EVALUATING ORANGUTAN CENSUS TECHNIQUES USING NEST DECAY RATES: IMPLICATIONS FOR POPULATION ESTIMATES

P. D. Mathewson,[1] S. N. Spehar,[1,4] E. Meijaard,[1,2,5] Nardiyono,[1] Purnomo,[1] A. Sasmirul,[1] Sudiyanto,[1] Oman,[1] Sulhnudin,[1] Jasary,[1] Jumali,[1] and A. J. Marshall[3]

[1]*The Nature Conservancy-East Kalimantan Program, Jl. Polentas 5, Markoni, Balikpapan 76122, East Kalimantan, Indonesia*
[2]*School of Archaeology and Anthropology, Building 14, Australian National University, Canberra, ACT 0200, Australia*
[3]*Department of Anthropology and Graduate Group in Ecology, One Shields Avenue, University of California,
Davis, California 95616-8522 USA*

Abstract. An accurate estimate for orangutan nest decay time is a crucial factor in commonly used methods for estimating orangutan population size. Decay rates are known to vary, but the decay process and, thus, the temporal and spatial variation in decay time are poorly understood. We used established line-transect methodology to survey orangutan nests in a lowland forest in East Kalimantan, Indonesia, and monitored the decay of 663 nests over 20 months. Using Markov chain analysis we calculated a decay time of 602 days, which is significantly longer than times found in other studies. Based on this, we recalculated the orangutan density estimate for a site in East Kalimantan; the resulting density is much lower than previous estimates (previous estimates were 3–8 times higher than our recalculated density). Our data suggest that short-term studies where decay times are determined using matrix mathematics may produce unreliable decay times. Our findings have implications for other parts of the orangutan range where population estimates are based on potentially unreliable nest decay rate estimates, and we recommend that for various parts of the orangutan range census estimates be reexamined. Considering the high variation in decay rates there is a need to move away from using single-number decay time estimates and, preferably, to test methods that do not rely on nest decay times as alternatives for rapid assessments of orangutan habitat for conservation in Borneo.

Key words: Borneo; decay rate; decomposition rate; Indonesia; Markov chain analysis; nest count; orangutan; Pongo pygmaeus; *primate; survey methodology; transect.*

INTRODUCTION

For most animals, accurate delineation of population distribution and effective monitoring of trends in population size are necessary to determine areas for conservation and to implement effective conservation strategies. This requires a reliable census method conducted uniformly across a species' range, which can be especially challenging to implement for forest-dwelling species that are difficult to observe directly. One important example is the endangered orangutan (*Pongo* spp.), found only on the islands of Borneo and Sumatra and severely threatened by habitat loss and hunting (Rijksen and Meijaard 1999, Yeager 1999, Singleton et al. 2004). All wild orangutan populations for which we have good data are in decline, and unless effective conservation measures are quickly enacted, orangutans are likely to disappear almost entirely from the wild in this century (Singleton et al. 2004, Meijaard and Wich 2007; Marshall et al., *in press*). Characteristics

making orangutans particularly vulnerable to extinction include large body size, low reproductive rate, and reliance on large contiguous patches of forest. The Bornean orangutan (*P. pygmaeus*) is listed by the IUCN as endangered (IUCN 2006), having experienced population declines of >90% since the early 20th century. It is now living in increasingly fragmented populations, and its distribution, particularly outside of protected areas in Indonesian Borneo, is poorly understood (Rijksen et al. 1995, Rijksen and Meijaard 1999, Goossens et al. 2006).

Population estimates based on direct counts of orangutans are usually impractical because wild orangutans are relatively rare and quite cryptic in their behavior, particularly in areas where they have been subject to hunting pressure, and encounter rates are therefore very low. Instead, the density of orangutan nests (d_{nest}) is almost universally used by researchers for estimating orangutan population density (e.g., van Schaik et al. 1995, Buij et al. 2003). It is calculated by the following formula:

$$d_{nest} = N/(L \times 2w) \quad (1)$$

where N is the number of nests observed along the transect, L is the length of the transect covered (km), and w is the estimated strip width (km), or the perpendicular distance on either side of a transect from

which all nests are assumed to be sighted. Orangutan densities (d) can then be obtained from nest counts by using the following equation:

$$d = d_{nest}/(p \times r \times t) \qquad (2)$$

where p is the proportion of nest builders in the population, r is the rate at which nests are produced (nests/day/individual), and t is the nest decay time (days), or the time over which a nest remains visible after it is constructed.

This technique utilizes many parameters that are difficult to estimate accurately, so population estimates clearly have limited reliability; this has been acknowledged in several studies (e.g., van Schaik et al. 1995, Singleton 2000, Buij et al. 2003). Any changes in parameters p, r, or t produce directly proportional changes in the resulting orangutan density estimate. As no other practical method for estimating orangutan population size currently exists, most estimates of orangutan densities and population trends have been made using nest surveys. Most orangutan researchers express confidence in this method (van Schaik et al. 1995, Buij et al. 2003, Morrogh-Bernard et al. 2003, Johnson et al. 2005), and where these surveys have been validated by known populations, they seem to provide accurate estimates (e.g., Sumatra: van Schaik et al. 1995). However, many recent Bornean studies and conservation assessments (e.g., Russon et al. 2001, Morrogh-Bernard et al. 2003, Johnson et al. 2005), have relied entirely on nest counts to estimate orangutan population density, without the benefit of validation against known populations. Furthermore, the only study in Borneo in which orangutan densities derived from these methods were compared to known densities (van Schaik et al. 2005) demonstrated that line transects underestimated orangutan densities and ultimately questioned the accuracy of the method.

A reassessment

A recently conducted survey in lowland forests in the Lesan Protected Area, East Kalimantan, Indonesia, using established rapid assessment techniques produced implausibly high orangutan densities ranging from 5.2 to 13.1 orangutans/km^2 (Marshall et al. 2006). Marshall et al. (2006) attributed these high density estimates to temporary compression effects from logging near the survey area, but they suggested that inaccurate estimates of population parameters (particularly nest decay time) may have also contributed to this result. Because no site-specific nest decay times were available, this analysis relied on tree-specific nest decay rates determined in Sabah, Malaysia (Ancrenaz et al. 2004a). As the extremely high population density estimates for Lesan were assumed to be localized and well above carrying capacity, Marshall et al. (2006) did not estimate a population for the area sampled.

In order to estimate the size of the Lesan orangutan population, we established a long-term research project to gather additional data on nest density and to determine a site-specific nest decomposition time. Here we provide a reassessment of orangutan population densities at Lesan based on this research. If this study indicates that initial density estimates were incorrect due largely to inaccurate decay times, it would suggest that other previous studies could have been subject to the same type of error.

A better understanding of the factors contributing to variation in decay rate is essential because errors in estimates of nest decay rate can have major implications for orangutan conservation. We thus reexamine the appropriateness of the standard technique for estimating t in short-term studies and reconsider the accuracy of nest surveys as means of estimating population densities for these endangered species.

