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Estimating Orangutan Densities Using the Standing Crop and Marked Nest Count Methods: Lessons Learned for Conservation

Stephanie N. Spehar[1]

Anthropology, Department of Religious Studies and Anthropology, University of Wisconsin-Oshkosh, 800 Algoma Blvd., Oshkosh, Wisconsin 54901, U.S.A.

Paul D. Mathewson

Nelson Institute for Environmental Studies, University of Wisconsin-Madison, 550 N. Park Street, 70 Science Hall, Madison, Wisconsin 53706, U.S.A.

Nuzuar

Sumatran Orangutan Conservation Programme, Jl. K. H. Wahid Hasyim NO 51/74, Medan Baru, Medan 20154, Sumatera Utara, Indonesia

Serge A. Wich

Anthropological Institute and Museum, University of Zurich, 8057 Zurich, Switzerland
PanEco, Foundation for Sustainable Development and Intercultural Exchange, Berg am Irchel, Switzerland

Andrew J. Marshall

Department of Anthropology and Graduate Group in Ecology, University of California at Davis, One Shields Avenue, Davis, California 95616, U.S.A.

Hjalmar Kühl

Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany

Nardiyono

The Nature Conservancy, Indonesia Forest Program and Orangutan Conservation Services Program, Jalan Polantas No. 5, Markoni, Balikpapan, East Kalimantan, Indonesia

and

Erik Meijaard

People and Nature Consulting International, Kerobokan, Badung 80361, Bali, Indonesia
School of Archaeology and Anthropology, Building 14, Australian National University, Canberra, ACT 0200, Australia

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ABSTRACT

Reliable estimates of great ape abundance are needed to assess distribution, monitor population status, evaluate conservation tactics, and identify priority populations for conservation. Rather than using direct counts, surveyors often count ape nests. The standing crop nest count (SCNC) method converts the standing stock of nests into animal densities using a set of parameters, including nest decay rate. Nest decay rates vary greatly over space and time, and it takes months to calculate a site-specific value. The marked nest count (MNC) method circumvents this issue and only counts new nests produced during a defined period. We compared orangutan densities calculated by the two methods using data from studies in Sumatra and Kalimantan, Indonesia. We show how animal densities calculated using nest counts should be cautiously interpreted when used to make decisions about management or budget allocation. Even with site-specific decay rates, short studies using the SCNC method may not accurately reflect the current population unless conducted at a scale sufficient to include wide-ranging orangutan movement. Density estimates from short studies using the MNC method were affected by small sample sizes and by orangutan movement. To produce reliable results, the MNC method may require a similar amount of effort as the SCNC method. We suggest a reduced reliance on the traditional line transect surveys in favor of feasible alternative methods when absolute abundance numbers are not necessary or when site-specific nest decay rates are not known. Given funding constraints, aerial surveys, reconnaissance walks, and interview techniques may be more cost-effective means of accomplishing some survey goals.

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Key words: Borneo; density estimate; great ape; Indonesia; *Pongo*; population census; primate; Sumatra.

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[1]Corresponding author; e-mail: spehars@uwosh.edu

EXCEPTING HUMANS (*Homo sapiens*), the rest of the great apes—comprising gorillas (*Gorilla gorilla*, *Gorilla beringei*), chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), and orangutans (*Pongo abelii*, *Pongo pygmaeus*)—are considered endangered or critically endangered (IUCN 2009). Their populations are thought to have declined by more than 50 percent, and in some cases by as much as 90 percent, within the last 40 yr (Rijksen & Meijaard 1999, Walsh *et al.* 2003, Oates 2006, Campbell *et al.* 2008, Wich *et al.* 2008, IUCN 2009). These precipitous declines are caused by widespread deforestation and habitat fragmentation due to commercial logging, habitat conversion, hunting, and in some cases, forest fires, infectious disease, and the wildlife trade (Walsh *et al.* 2003, Bermejo *et al.* 2006, Hart *et al.* 2008, Wich *et al.* 2008). Immediate, large-scale conservation action is urgently needed to prevent further declines and possible extinction of remaining great ape populations.

Assessments of the population status of great apes, including distribution, abundance, and trends in absolute or relative abundance, are often used to inform conservation decisions. Density estimates can be particularly useful, as they can be used to assess the impact of particular threats, determine priority populations for conservation, and assess the effectiveness of enacted conservation measures (Kühl *et al.* 2008). It is notoriously difficult, however, to obtain accurate density estimates for great apes. They are elusive, often flee from surveyors, and their low densities make direct counts impractical for many studies (Plumptre & Reynolds 1996, 1997; Walsh & White 2005). Furthermore, their densities can fluctuate substantially, due to supra- and intra-annual variation in movement patterns, home range size, and grouping patterns (Buij *et al.* 2002, Poulsen & Clark 2004, Wich *et al.* 2004, Devos *et al.* 2008).

