources for orangutans. A detailed understanding of the impact of variation in habitat quality (either through disturbance or at higher elevations) on orangutans is critical for the design and management of protected areas as well as for possible rehabilitation and reintroduction efforts.

The long term protection of wild orangutans requires a large-scale and multi-faceted approach. Many of the most critical steps lie outside the jurisdiction of conservation biology: they involve adequate protection of Indonesia's national parks by national and local governments unable or unwilling to do so; economic incentives and alternatives to discourage illegal logging, forest conversion, and animal trafficking; and increased in-country awareness of this species' status and needs. However, researchers do have at least one invaluable role: the identification and monitoring of remaining viable populations. This makes it crucial that researchers have a standardized methodology with which to derive accurate and directly comparable estimates. Based on the results of this study, we strongly recommend that second counts be a standard element of nest-based census methodology in order to ensure comparable and more accurate population figures.

Although nobody knows exactly what constitutes a "viable" orangutan population, the basic principles of conservation biology suggest that the most effective strategy is to focus conservation efforts on the few remaining large wild populations. Our findings indicate that Gunung Palung National Park is one of a very limited number of areas left in the world that contains a population large enough to have the potential for long-term viability.

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