Methods

Study area

We conducted nest surveys in the Lesan Protected Area, a Nature Conservancy-run site in the Berau district of East Kalimantan, Indonesia (1°36′ N, 117°10′ E, mean elevation ~75 m above sea level). This site is a former logging concession (logging ceased six years previous to the study) and consists of 115 km^2 of secondary and mixed primary and secondary forest in a much larger secondary forest landscape. The unlogged lowland forest portion of the site is a mix of lowland dipterocarp forest, with high floristic diversity and the multitiered structure characteristic of mature diptero-carp forest, and heath (or kerangas) forest, with lower plant diversity and shorter, less well-structured vegetation. The site is topographically variable, incorporating rivers and streams as well as large hills and ridges. The maximum altitude gain from streambeds to hill or ridge tops is 400 m.

Nine parallel line transects, each 4 km long, were cut along a midline with ~500 m between transects (Fig. 1). The transects were cut due north–south from the midline without regard for topography or vegetation (adhering to the line-transect method assumption that transects be placed randomly in respect to the terrain [Buckland et al. 2001]) and cover a representative sample of the Lesan Protected Area.

Field surveys

This study was carried out between February 2005 and September 2006. A team of trained observers conducted all nest surveys under supervision of an experienced coordinator with more than five years surveying experience (Nardiyono). At the start of the study (February 2005), observers located 672 nests by walking slowly along line transects, and for each nest the perpendicular distance from the transect (measured by tape measure), location along transect, direction from transect, nest height, tree diameter at breast height (dbh), and tree species were recorded. Survey team members were trained and tested in the area's botany,
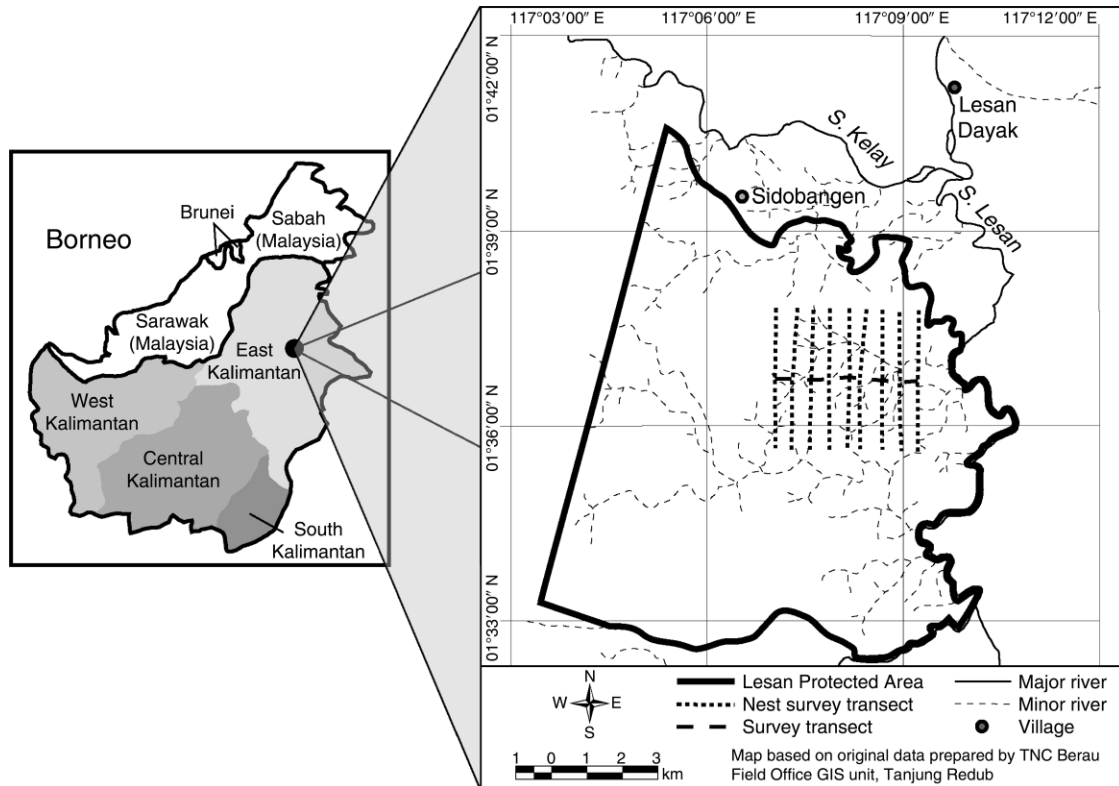
Fig. 1. Map of the Lesan Protected Area, East Kalimantan, Indonesia, and nest survey transects (shown to scale).

and we are confident of tree identification at a minimum to the genus level despite the potential variation in local ethnotaxonomy. The decay state of each nest was recorded as one of five possible states: (A) fresh, leaves still green; (B) still fairly fresh, mixture of green and brown leaves; (C) nest is brown, but remains intact; (D) nest has begun to fall apart, chunks of the nest and leaves missing; and (E) leaves are gone, and only the branch and twig structure of the nest remains (e.g., Johnson et al. 2005). In the second or third week of each month (except July 2005, when no data were collected), the team resurveyed each transect and assessed the decay stage of each nest. They also anecdotally recorded any new nests produced since the previous survey to increase sample size. By the end of the study, a total of 807 nests had been monitored.

To investigate the effects of rainfall on decomposition, we estimated local monthly rainfall using data from the nearest active weather station located 75 km from the study area.

The data set

Observed nests.—Of the 807 nests monitored in this study, 144 nests were discarded because of problems with data collection, including missing nest scores (40% of discarded nests) and inconsistencies in scoring. These inconsistencies were likely due to possible reuse of nests (10% of discarded nests) and cases where recorded nest state fluctuated between states due to the intrinsic subjective nature of describing nest state, particularly the later stages of decay (50% of discarded nests). The remaining data set used in the analysis consisted of 663 nests.

Data on nest decay were not collected in July 2005. In order to create a single continuous data set for the purposes of the Markov chain analysis, we estimated the likely state of the nest in July 2005 by scoring single-step transitions conservatively (i.e., transitions happened sooner rather than later) and for all two-step transitions, scoring the intermediate step, as this has minimal effect on decay rate calculations. We reanalyzed the data set omitting July 2005 to determine whether the inclusion of estimated states for July 2005 altered our results.