As direct counts are impractical for assessing great ape densities over large areas given the time and resource demands of such studies, indirect methods are overwhelmingly employed. The most common technique involves counting nests (Ghiglieri 1984, van Schaik *et al.* 1995, Plumptre 2000, Kühl *et al.* 2008). All great apes build nests made of branches, leaves, and other vegetation that can remain visible for weeks, months, or even years (Mathewson *et al.* 2008). Nests are counted using line transect techniques (Buckland *et al.* 2001, Thomas *et al.* 2010) and then ape densities are calculated by applying parameters that correct for nest construction and decay and for the proportion of the population that builds nests.

This technique, called the standing crop nest count (SCNC) method, has many advantages. Unlike apes themselves, nests are stationary and more easily detected. Additionally, as nests are generally long lasting (for orangutan nests, 200–400 d at most sites, but sometimes more, see Mathewson *et al.* 2008), SCNC methods integrate population densities over extended periods, providing a general estimate of ape abundance that is less sensitive to short-term fluctuations in population density. One obvious shortcoming is that the method will be unable to detect rapid population declines. Furthermore, the accuracy of SCNC population density estimates is largely dependent on the parameters used when converting nest counts to estimates of population density. These parameters are often difficult to estimate accurately without long-term study (Buij *et al.* 2003, Ancrenaz *et al.* 2004, Johnson *et al.* 2005, Mathewson *et al.* 2008). Each parameter carries an associated error, and the cumulative effect of combining these factors can lead to imprecise ape density estimates that are not easily comparable across sites (Plumptre 2000, Devos *et al.* 2008, Molyneaux 2008).

There is some variation in the proportion of nest builders and nest building rate between sites for all great apes (Buij *et al.* 2003, Morgan *et al.* 2006, Kühl *et al.* 2008); however, this variation is slight and has a proportionately small impact on resulting density estimates when compared with the variation in nest decay time. Nest decay time seems to be affected by a variety of factors (*e.g.*, plant species used in next construction and local climatic conditions), and varies by more than an order of magnitude across time and space (Tutin *et al.* 1995, Wich *et al.* 2004, Walsh & White 2005, Mathewson *et al.* 2008). Thus, the need for accurate local nest decay estimates is acute. This makes rapid population density assessments impractical for areas in which decay rates are unknown, as determining a reliable decay time for an area is labor-intensive and time-consuming, requiring regular surveys over at least 6 mo in the case of orangutans (Mathewson *et al.* 2008). Therefore, developing alternative methods that eliminate the need to use decay rates should be of high priority to ape researchers (Marshall & Meijaard 2009).

The marked nest count (MNC) method (Hashimoto 1995) circumvents the nest decay time variable by replacing it with a known parameter, the inter-survey period. This method entails conducting two surveys, separated by a period of time short enough to not allow newly built nests to decay within that time. All nests seen on the first survey are marked, and the second survey records new nests produced since the initial survey.

In addition to assumptions attendant to standard distance sampling (Buckland *et al.* 2001), the MNC method carries two additional assumptions: (1) no preexisting nests that were overlooked in the first survey are counted as new nests in subsequent studies and (2) no nests are built and completely decay during the inter-survey period.

The MNC method has been used to estimate densities of chimpanzees (Hashimoto 1995, Plumptre & Reynolds 1996, Furuichi *et al.* 2001, Plumptre & Cox 2006, Devos *et al.* 2008), gorillas (Kühl *et al.* 2007, Devos *et al.* 2008), and orangutans (Singleton 2000, Buij *et al.* 2003) and to study seasonal shifts in forest use by orangutans (Buij *et al.* 2002). In this paper, we examine this method using data gathered from long-term orangutan nest monitoring studies at a site in Borneo and in Sumatra, and compare these results with those obtained using the SCNC method. We discuss the implications of our findings for using nest surveys as part of orangutan conservation programs and evaluate the proper role of these methods, as well as alternatives, given specific conservation objectives.

METHODS

STUDY SITES.—The Ketambe research area (3°41′ N, 97°39′ E; Fig. S1A) is located in Gunung Leuser National Park, Sumatra, Indonesia, with an elevational range of 320–1000 m asl. Orangutan research started in 1971 and continues until today with a 1-yr break in most research activities in 2002–2003. The study area consists of primary mixed dryland rain forest and some alluvial forests poor in dipterocarps along the Ketambe and Alas rivers (Rijksen 1978, van Schaik & Mirmanto 1985). The site experiences two wetter and two drier periods per year and has a mean annual rainfall of 3288 mm (Wich & van Schaik 2000). The three transects used for this study had a combined length of 6.24 km and are a subset of transects used in a previous study (see Buij *et al.* 2002).