Estimating parameters for population estimates

Parameters p, r, and w.—The proportion of nest builders in the population (p) and the rate at which nests are produced (r) must be based on observed values from known populations (MacKinnon 1974, van Schaik et al. 1995, Singleton 2000). All orangutans, with the exception of dependent infants, build nests (Johnson et al. 2005). No significant variation in the proportion of nest builders has been found between Sumatran and Bornean populations, so we used the typically cited p value of 0.9 (van Schaik et al. 1995, Johnson et al. 2005). The rate at which nests are produced does seem to differ signifi-

cantly between the two islands, with Sumatran orang-utans building nests at a rate of 1.7 nests per day (van Schaik et al. 1995, Singleton 2000) and Bornean orangutans building at a rate of 0.9–1.2 nests per day (Morrogh-Bernard et al. 2003, Ancrenaz et al. 2004a, b, Johnson et al. 2005). We used an average Borneo-specific r value of 1.08 in this study (Ancrenaz et al. 2004b, Johnson et al. 2005)

In calculating nest density, nest number (N), and strip width (w), only the 672 nests found in the first survey in February 2005 were used. We determined strip width using DISTANCE 4.1 (Thomas et al. 2004), which takes into account the total number of nests, total transect length, and perpendicular distance from nest to transect. DISTANCE software has been shown to be reliable (Cassey and McArdle 1999) and has been used in previous studies of orangutan densities (e.g., Buij et al. 2003, Morrogh-Bernard et al. 2003, Johnson et al. 2005). See Buij et al. (2003) and Johnson et al. (2005) for detailed discussions on estimating w.

Nest duration (t).—Nest decay rate (t) is more difficult to estimate accurately, and variation in t also produces directly proportional variation in orangutan density estimates. Measuring t has thus been the subject of a number of studies (van Schaik et al. 1995, Russon and Susilo 1999, Singleton 2000, Russon et al. 2001, Buij et al. 2003, Felton et al. 2003, Morrogh-Bernard et al. 2003, Ancrenaz et al. 2004a, Johnson et al. 2005). These studies demonstrate that there is a great deal of variation between sites in nest decay estimates, with published decay rates ranging from 72 to 424 days. What causes these differences is not clearly understood, although climatic factors, altitude, the purpose for which the nest was constructed (night or day nest), soil pH, nest height, and tree species in which the nest is built have been suggested as explanations for some of the variation (van Schaik et al. 1995, Singleton 2000, Buij et al. 2003, Ancrenaz et al. 2004a, Johnson et al. 2005). It is agreed that nest decay rate varies substantially with habitat and site and should ideally be determined separately for each site.

1. *Direct observation.*—Nest monitoring provides the most accurate estimate of t, but requires laborious and time-consuming data collection that can take years. Only 127 of the 663 nests used in this study were discovered in states A or B (accounting for 19% of all nests) and, of these, 41% (52 nests) disappeared during the course of the 20-month study. These 52 nests observed from state A or B to disappearance account for only 8% of all nests used in the analysis. These nests are not a representative sample of the entire data set, as this sample is biased; these are inherently the shortest-lived of all the nests, as they must have a life span encompassed by the 20 months of surveys. By all indications, the nests at Lesan have exceptionally long life spans. For example, of the 557 nests discovered in the first month of the study in any decay state, 249 (45%) were still present at the final survey in September 2006. Because so few nests were observed from state A to

disappearance, and as these nests are not representative of the entire data set, we estimated nest duration using an indirect method (see *Methods: The matrix technique*).

2. *The matrix technique: the Markov chain analysis.*—Many researchers have understandably looked for shortcuts for estimating decay rates that require far less time in the field than monitoring nest decay directly. A Markov chain analysis (Kemeny et al. 1956) has been used to estimate decay rate by several previous studies (van Schaik et al. 1995, Russon et al. 2001, Buij et al. 2003, Morrogh-Bernard et al. 2003, Johnson et al. 2005). This technique uses matrix mathematics to estimate nest duration based on transition rates between decay states, allowing the use of "censored" nests (nests that were not found in state A, or had not disappeared within the study period) because it does not depend on actual nest duration. However, a sufficient number of nests must disappear in order to apply the matrix technique to a data set (Buij et al. 2003, Johnson et al. 2005). This method allows the process of nest decay to be modeled and provides an estimate of t from as few as two surveys of decaying nests (van Schaik et al. 1995). It has also been suggested as an acceptable technique for use in short-term rapid assessments of orangutan densities (Buij et al. 2003).

Markov chain analysis assumes that for every process (in this case, an orangutan nest transitioning through decay states until it disappears), there is a matrix of the probabilities of transitioning from one state to another, and from this one can calculate the sojourn time spent in each state before the process ends (Kemeny et al. 1956). For use in orangutan nest decay, sojourn time is the cumulative number of survey intervals a nest remains in a given state. Application of this method relies on known transition rates between the "nonabsorbing" states in this matrix, that is, the states from which nests can make a transition. In the case of orangutan nest decay, transitions through stages are unidirectional, and there is only one "absorbing" state: when the nest is gone. A matrix with only the nonabsorbing states is called the transition matrix (Q). Squaring this matrix will yield the probabilities of given nest transitions after two study intervals, cubing it will give probabilities after three study intervals, and so on.

From matrix (Q), one can calculate the Markov chain's underlying fundamental matrix, N (Wong et al. 2006):

$$\mathbf{N} = \sum_{k=0}^{\infty} \mathbf{Q}^k \qquad (3)$$

where k equals the number of study intervals. The fundamental matrix can be calculated using matrix calculators with the following equation:

$$\mathbf{N} = (\mathbf{I} - \mathbf{Q})^{-1} \qquad (4)$$

where I is an identity matrix.

Each entry in the fundamental matrix represents the expected sojourn time in each decay state. Applied to

orangutan nest decay, these entries would estimate the amount of time a nest would spend in a given state given a certain starting state. Summing across a row in the fundamental matrix **N** gives the total amount of time a nest is expected to be visible from a certain starting state.

Our 20-month study produced 19 one-month transition matrices, which were pooled to create one transition matrix representing one "typical" month in the study period. Bimonthly survey periods were also used to compare to other studies. All matrix calculations in this paper were done with an on-line matrix calculator (S. Waner, *unpublished software*).

3. *Correction factor (Cf).*—Where they have been calibrated against actual decay rates, Markov analyses tend to overestimate nest duration (van Schaik et al. 1995, Buij et al. 2003, Johnson et al. 2005), due to an inherent bias of the method. Longer-lasting nests are more likely to be observed and included in a given sampling effort than are nests of flimsier construction, such as day nests, which can decay completely within days (van Schaik et al. 2005). A correction factor (Cf) is usually applied to provide a more accurate estimate of duration. This Cf is calculated by comparing observed nest duration with results obtained from a Markov analysis, and, like nest durations themselves, seems to be very site-specific; published correction factors range from 0.60 (van Schaik et al. 1995) to 0.89 (Johnson et al. 2005). Because an insufficient number of nests were observed from state A to disappearance ($n = 52$; see *Methods: Direct observation*) and because these nests were censored, biased observations, we were unable to obtain a Cf specific to our study site. Other studies with insufficiently long observation periods have applied Cfs from other study sites, so for comparison with these studies we applied a conservative Cf of 0.75, recommended by van Schaik et al. (1995), and a Cf of 0.89, perhaps more appropriate for Borneo (Johnson et al. 2005).

Adjustments for comparison to previous study and reassessment

Methods used to estimate Lesan's orangutan density in the previous study (Marshall et al. 2006) differed slightly from those used in our study, and some adjustments were necessary when comparing our results to the previous study.

When calculating nest density for this study, only those nests found during the first survey in February 2005 were used. Line-transect methodology assumes that all nests above a transect are observed during a survey; however, Johnson et al. (2005) and Marshall et al. (2006) reported that walking a transect a second time found 16–35% more nests. To avoid violating line-transect methodology, a missed-nest correction factor can be applied when calculating nest densities based on a single survey. This study used an average correction factor of 1.25 (Johnson et al. 2005, Marshall et al. 2006) when comparing results to the previous study. Following Marshall et al. (2006), decay rates were adjusted for

tree taxa by dividing the sample into four groups based on nesting tree taxonomy (Dipterocarpaceae trees, Myrtaceae trees, *Eusideroxylon* trees, and all other trees), and decay rate was determined for each group using the matrix method. Each group's decay rate was multiplied by the proportion of the total sample that group comprised; these four products were summed for a weighted average decay rate. A further correction factor (0.07 × average altitude of survey area) for altitude was added to this total decay rate (Johnson et al. 2005, Marshall et al. 2006). This is not a promotion of these methods, as we have no means of validation for this study; it is simply done to obtain results comparable to the previous study in Lesan.

Subsets

As some studies employ small sample sizes and are conducted over short periods of time, we were interested in assessing the effects of sample size and study length (regardless of the time of year in which the studies were conducted) on the precision and accuracy of the resulting t values obtained by the matrix technique.

From our complete set of 663 nests, we randomly selected 10 subsamples each of 75, 150, 300, and 500 nests, for a total of 40 nest subsets. Using these subsets, we performed Markov chain analyses simulating study lengths of 1, 3, 6, 12, and 15 months, starting in each of the different months encompassed by this study. After March 2006, there were not sufficient nests in all age classes to perform Markov chain analyses on individual months.

For each of the 40 subsamples of different size (75, 150, 300, 500), there were 49 "studies" of different length and start month for a total of 1960 studies. For analysis, we grouped the subsamples by study length and nest sample size to form 20 sample populations. While these simulated populations are not independent, they permit exploration of how study length and nest sample size influence decay time calculations.

Data analysis

We analyzed nest density using DISTANCE 4.1 (Thomas et al. 2004), and, following Buckland et al. (2001), nest density was calculated using five suggested models: half-normal with cosine or simple polynomial expansions, hazard rate with either cosine or simple polynomial expansions, and uniform with cosine expansion. Data were analyzed with 4- and 5-m interval cut-off points, and the model resulting in the lowest value for Akaike's information criterion (AIC) that still resulted in an insignificant goodness-of-fit statistic to the distribution of data was selected.

Statistical tests were performed using StatView 4.5 (Abacus Concepts 1995) and SPSS 14.0 (SPSS 2005).

RESULTS

Transition rates

The proportion of nests that transitioned between states each month varied considerably between months,
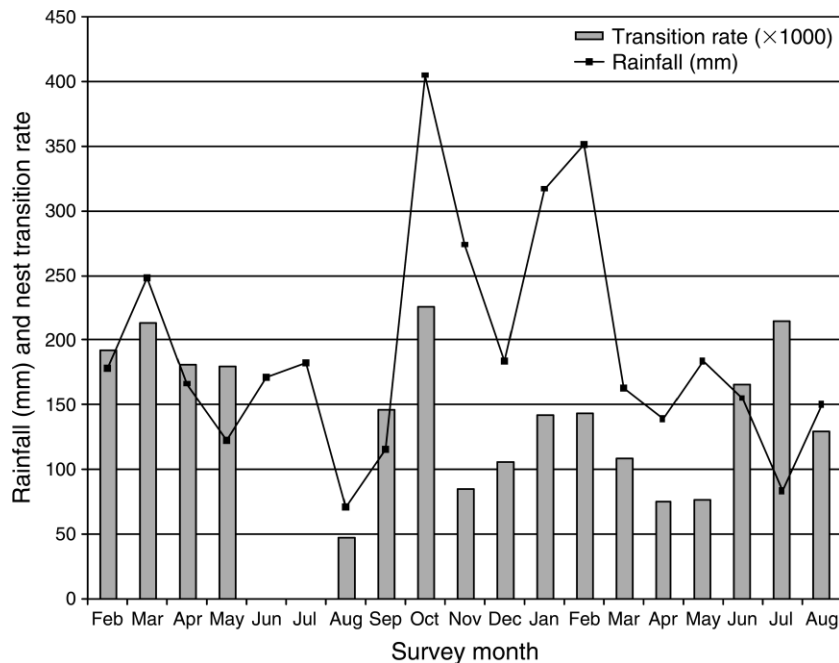
Fig. 2. Monthly nest transitions and rainfall from February 2005 to August 2006. No data were collected in July 2005; thus, no transition rates could be calculated for June and July 2005. Nest transition rate was calculated by determining what proportion of all nests surveyed in a given month were found in a more advanced decay state in the following month's survey. This rate was multiplied by 1000 so it could be visually compared to rainfall.

from a low of 0.05 in August 2005 to a high of 0.23 in October 2005 (Fig. 2). Overall, although an increase in monthly rainfall appears to result in higher transition rates (Fig. 2) the amount of rainfall per month did not correlate significantly with transition rate ($n = 19$ months, Spearman rank correlation, $n = 17$, $r^2 = 0.16$, $P = 0.54$). When we excluded early stage transitions (A–B, A–C, and B–C), as these occur within a month and would not be noticeably accelerated by rainfall, there was still no significant correlation.

Markov results for nest duration (t)

The data were analyzed in two forms: "with July 2005" and "without July 2005." The without July 2005 Markov results do not include the transitions between June and July 2005 and July and August 2005, as these data were missing. To create the with July 2005 data set, we filled in the likely nest states for July to obtain a

continuous data set (see *Methods*). As the overall nest durations (t) for the with July 2005 and without July 2005 data sets are comparable (Table 1), we use the uninterrupted sample (with July 2005) throughout the rest of this paper.

As noted earlier, this study uses five transient states to categorize nest decay, rather than four, as sometimes used in other studies. To make our data more comparable to other studies, we converted our data so that only four transient states were possible (by combining the categories B and C, as both states fall into the second decay stage of a four class categorization) and performed a Markov chain analysis on this data set. The results are comparable to the result obtained using all nest states (see Table 1). A previous study (Buij et al. 2003) also found little difference in calculated decay times using both four and five age classes to characterize nest decay.

TABLE 1. Decay time for orangutan nests in Lesan, East Kalimantan, Indonesia, obtained using the Markov chain method.

Data set	Study length (d)	Decay time (d)	Cf	Corrected decay time (d)
With July 2005†	547	676.95	0.75‡/0.89§	507.71/602.49
Without July 2005	486	661.06	0.75‡/0.89§	495.79/588.35
Combined states B and C	547	677.31	0.75‡/0.89§	507.98/602.81
Bimonthly	547	683.77	0.75‡/0.89§	512.83/608.56

† Data "with July 2005" are analyzed in this paper.
‡ Correction factor (Cf) obtained from van Schaik et al. (1995).
§ Cf obtained from Johnson et al. (2005).