The Lesan protected area is a Nature Conservancy (TNC)-facilitated conservation area in East Kalimantan, Indonesia (1°36′ N, 117°10′ E; mean elevation 75 m asl; Fig. S1B). This site is a former logging concession (selective timber extraction ceased 6 yr before the study) and consists of 115 km^2 of mixed primary and logged forest in a much larger selectively logged and partially clearcut forest landscape. The unlogged lowland forest portion of the site is a mix of dipterocarp forest and heath forest. The average annual rainfall over the past 20 yr at a weather station 75 km from the study area is 2085 mm (F. Buschman, pers. comm.). Nine parallel line transects, each 4-km long and separated by *ca* 500 m, were established for the study (Mathewson *et al.* 2008). See Appendix S1 and Fig. S2 for an evaluation of transect length and coverage in this study.

NEST SURVEYS.—Nest monitoring was conducted during January 2003–November 2004 (Ketambe) and February 2005–September 2006 (Lesan). Teams of extensively trained and experienced observers conducted the nest surveys along line transects. These teams were able to distinguish between orangutan nests and those made by other species (*e.g.*, squirrels *Ratufa* sp. and sun bears *Helarctos malayanus*) due to observable differences in nest construction, nest size, and/or other accompanying sign (*e.g.*, claw marks on trees made by sun bears). Nest locations were marked along the transect or on a map so that old and new nests could be differentiated on future surveys. The teams re-surveyed each transect monthly (except July 2005 at Lesan), assessing the decay stage of each nest, and recording new nests. Nest decay at Lesan was measured in a five-class system: (A) fresh, leaves still green; (B) fairly fresh, mix of green and brown leaves; (C) nest is brown but remains intact; (D) leaves missing and holes appearing in nest; and (E) leaves are gone, only branch structure of nest remains. Ketambe used a four-class system in which classes (A) and (B) from the five-class system used at Lesan were combined.

CALCULATING DENSITY ESTIMATES.—Orangutan density estimates calculated using the SCNC method used the following equation to convert nest counts to ape density: $\hat{D}_{\mathrm{ind}} = N/(2\mu L\hat{p}\hat{r}\hat{t})$, where $\hat{D}_{\mathrm{ind}}$ is the density of individuals, N is the number of nests observed along the transect, μ is the effective strip width of the transect, L is the transect length, $\hat{p}$ is the proportion of nest builders in the population, $\hat{r}$ is the nests built per individual per day, and $\hat{t}$ is the nest decay time (Ghiglieri 1984).

When using the MNC method, nest counts were converted to ape densities using the following equation: $\hat{D}_{\mathrm{ind}} = N_{\mathrm{newnest}}/(2\mu L\hat{p}\hat{r}i)$, where N_{newnest} is the number of nests built during the inter-survey period and i is the inter-survey period. Other parameters are the same as in the SCNC equation (Hashimoto 1995).

We calculated orangutan density estimates separately for each month using the MNC and SCNC methods. We also pooled new nest counts from all months to obtain an overall orangutan density estimate using the MNC method. We then calculated orangutan density estimates with the SCNC method using three nest counts: (1) the standing stock of nests at the first survey; (2) the standing stock at the last survey; and (3) the average standing stock of nests from all surveys.

PARAMETER ESTIMATION.—Parameters used are listed in Table 1. Nest decay (t) was calculated for Ketambe using a Kaplan–Meier survival analysis (Husson *et al.* 2009, S. A. Wich, unpubl. data). At Lesan, most nests were not decayed by the end of the study, so survival probability on day j at Lesan was calculated using a Markov model approach: $p_j = \prod_{j=1}^{j=n} \frac{1}{1+e^{-p_s}}$, where j is time in number of days from nest construction (j = 1) to decay (j = n), and p_s is the estimated parameter. After estimating p_s we then calculated mean decay time by integrating over 1000 d. We then used bootstrapping to derive 95% confidence intervals (CIs).

This method allows the use of nests that have not decayed completely by the end of the study, but does require that only nests found in the freshest decay stage be included. At Lesan, 88 nests were found in stage A and these were the only nests used in the decay time estimation used here. The mean decay time (603.7 d) was essentially the same as that estimated using a Markov chain analysis that used of nests not found in the freshest decay stage (corrected estimate = 602.5 d, N = 663 nests; Mathewson *et al.* 2008).