TABLE 2. Uncorrected nest decay times for classes of different tree characteristics, obtained using the Markov chain analysis.

Tree characteristic	Class	N	Decay time (d)
Wood durability†	I, I/II, II	118	715.80
	III, III/IV	277	707.80
	V, IV/V, V	181	623.87
Nesting tree dbh (cm)	0–9	26	797.79‡
	10–19	286	744.86‡
	20–29	181	629.89
	30–39	84	622.81
	40–49	45	691.81§
	50+	41	550.75§
Nest height (m)	0–9	245	692.12
	10–19	369	697.62
	20+	49	487.62

† From Hildebrand (1952); I is most durable, and V is least durable.
‡ Combined decay time for these two classes is 747.63 days.
§ Combined decay time for these two classes is 619.70 days.

Effect of tree type, tree size, and nest height on nest duration (*t*)

We examined differences in nest decay time between nests built in different tree types, at different heights, and in different tree sizes (based on tree dbh). A significant difference in nest decay time was found at both the family ($\chi^2 = 463.95$, df = 14, $P < 0.001$) and genus ($\chi^2 = 630.16$, df = 20, $P < 0.001$) level (see Appendix for specific values). When nests are grouped by wood durability classes (from Hildebrand 1952), there is a clear difference in nest decay time between nests built in the harder trees (I–III) and in the softer trees (IV and V) (Table 2). A significant difference was also found for nest height ($\chi^2 = 52.91$, df = 3, $P < 0.001$), and tree dbh ($\chi^2 = 60.05$, df = 5, $P < 0.001$) (Table 2). The latter two variables are positively correlated (Spearman rho = 0.57, $P < 0.001$).

Estimate of orangutan density

Estimation of orangutan nest density and population size.—Data analysis gave a nest density of 968.89 nests/km² (95% CI, 878.90–1068.10). When using the correction factor (0.89) for nest decay time calculated using the Markov method, this nest density translated into 1.65 (95% CI, 1.50–1.82) orangutans/km² and a population estimate of 190 orangutans in Lesan. All parameters used in the estimate of orangutan density in the Lesan Protected Area are listed in Table 3.

Reassessment.—To compare these results to the previous study done in the Lesan area (Marshall et al. 2006) we made comparable adjustments to our calculated *t* values, as explained in *Methods: Adjustments for comparison.* When the site-specific decay times from this study were applied to the previous study, orangutan density was slightly higher than the density presented in this paper (Table 4). As the previous surveys were conducted in 2003, the disparity in orangutan density may be indicative of a population loss in the two years between surveys or a reduction in the compression effect from logging.

Variations in decay times using Markov chain analysis

Length of study.—Some researchers have suggested that studies employing the Markov method can provide accurate estimates of nest duration in a study length as short as one month (e.g., Buij et al. 2003). To test the accuracy of the Markov analysis when applied to short study periods, we performed Markov analyses on each cumulative month of our study data. Nest duration calculated using the Markov analysis varies widely in the early months of the study, both over and underestimating the duration of nests, before stabilizing later in the study (Fig. 3). As the Markov process uses transition rates to determine nest duration, and transition rates vary significantly between months (see Fig. 2), these results are not surprising. When we performed Markov analyses based on the decay data for each month in this study, we found that the results for individual months varied significantly ($n = 16$ months, mean 705.87 days, range 226.65–1563.94, $\chi^2 = 2294.60$, $P < 0.001$). Monthly decay times showed a significant inverse correlation with monthly transition rates (Spearman rank correlation, $n = 15$, $r^2 = -0.621$, $P = 0.01$; Fig. 4).

Subsets.—While the subset studies do not form true populations and thus cannot be statistically tested, they do serve to illustrate certain trends when looking at the influence of study length and nest number on the calculated decay time using the Markov chain method. The shorter studies produce a much wider range of

TABLE 3. Parameters used in estimating orangutan density.

Parameter	Value	Notes
Nest density (d_{nest}; no./km²)	968.89	analyzed in DISTANCE 4.1 using the half-normal with hermite expansion model and 5-m intervals (AIC: 1525.97)
Nest number (N)	672	all nests observed in first survey (February 2005)
Total transect length (L; km)	36	
Effective strip width (w; m)	9.63	survey data analyzed in DISTANCE 4.1 using the half-normal with hermite expansion model and 5-m intervals
Proportion of nest builders (p)	0.9	accepted value (van Schaik et al. 1995, Buij et al. 2003)
Daily nest-building rate, r (no. nests per day per individual)	1.08	average rate for Bornean populations (Ancrenaz et al. 2004*b*, Johnson et al. 2005)
Nest decay time (t; d)	602.49	Markov chain analysis; correction of 0.89 from Johnson et al. (2005)

TABLE 4. Reassessment of orangutan density in the Lesan protected area (LPA).

Study	Nest density (no./km²)	Orangutan density (no./km²)	Extrapolated LPA population
Previous study†	1512.21	8.95	N/A‡
Previous study, new *t* values§	1512.21	2.54	296
TNC¶	968.89	1.65	189
TNC (t_{corr})#	1211.49	2.05	236

† From Marshall et al. (2006); $N = 2685$, $p = 0.9$, $r = 1.08$, $L = 44.5$, $w = 19.95$ m, $t = 173.9$ d. Parameters are defined in Table 3.

‡ No population estimate made; nest density figures for this area discarded by study (see *Introduction: A reassessment*).

§ Results from Marshall et al. (2006) using new decay times; $N = 2685$, $p = 0.9$, $r = 1.08$, $L = 44.5$, $w = 19.95$ m, $t = 613.23$ d.

¶ TNC, The Nature Conservancy; $N = 672$, $p = 0.9$, $r = 1.08$, $L = 36$, $w = 9.63$ m, $t = 602.49$ d.

Nest decay time t corrected for tree species and altitude, N corrected for missed nests; $N = 840$, $p = 0.9$, $r = 1.08$, $L = 36$, $w = 9.63$ m, $t = 608$ d.

decay times than longer ones, and with one exception, as nest number increased, the range of decay times decreased (Fig. 5.) The results from the one month/75 nest population are somewhat misleading, as there were a number of studies within this sample population in which not enough nests made the transition to the absorbing state to obtain a decay time. For this reason, the one month/75 nest sample population produced no results in the times of year (for example, February 2005) yielding the highest decay times. Had we been able to calculate a decay time for all studies in this population, its results would most likely be similar to that of the one month/150 nest population. While the mean decay times did not differ for the most part between sample populations, the reliability of the resulting decay times did differ. The mean values of the short-term studies do not differ significantly because they are the product of averaging repeated studies over the course of the study period, which eliminates the between-month variation found in this study (see Fig. 4). Because researchers must normally base conclusions on just one study, a long-term study would give a much more reliable decay rate, as short-term studies tend to be prone to enormous amounts of variation regardless of nest number.
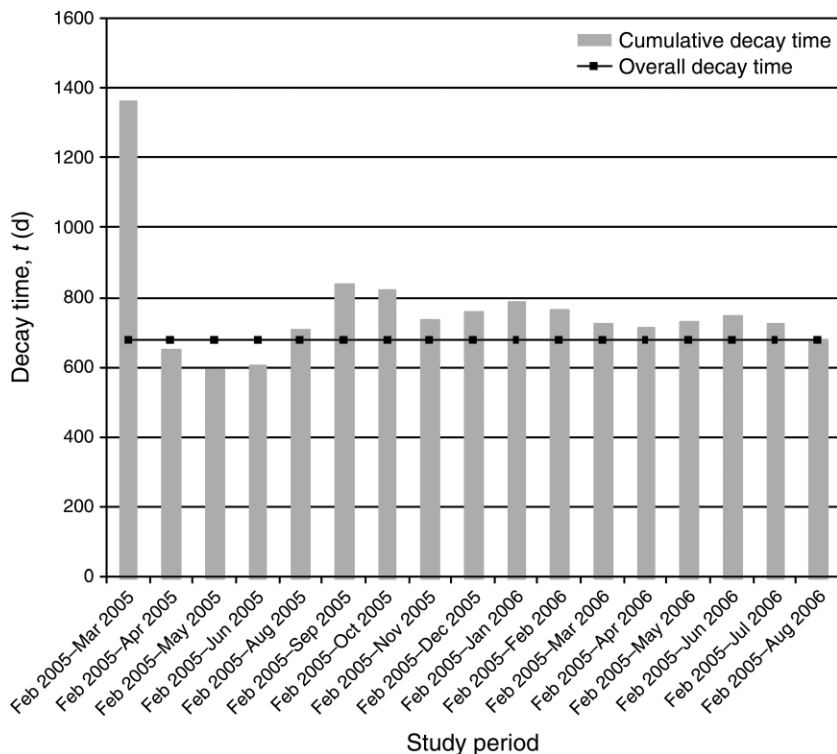

FIG. 3. Cumulative nest decay times calculated using the Markov method. The final uncorrected decay time of 676.95 days is represented by the solid black line.
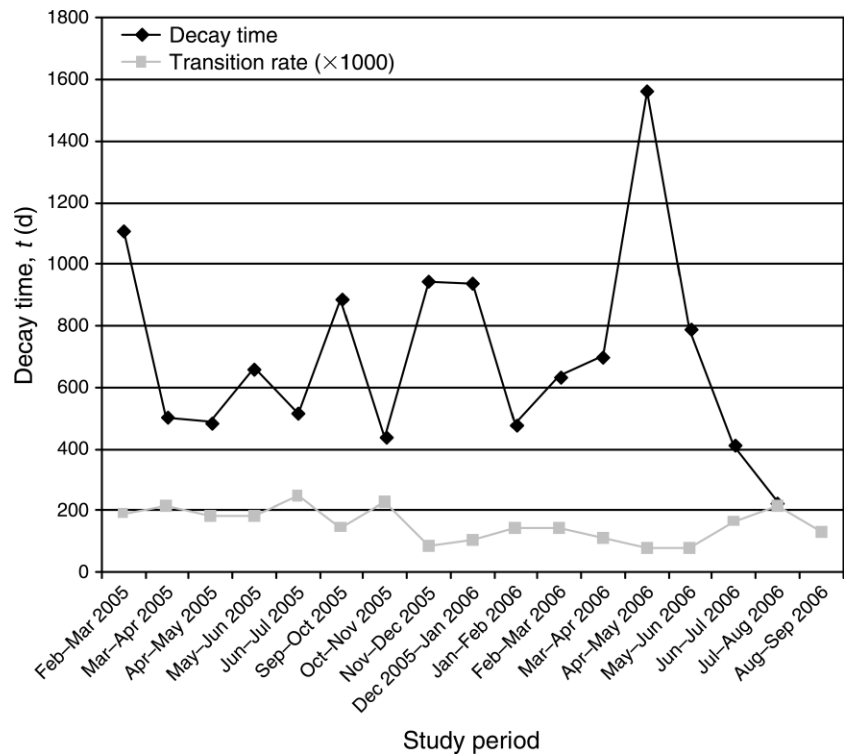
Fig. 4.   Monthly transition rate and decay times calculated using the Markov method. No data were collected in July 2005, and no nests transitioned into the absorbing state in August 2005.
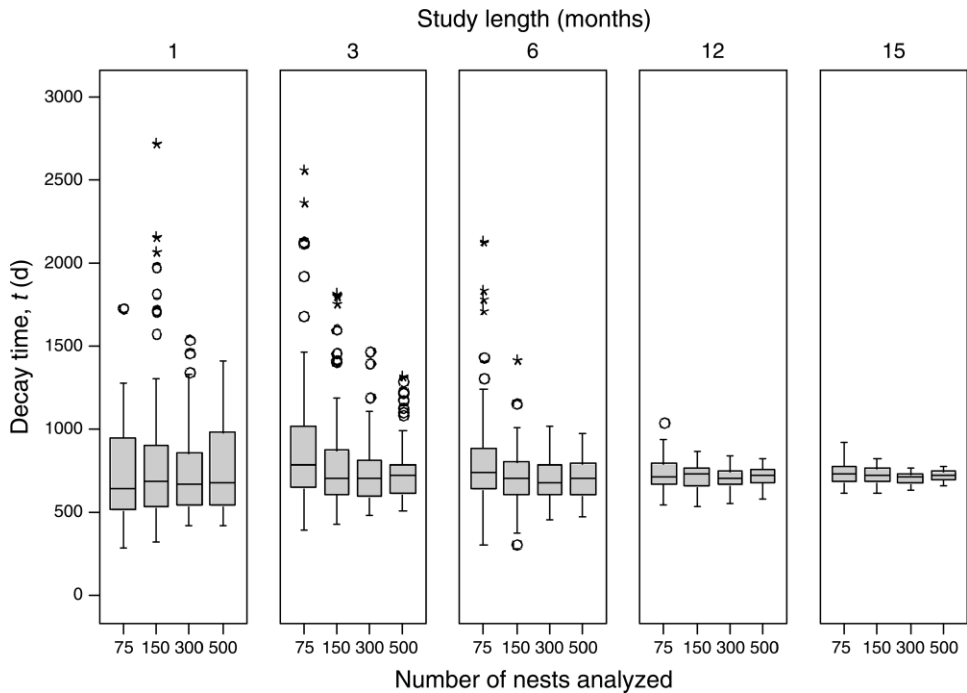

Fig. 5.   Box plot of nest decay time from subsets of different study lengths and nest numbers, grouped by study length. The boxes represent the interquartile (IQ) range, that is, the middle 50% (25th to 75th percentile) of the data being displayed. The horizontal line in the box represents the data set's median value. The upper and lower whiskers reach out to the highest and lowest data points not considered outliers. Outliers are represented by open circles and are defined as being greater than 1.5 times the IQ range from the middle 50% of the data. Extreme outliers, represented by stars, are defined as being greater than three times the IQ range from the middle 50% of the data.