The effective strip width (μ) at the sites was calculated using DISTANCE 4.1 (Thomas *et al.* 2004) by pooling all nests found during the respective studies. Models were selected following Buij *et al.* (2003). This value was used in every density calculation rather than calculating separate values for each survey. Given the small number of new nests found in 1 mo, strip width calculations based on single months would be subject to considerable sampling error. At each site, the same survey team was used throughout the study, and we have no reason to believe that their ability to detect nests varied between months. The same overall site-specific nest decay parameter ($\hat{t}$) was used in all population density calculations using the SCNC method at the respective sites.

QUANTIFYING ORANGUTAN DENSITY ESTIMATE PRECISION.—We used the delta method to calculate the coefficient of variation (CV) and CIs for our orangutan density estimates. The delta method accounts for variation in nest counts and parameters $\hat{p}$, $\hat{r}$, and $\hat{t}$ to obtain the CV for orangutan density $\hat{D}$: $\left[cv(\hat{D})\right]^2 = [cv(N)]^2 + [cv(\hat{p})]^2 + [cv(\hat{r})]^2 + [cv(\hat{t})]^2$.

The CV for nest encounter is given by DISTANCE 4.1 and includes the probability density function evaluated at distance 0. This CV was based on the analysis of all nests found during the course of the respective studies and was used for all estimates. This was done for consistency because many monthly new nest counts were too low to reliably calculate a separate CV. The CVs for $\hat{p}$ and $\hat{r}$ were calculated based on island-specific studies of these parameters. On Sumatra, the two studies reporting $\hat{p}$ values both report values of 0.9 (van Schaik *et al.* 1995, Singleton 2000),

TABLE 1. *Parameters used in orangutan density calculations.*

	Ketambe		Lesan	
Parameter	Value	Notes	Value	Notes
Total transect length (L, km)	6.24		36	
Effective strip width (μ, m); (SD)	30.1 (25.4–35.6)	Pooled survey data analyzed in DISTANCE 4.1 using the half-normal with hermite expansion model, 7.5 m intervals, and 45 m cut-off	9.27 (8.77–9.80)	Pooled survey data analyzed in DISTANCE 4.1 using the half-normal with hermite expansion model and 9 m intervals
Proportion of nest builders ($\hat{p}$)	0.9	Average value for Sumatran populations (van Schaik *et al.* 1995, Singleton 2000)	0.88	Average value for Bornean populations (Ancrenaz *et al.* 2004, Johnson *et al.* 2005, van Schaik *et al.* 2005; H. C. Morrogh-Bernard, unpubl. data, in Husson *et al.* 2009)
Daily nest-building rate ($\hat{r}$, number of nests per day per individual)	1.7	Ketambe-specific value (van Schaik *et al.* 1995)	1.12	Average rate for Bornean populations (Ancrenaz *et al.* 2004, Johnson *et al.* 2005, van Schaik *et al.* 2005; H. C. Morrogh-Bernard, unpubl. data, in Husson *et al.* 2009)
Nest decay time ($\hat{t}$, d)	180 (158–202)	Calculated using a Kaplan–Meier survival analysis	604 (469–793)	Calculated using a Markov model

and there is a single site-specific $\hat{r}$ value for Ketambe (van Schaik *et al.* 1995). Thus, the CV for both $\hat{p}$ and $\hat{r}$ is 0 in the Ketambe calculations. CVs for $\hat{t}$ were calculated using site-specific nest decay data. The CV for orangutan estimates using the MNC method was calculated in the same way, but without the inclusion of decay time variance. These CVs were then used to calculate 95% CIs for our orangutan density estimates following Ancrenaz *et al.* (2004, equations 3–4).

RESULTS

At Lesan, there was a large drop in the number of new nests found after the second month of the study (Table S1). It is possible that some of the new nests found during that survey ($N = 33$) represent nests that were missed on the initial survey but found in the subsequent survey after they had progressed to a later decay state and were easier to spot. All but one of these nests, however, were in the two freshest decay stages. While the one older nest may have been missed during the initial survey, the remaining nests were likely new nests built after the initial survey, because only one nest in the entire study ($N = 810$) was observed to remain in either of the two freshest decay stages for more than 1 mo.

Monthly orangutan density estimates calculated using the MNC method and the SCNC method are presented in Figures 1A and B. The Lesan data show a clear discrepancy between the densities calculated using the two methods (Spearman's rank correlation, $N = 18$ mo, $r = 0.13$, $P = 0.59$). The MNC and SCNC methods are well correlated throughout the Ketambe study (Spearman's rank correlation, $N = 22$, $r = 0.57$, $P < 0.01$). As the sample size of new nests in a single month was quite small, we pooled the nest count data into 3 mo sets ($N = 7$) and 6 mo sets ($N = 3$) to minimize the effect of sample size and more clearly examine temporal variation in density estimates obtained using the MNC method (Table 2). The pooled 6-mo datasets at Lesan show up to a twofold difference in density estimates. At Ketambe, with much larger sample sizes, the 6-mo pooled data still produced density estimates differing by close to 20 percent between the first and the last 6 mo of the study.

SCNC-calculated densities based on a single survey at the beginning and end of the study differed significantly at Ketambe, but not at Lesan. The density estimate calculated using the MNC method pooled across all months was significantly lower than the average SCNC estimate at Lesan, but not at Ketambe (Table 3).

DISCUSSION

This study highlights the strengths and weaknesses of the MNC and SCNC methods, as well as the difficulties of meeting some methodological assumptions. Furthermore, three primary lessons emerged: (1) utilizing transects at the appropriate spatial scale is crucial for effective use of traditional line transects for orangutan surveys; (2) despite avoiding the issue of calculating decay time, MNCs may not require substantially less time and effort than SCNC methods; and (3) depending on the research question, alternative methods may be appropriate, cost-effective options.

EXAMINING THE ASSUMPTIONS OF THE MNC METHOD.—The assumption that no preexisting nests, overlooked during the first survey, are counted as new nests in subsequent studies, can be a concern, particularly for inexperienced surveyors. Re-survey data from other sites indicate that even experienced observers can miss 12–24 percent of nests visible from a transect (Johnson *et al.* 2005, van Schaik *et al.* 2005, Marshall *et al.* 2006). Re-survey data from Ketambe,

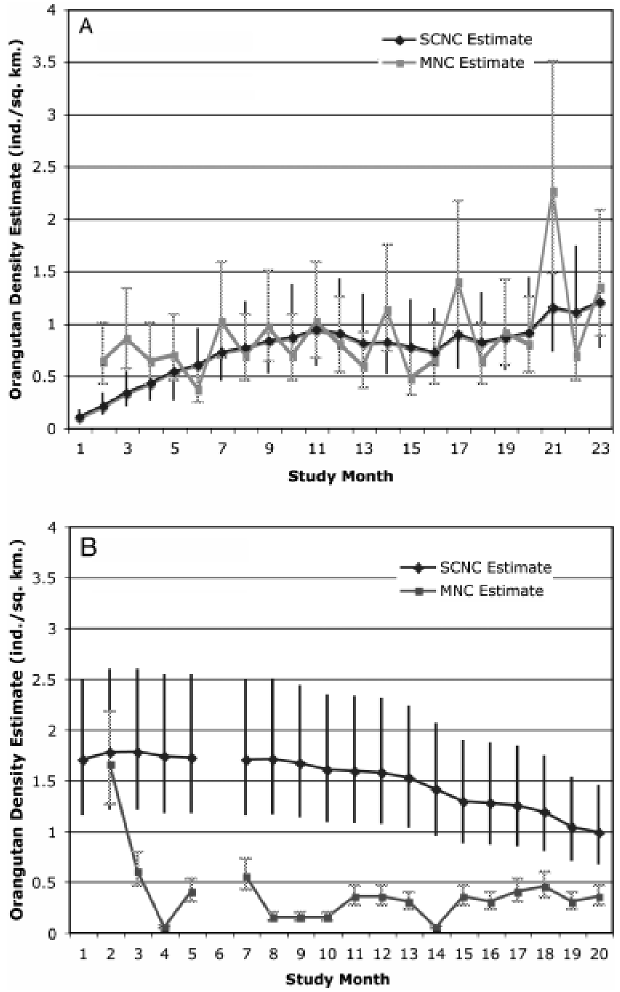

FIGURE 1. Monthly orangutan density estimates (individual/km^2), with 95% CI, calculated using the standing crop nest count method (SCNC) and the marked nest count method (MNC) at (A) Ketambe, Indonesia and (B) Lesan, Indonesia. No data were collected in study month 6 (July 2005).

TABLE 2. *New nest data pooled into 3- and 6-mo groups to obtain a sufficient sample size, and the calculated orangutan density estimate using the marked nest count method.*

Months pooled	Ketambe		Lesan	
	New nests	Density (95% CI)	New nests	Density (95% CI)
2–4	40	0.72 (0.46–1.11)	46	0.77 (0.59–1.01)
5–7	39	0.70 (0.46–1.08)	19	0.32 (0.24–0.42)
8–10	44	0.79 (0.51–1.22)	9	0.15 (0.11–0.20)
11–13	45	0.81 (0.53–1.25)	20	0.33 (0.25–0.44)
14–16	42	0.76 (0.49–1.17)	14	0.23 (0.18–0.31)
17–19	55	0.99 (0.64–1.52)	23	0.38 (0.29–0.50)
20–22	70	1.26 (0.81–1.94)	—	—
2–7	79	0.71 (0.46–1.09)	65	0.54 (0.41–0.71)
8–13	89	0.80 (0.52–1.24)	29	0.24 (0.18–0.32)
14–19	97	0.87 (0.57–1.35)	37	0.31 (0.24–0.41)

however, indicate that the survey team only missed 1–2 percent of visible nests (S. A. Wich, unpubl. data). At Lesan, all but one of the nests found in the second survey were in the two freshest decay stages. It was not until the 15th survey that any other new nests not in the freshest decay stages were discovered, making it improbable that these nests were present at the initial survey.