DISCUSSION

The primary finding of this study is an extremely long decay rate for orangutan nests at Lesan in East Kalimantan. The 602 days we calculated from this long-term nest monitoring study is about three times longer than the previously assumed decay rate of between 176 and 237 days at Lesan using the best available information (Marshall et al. 2006). This decay time is much greater than any previously reported for any site, and our findings substantially increase the already extreme between-site variation exhibited by orangutan nest decay rates (Table 5), which are far more variable than those reported for other apes. While variations in nest decay rates have been reported for both chimpanzee (*Pan troglodytes*) and gorilla (*Gorilla* sp.) nests (Furuichi et al. 1997, Plumptre and Reynolds 1997, Hall et al. 1998, Blom et al. 2001, Brugiere and Sakom 2001, Pruetz et al. 2002), the magnitude of variation is nowhere near that found for orangutan nests: chimpanzee nest decay times vary between 41 and 113 days, and gorilla nests vary between 50 and 170 days. Why orangutan nest decay varies so much and whether management decisions based on population estimates derived from nest monitoring are appropriate for this species are two important questions facing the conservation community.

It is widely understood that decay rates for any biological index are variable throughout the year, particularly in areas that experience seasonal rains, with decay rates being markedly lower in dry seasons (Tutin et al. 1995, White 1995, Brugiere and Sakom 2001, Laing et al. 2003). This is especially true for long-lived indices such as orangutan nests that are inherently subject to greater variability. This study found significant inter-month differences in nest decay rates; while rainfall is one of the more obvious potential correlates with decay rate, we did not find a significant direct correlation between monthly rainfall and transition rates (see Fig. 2). However, there is clearly a relationship between the two variables, and it is likely that the correlation between rainfall and decay rate is mitigated by the effect of the many other factors that can influence decay rate. This study found that decay rate was related to nesting height, tree size, and tree type. Nest height was positively correlated with tree size, and higher nests decay more quickly as they are presumably more exposed to damaging wind and rain. Nests built in hardwood trees decay slower than those built in softer-wooded trees, as expected. In addition to wood type, leaf color change and oxidation that dictate a nest's observable transition through decay states are also related to the specific phytochemistry of individual tree species (M. Grote, *personal communication*).

Recent studies (e.g., Ancrenaz et al. 2004a, Marshall et al. 2006) have proposed moving away from a single-number estimate of decay time in favor of tree taxa-dependent decay times, given the correlation found between different tree types and nest decay found in this and other studies. Ancrenaz et al. (2004a) suggested that the effect of physical characteristics such as tree type on decay rate should remain similar between sites; this study provides evidence that this is not the case (Table 6). The daunting reality is that a model needs to also incorporate other factors that may influence decay rate, which include (but are not limited to) altitude (van Schaik et al. 1995, Buij et al. 2003, Johnson et al. 2005), soil pH (Buij et al. 2003, Wich et al. 2004), decomposer abundance, the sample's nest age composition at any given time, seasonality, nest reuse rates (Singleton 2000), orangutan "mood" (Rijksen 1978), and other possible behavioral or cultural differences between different orangutan populations (Singleton 2000; M. Ancrenaz, *personal communication*).

Until the interaction between these factors is properly understood, it appears virtually impossible to accurately predict or model nest decay, as the factors vary both between sites and over time. Nevertheless, most researchers have relied on nest census methods and accompanying studies of nest decay rate because it is currently the only practical method of censusing orangutans. Other studies have outlined the appropriateness of using nest-count surveys to estimate orangutan population size (e.g., van Schaik et al. 1995, Buij et al. 2003, Johnson et al. 2005), and some have suggested that short-term studies of nest decay rate (1–2 months in length) can provide reliable accurate estimates of nest decay time for use in population estimates. The appeal of such rapid methods is understandable, as direct monitoring requires a substantial investment of time and labor, commodities that are not always readily available. While previous studies have acknowledged that the Markov method (e.g., van Schaik et al. 1995) is less precise than direct monitoring, they have concluded it could still produce a reliable estimate from a short study.

Given all the factors affecting nest decay rate and given how many of these factors are variable over time, it is difficult to believe one could conduct a short-term study and then extrapolate those nest decay results to obtain an accurate population estimate. A short-term study assumes a representative, stable decay rate in spite of documented variability, resulting in biases of tens of percent when the decay rate is used to estimate animal abundance (e.g., Walsh and White 2005). This study provides evidence that shorter studies of orangutan nest decay may be quite unreliable. The preliminary subset analysis presented here suggests that studies less than six months in length produce a wide range of decay times; relying on a single calculation in such a study could be risking great error. Further research and rigorous statistical testing on the reliability of shorter-length studies should be conducted to determine whether this is unique to our present study site. Through such testing, minimum standards for study design considerations, such as sample size and study duration, might be extracted.

TABLE 5. Decay times for orangutan nests calculated using direct monitoring (DM) and Markov chain analysis (Markov) at sites in Borneo and Sumatra; findings from this study are in bold.

Location	Forest type	Study length (d): DM/Markov	Sample period	No. nests	Decay time (d)	
					DM	Markov
W. Kalimantan	lowland	1795/365	bimonthly	258	259	291.5
	peat	1795/365	bimonthly	35	399	424.4
Sabah, Malaysia	lowland	850†	21 days	115	202	N/A
Sumatra	transit swamp	850/850	monthly	735	206.4	246.4
	hills	850/850	monthly	470	227.7	249.4
	backswamp	850/850	monthly	601	192.7	234.1
	transit swamp	850/850	bimonthly	735	N/A	240.4
	hills	850/850	bimonthly	470	N/A	269.4
	backswamp	850/850	bimonthly	601	N/A	228.7
W. Kalimantan	peat	122‡	monthly	621	N/A	72§
C. Kalimantan	peat	30‡	monthly	86	N/A	284
W. Kalimantan	swamp	38‡	monthly	264	N/A	193.7
Sumatra	hills	~665†	monthly	45	319	N/A
	swamp	~665†	monthly	55	228	N/A
E. Kalimantan	lowland	43‡	43 days	79	N/A	319
Sumatra	lowland	31‡	monthly	83	N/A	118
	highland	31‡	monthly	35	N/A	247
	peat swamp	17‡	17 days	106	N/A	96
Sumatra	hills	~395†	monthly	30	81	N/A
E. Kalimantan	**lowland**	**547‡**	**monthly**	**663**	**N/A**	**676.95**

Note: "N/A" stands for not applicable.
† Only DM calculated for this study.
‡ Only Markov calculated for this study.
§ Not enough nests entered absorbing state; decay time only through three of four decay states.
¶ Cf obtained from van Schaik et al. (1995).
# Cf obtained from Johnson et al. (2005).