The validity of the assumption that no nests were built and disappeared between surveys is difficult to assess; however, the error associated with violating this assumption is likely much smaller than error associated with nest decay rates. Orangutan nests are generally longer lasting than chimpanzee or gorilla nests, and the number of nests that are built and decay within a month is likely quite low. At Lesan, < 1 percent of nests in any stage disappeared in the month following their discovery. The effect of violating this assumption, while still low, is likely to be greater in areas with faster nest decay times. At Ketambe, where the average nest decay time is a quarter of the Lesan decay time, 5.8 percent of nests disappeared within a month.

COMPARISON OF NEST COUNT METHODS.—The primary difference between the two methods examined is their temporal scope. Density estimates calculated using the MNC method reflect current orangutan abundance. The method is sensitive to both density increases and decreases, making it well suited to mapping animal movement within an area or charting seasonal habitat use (Buij *et al.* 2002, Devos *et al.* 2008). Density estimates obtained using the MNC method, however, represent only a snapshot in time. Orangutans can range widely at certain times of the year (Rijksen & Meijaard 1999) and can have very large home ranges (Singleton & van Schaik 2001, Singleton *et al.* 2009), hence either repeated surveys or surveys covering these large areas are needed to account for this movement when estimating an area's average orangutan density.

The SCNC method is able to integrate abundance over a longer period of time, using information from the past in the form of old nests, which provides a better overall indication of an area's average orangutan density. This affects the method's ability to reliably capture an area's current population. The SCNC method will be slow to detect population declines, particularly in areas with long nest decay times, as evidence of a population decline will be masked by the nests remaining from the previous, larger population. This is illustrated by the Lesan data, which indicate that there was a larger population before this study than was present during the study itself. A previous population estimate at Lesan

TABLE 3. *Comparing orangutan density estimates (individual/km^2) calculated using the standing crop nest count (SCNC) and marked nest count (MNC) methods (with 95% CI). We used three nest counts extracted from the studies to calculate estimates using the SCNC method: (1) the standing stock of nests at the first survey; (2) the standing stock at the last survey; and (3) the average monthly standing stock of nests from all surveys.*

	Ketambe		Lesan	
	Nest density	OU density	Nest density	OU density
MNC overall pooled[a]	943	0.89	207	0.38
	(811–1136)	(0.57–1.36)	(196–219)	(0.29–0.50)
SCNC first month	31.4	0.11	1007	1.70
	(27.0–37.9)	(0.07–0.17)	(952–1064)	(1.16–2.47)
SCNC last month	346	1.21	584	0.98
	(297–416)	(0.77–1.89)	(553–618)	(0.68–1.44)
SCNC average month	216	0.76	888	1.50
	(186–261)	(0.48–1.18)	(840–939)	(1.03–2.18)

[a]Nest density in this row refers to new nest density.

used the nest density from the first survey to calculate the orangutan density (Mathewson *et al.* 2008). New nests were not built at a rate fast enough to maintain a steady standing stock throughout the study. The effect of the area's exceptional nest duration was such that even after 20 mo, the standing stock had not been reduced to a level that reflected the current orangutan population suggested by the MNC method (Fig. 1B). While the SCNC method may be slow to detect a population decline, the Ketambe data show that the method can be sensitive to a population increase (Fig. 1A).

LESSON 1: UTILIZING TRANSECTS ON THE APPROPRIATE SPATIAL SCALE IS CRUCIAL FOR EFFECTIVE USE OF TRADITIONAL LINE TRANSECTS.—This study highlights the importance of carrying out line transect nest surveys at an appropriate scale to capture wide-ranging orangutan movement. A single survey of the standing stock at Ketambe in study month 1 would indicate a low-density orangutan population, while one in study month 23 would show a high-density population. Although the SCNC density estimates at Lesan in the first and last months do not differ significantly, they do indicate a downward trend in orangutan density at the site over the course of the study. This trend becomes clearer when combined with evidence suggesting that long-lasting nests can mask recent changes in orangutan density at Lesan (above). The unidirectional trends shown by the density estimates at both sites suggest large-scale movements by orangutans, inconsistent with yearly fluctuation in fruit availability that has been reported at sites like Ketambe (Buij *et al.* 2002). Supra-annual fruiting events at the community level (mast-fruiting) could perhaps be a factor involved in such large density fluctuation, although no such events were recorded during either study. At Lesan, the high density before the present study could have been the result of temporary compression effects from logging and other land conversion in surrounding areas (Marshall *et al.* 2006). At Ketambe, the density fluctuation might also be influenced by changes in the number of reproductive females in the area and the low numbers of males in the area during certain periods (Wich *et al.* 2006, S. A. Wich, unpubl. data).

Thus, while both sites were sampled sufficiently to avoid clumping effects resulting from unevenly distributed animal signs (Fig. S2), the sampling was not extensive enough to account for wide-ranging orangutan movement. To obtain reliable population density results when using line transects to conduct nest counts, researchers must be sure that transect placement can capture this large-scale movement. This is a daunting task considering that males can have home ranges up to 10,000 ha (Singleton & van Schaik 2001).

LESSON 2: DESPITE AVOIDING THE ISSUE OF CALCULATING DECAY TIME, MNCS MAY NOT REQUIRE LESS TIME AND EFFORT THAN THE SCNC METHOD.—The presumed reduction in time and resource investment required to obtain a reliable decay time is a principal justification for replacing the SCNC method with the MNC method (Hashimoto 1995). Our data, however, show that a substantial investment is still needed to obtain reliable density estimates using the MNC method. This is illustrated by the large inter-month variation in density estimates found in this study. This variation is likely caused by a combination of orangutan movement and sampling error resulting from small numbers of new nests found in a given month. The relative importance of these two sources of variation is unknown. Plumptre *et al.* (2003) recommended a minimum sample size of approximately 50 nests for a robust density estimate using the MNC method. For orangutans, which live at low densities, finding 50 new nests in a single survey at many sites would require a substantial survey effort. At a site like Lesan, this would require $>$ 200 km of transects (Table S2).

Even when a sufficient number of new nests are found in a single survey, relying on such an estimate would assume a steady population density in the survey area. This may not be a valid assumption. After pooling the MNC data into 6-mo intervals to obtain sufficient sample sizes, we still found up to a twofold variation in orangutan density estimates between intervals. This variation likely reflects the orangutan movement discussed earlier. Thus, a density estimate obtained from a short-term study using the MNC method is still subject to substantial error due to localized density fluctuations unless one is able to effectively sample the entire range of the study population, which can be a challenging undertaking, as explained above.

The MNC method may provide a more reliable means of monitoring population densities than the SCNC method, as nest decay time calculated from one crop of nests may not be uniformly applicable to nest counts at a site over time due to the effect of variable climactic conditions on decay times (Plumptre *et al.* 2003, Walsh & White 2005). Therefore, we recommend that where a long-term monitoring program can be established using a capable team, a combination of nest count methods be used to maximize the value of invested resources. When a reliable nest decay time can be calculated, the SCNC method can be applied to the initial standing crop of nests to effectively extend the study for a period of time equal to the average nest decay duration. This would also contribute to the body of knowledge about nest decay rates, which could be used to improve SCNC methodology.

Lesson 3: Depending on the research question, alternative methods may be appropriate, cost-effective options.—While line transect methodology is currently the standard ape survey method (Kühl *et al.* 2008), our understanding of the methodology, and its limitations, has greatly improved in recent years. It has become clear that short-term line transect surveys have limited ability to produce reliable density estimates (present study, Mathewson *et al.* 2008), while still requiring relatively high effort and costs.

The cumulative variability of all the parameters used to calculate orangutan densities for both the SCNC and MNC methods results in orangutan density estimates with wide CIs (Figs. 1A and B). The imprecision of these estimates makes it difficult to detect changes in orangutan density. For example, there is no significant difference between the orangutan density estimate calculated for Lesan using the SCNC method in the first and last months, despite a > 40 percent decline in the point estimate. This suggests that traditional nest count methods may not provide a large enough advantage over possible alternatives to warrant the extra expenditure necessary to carry out the studies.

Imminent threats and the limited funding available for orangutan conservation necessitate a methodology that can rapidly assess large areas with minimal resource expenditure. In Borneo alone there are approximately 300 distinct orangutan populations (Wich *et al.* 2008) dispersed over 130,919 km^2 as of 2004 (Meijaard & Wich 2007). Given budgetary constraints and the investment generally required to obtain reliable results using traditional nest count methods, only a small portion of this area or a small number of these populations could be effectively surveyed and monitored using these methods.

Furthermore, accurate density estimates, and, by extension, standard line transect methodology, may not always be necessary, depending on the goals of a given survey. In some circumstances absolute abundance numbers will be needed (*e.g.*, conducting population viability analyses and providing a population census to gain political support for a conservation project). Currently, traditional line transects are still the best available method for this purpose, provided that site-specific nest decay rates are available. For other questions (*e.g.*, searching for potentially viable populations in need of conservation attention) where information on absolute abundance is not required, nest counts using standard line transects may not be necessary or the most efficient use of limited funds, particularly given their lack of precision. Alternative methods may be able to accomplish the same task at a fraction of the cost while also providing more extensive spatial coverage (Table 4).