Another source of potential error in calculating orangutan densities from nest surveys is the inherent difficulty and subjectivity of scoring nest state. This is of particular concern for short-term studies that rely on the Markov method for decay time calculations, as the analysis is so sensitive to transitions between states. A related issue is that of nest reuse. For example, our best estimate is that 10% of the discarded nests in this study were reused by orangutans, but it is likely that other reused nests went undetected. It is difficult to identify reuse without direct observation, and reused nests may be inadvertently included in a study, artificially inflating decay times. Reuse rates are poorly understood and vary between sites, from 14.6% in Sabah, Malaysia (Ancrenaz et al. 2004a) to 5% in Sumatra (Singleton 2000). Our use of the lower Bornean-specific r value reflects in part the higher nest reuse rate documented in Bornean orangutans (Ancrenaz et al. 2004a). However, we must note that this r value may not fully account for an unknown nest reuse rate, and the effect of not knowing the reuse rate in Lesan on our calculations of decay time is unknown.

The reassessment of orangutan density in the Lesan Protected Area highlights the importance of reliable estimates of nest decay and questions how much we really know about orangutan numbers in Borneo where estimates have not had the benefit of validation. The most serious concern raised is whether other studies that did not develop complete site-specific decay rates could have presented incorrect orangutan population esti-

mates. The nest density numbers in the previous study at Lesan were so implausibly high that while interest was piqued, no estimate was made; however, there could be cases where estimates based on questionable decay times fall into expected ranges, and are simply accepted.

One of the most pressing needs for orangutan conservation is a better understanding of orangutan distribution throughout Borneo in the face of rapidly shrinking forest habitat. Effectively determining distribution throughout their entire range might be better done using indirect methods such as a combination of forest reconnaissance (e.g., Hall et al. 1998, Rijksen and Meijaard 1999), estimates of hunting pressure, and developing a fruiting tree density correlation to orangutan presence. This combination of methods has been successfully used for identifying healthy chimpanzee populations in Africa (Balcomb et al. 2000). Strangler fig density has been found to be a reliable index of orangutan density in Sumatra (Wich et al. 2004), but not in East Kalimantan (Marshall et al. 2006, 2007); however, neither study examined the density of all large fleshy-fruiting trees that might attract orangutans. While relying solely on ecological indicators to estimate orangutan density has not been well-tested and could be as misleading, if not more, than nest censuses when estimating population size, the combination of this method and forest reconnaissance could provide a cost-effective means to obtain a reliable understanding of orangutan distribution. This may also help reduce error resulting from under- or overestimating populations in

TABLE 5. Extended.

Corrected Markov (d)	Cf	Study
259	0.89	Johnson et al. (2005)
377.7	0.89	
N/A	N/A	Ancrenaz et al. (2004)
206.48	0.838	Buij et al. (2003)
227.7	0.913	
192.66	0.823	
201.46	0.838	
245.96	0.913	
188.22	0.823	
N/A	N/A	Felton et al. (2003)§
217	0.763¶	Morrogh-Bernard et al. (2003)
145	0.75¶	Russon et al. (2001)
N/A	N/A	Singleton (2000)
N/A	N/A	
242	0.76¶	Russon and Susilo (1999)
89.68	0.76	van Schaik et al. (1995)
187.72	0.76	
72.96	0.76	
N/A	N/A	Rijksen (1978)
507.71/602.49	**0.75¶/0.89#**	**TNC**

an area due to the poorly understood seasonal movements of orangutans (Singleton 2000, Buij et al. 2002). Examining only the presence or absence of nests in an area might not take into account the possibility that orangutans are present only part of the year, risking exclusion of critical orangutan habitat from conservation consideration.

While such indirect methods may aid in increasing overall understanding of orangutan distribution, they do not provide a quantitative estimate of population size, and are not sufficient in situations in which it is essential to have such an estimate. For example, there is an increasing need for wildlife managers to understand both population numbers and habitat carrying capacity when making decisions about reintroducing or translocating orangutans. Once orangutan distribution is better understood, more detailed and time-intensive surveys can be conducted in high-priority areas to make quantitative population estimates. Methods that do not employ nest decay time such as the marked nest count method (Plumptre and Cox 2006) may be more reliable for reasons outlined in this paper. The marked nest count method determines animal numbers by visiting study sites regularly and recording only the new nests that have appeared (van Schaik et al. 1995, Plumptre and Reynolds 1996). This technique requires a substantial time commitment, as a large sample size is needed for accuracy, and transects or plots have to be recounted within a period less than the minimum nest decay time (van Schaik et al. 2005), so there is still a need to establish minimum decay time. Recent studies have also demonstrated the potential of using helicopter aerial surveys for direct monitoring of distribution and estimating populations (Ancrenaz et al. 2005), as well as

the use of genetic research to monitor population trends (Goossens et al. 2005, 2006).

It should be noted that these alternative methods each have their own biases, flaws, and inaccuracies that may be just as serious as those present in nest monitoring. As the collective conservation community, we need to fully evaluate and develop such alternatives; a task beyond the scope of this paper. Whatever method is determined to be the most practical and reliable, it is critical that the methods used are uniform for comparison and the successful monitoring of orangutan populations and population trends (e.g., Morrogh-Bernard et al. 2003, Plumptre and Cox 2006).

Finally, considering the inaccuracy of all orangutan survey methods one wonders how useful such surveys are. The decay times from this study alone fluctuate by >20%, depending on what parameter estimation and correction factor are used. The annual changes in population density in areas where there is no major forest loss or hunting are unlikely to exceed a few percent, and given that present survey methods have large standard errors because of plug-in estimates, they are unlikely to reliably detect small changes in population size (Plumptre 2000). In areas where the main threats to orangutans, i.e., deforestation and hunting (Tilson et al. 1993, Rijksen and Meijaard 1999, Singleton et al. 2004), are high, monitoring those threats rather than their effect on population size will provide a good indirect measure of population change, and measuring the loss of orangutan habitat is much less difficult than measuring the change in population size. Thus, in terms of monitoring orangutan populations, we must strike a balance between approximate, threat-based monitoring methods and more detailed direct population counts. Finding this balance in a world where there is limited funding for conservation requires strategic choices between expensive and labor-intensive techniques vs. cheaper, indirect ones. The scientific and conservation community also needs to recognize that saving orangutans is ultimately a political choice. We need to provide the information that convinces politicians to take action, and such information may not necessarily be whether there are 1000 vs. 1050 orangutans in a particular area.

TABLE 6. A comparison of decay times among tree taxa between a site in Sabah, Malaysia (Kinabatangan) (Ancrenaz et al. 2004a) and East Kalimantan, Indonesia (Lesan).

	Decay time (d)	
Taxa	Kinabatangan†	Lesan‡
Dipterocarpaceae	205	636
Eusideroxylon	476	740
Myrtaceae	128	656
Sterculiaceae	135	602

† Decay time determined by direct observation.
‡ Decay time determined using Markov chain analysis and a correction factor of 0.89.

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APPENDIX

Taxonomic breakdown, decay times, wood durability, and local names of trees used for orangutan nesting in the Lesan Protected Area (*Ecological Archives* A018-006-A1).