CONCLUSION

We believe that use of a suite of currently available survey methodologies could more efficiently accomplish some orangutan survey goals than the continued sole reliance on, and preference for, traditional nest count methods. Careful selection and implementation of alternative survey methods may allow conservationists to allocate more of their limited resources toward the ultimate goal of reducing or eliminating threats to orangutan survival.

Aerial nest surveys or reconnaissance walks combined with interview-based methods are promising for gathering information on distribution and relative abundance over large areas and identifying potentially viable populations in need of conservation attention. Interview-based methods have the added benefit of contributing important information about hunting pressure, habitat loss, and local attitudes toward conservation.

Once potentially viable populations are identified, long-term monitoring of the highest priority populations should be undertaken to provide information on absolute abundance and population trends. Traditional nest surveys, if conducted at a proper scale, are still the best methods available for this purpose. Such monitoring programs should also include a research component dedicated to developing a better understanding of issues affecting nest count method accuracy, including nest detection problems, determinants of nest decay rates, and variation in nest building and reuse rates between populations. It is important that researchers continue to publish nest density estimates in addition to animal density estimates so that it is possible to compare estimates between sites and to re-evaluate population estimates using updated information.

Finally, we note that there can be considerable time lags between when a population is initially affected and detection of resultant declines, so population monitoring is not an alternative to enforcement (Marshall *et al.* 2009). Directly monitoring threats to orangutans, which can be accomplished in part using interview-based methods, and immediately enacting measures to mitigate or eliminate these threats, is perhaps more important to orangutan conservation than monitoring orangutan populations themselves (*cf.* Chades *et al.* 2008).

TABLE 4. *Strengths and weaknesses of alternative orangutan survey methods given different study objectives.*

Objective of study	Method	Advantages	Disadvantages	Comments
Obtaining distribution and absolute densities over large areas Obtaining estimates of relative population densities over large areas Obtaining distribution and relative abundance estimates Determining distribution and absolute densities over large areas	Aerial surveys Reconnaissance surveys or recce walks Interview-based methods	Aerial counts are significantly correlated to orangutan densities estimated by ground surveys (Ancrenaz *et al.* 2005), and if feasible, could be a cost-efficient means of surveying large areas Less effort required than line transects done on foot because it does not require establishing transect systems or measuring perpendicular distances Allows rapid surveys of much larger areas at a fraction of the cost of traditional line transect methods Can provide information, about not only animal density but other information that is equally important to conserving orangutans (*e.g.*, the intensity of local threats like hunting and habitat conversion, and human attitudes toward orangutans)	Has the same problems of converting nest counts to orangutan numbers as nest counts done through ground line transects Currently lacks the nest detection precision of ground surveys Unable to provide absolute density estimates Still requires much effort to conduct walks over large areas Human surveys are potentially unreliable in terms of providing an accurate density estimate (*cf.* Marchesi *et al.* 1995)	In a study by Ancrenaz *et al.* (2005), surveys from helicopters flying at 70 km/h covered 27.2 km of aerial lines per 'surveyor day' (effectively surveying 1.8–16.9 percent of the total forest area). In contrast, ground surveys covered only 0.5 km of line transects or recce walks per 'surveyor day' (effectively surveying 0.001–1 percent of the total forest area) Further reading: Payne (1987); Ancrenaz *et al.* (2004, 2005) Encounter rates from reconnaissance walks are well correlated with density estimates based on line transects for apes in Africa (Plumptre & Cox 2006) Further reading: Walsh and White (2005), Plumptre and Cox (2006) One method yielded density estimates comparable with those obtained through traditional transect techniques for some tropical forest species, including gorillas and chimpanzees (van der Hoeven *et al.* 2004) Integrated methods like these surveys are especially useful because the interviews can provide multi-dimensional information and may represent an appropriate compromise between seeking accurate estimates and using limited funds to accomplish conservation goals Further reading: van der Hoeven *et al.* (2004)

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Monthly standing crop of nests and new nests throughout the study periods at Ketambe and Lesan, Indonesia.*

TABLE S2. *Sampling effort (km) needed to find a minimum of 50 new nests in a single survey, assuming stable orangutan density in the area.*

FIGURE S1. (A) Ketambe study area site map and (B) Lesan study area site map.

FIGURE S2. Cumulative number of nests sighted per 100 m of transect at Lesan during the second survey.

APPENDIX S1. Evaluating transect length.

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