

Comparing spatial capture–recapture modeling and nest count methods to estimate orangutan densities in the Wehea Forest, East Kalimantan, Indonesia



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ABSTRACT

Accurate information on the density and abundance of animal populations is essential for understanding species' ecology and for conservation planning, but is difficult to obtain. The endangered orangutan (*Pongo* spp.) is an example; due to its elusive behavior and low densities, researchers have relied on methods that convert nest counts to orangutan densities and require substantial effort for reliable results. Camera trapping and spatial capture–recapture (SCR) models could provide an alternative but have not been used for primates. We compared density estimates calculated using the two methods for orangutans in the Wehea Forest, East Kalimantan, Indonesia. Camera trapping/SCR modeling produced a density estimate of 0.16 ± 0.09 – 0.29 indiv/km², and nest counts produced a density estimate of 1.05 ± 0.18 – 6.01 indiv/km². The large confidence interval of the nest count estimate is probably due to high variance in nest encounter rates, indicating the need for larger sample size and the substantial effort required to produce reliable results using this method. The SCR estimate produced a very low density estimate and had a narrower but still fairly wide confidence interval. This was likely due to unmodeled heterogeneity and small sample size, specifically a low number of individual captures and recaptures. We propose methodological fixes that could address these issues and improve precision. A comparison of the overall costs and benefits of the two methods suggests that camera trapping/SCR modeling can potentially be a useful tool for assessing the densities of orangutans and other elusive primates, and warrant further investigation to determine broad applicability and methodological adjustments needed.

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1. Introduction

Accurate information on the density and abundance of animal populations is essential to answering central questions in ecology and conservation biology. Such information allows us to test hypotheses about the relationship between environmental variables and abundance, expanding our understanding of the ecological factors that limit populations. It is also crucial for effective conservation planning, as such information can be used to assess threats to populations and species, set conservation priorities, and monitor populations (Seber, 1982; Williams et al., 2002; Borchers et al., 2003). However, obtaining accurate density and abundance estimates is challenging, especially for animals that are elusive, range widely, and live at low densities (Garshelis, 1992; Karanth, 1995; Thompson, 2004).

This is clearly illustrated in the case of the orangutan. Orangutans, the only Asian great ape, exhibit considerable geographic variation in ecology, behavior, and morphology (Wich et al., 2009). Their population densities also vary widely across their range, with Sumatran orangutans (*Pongo abelii*) generally exhibiting higher densities than Bornean orangutans (represented by the Northwest subspecies, *Pongo pygmaeus pygmaeus*; Central subspecies, *Pongo pygmaeus wurmbii*; and Northeast subspecies, *Pongo pygmaeus morio*) (Husson et al., 2009; Marshall et al., 2009a). Accurate information on orangutan densities across their geographic range, especially for the little-known Northeast Bornean orangutan (*P.p. morio*), is necessary if we are to fully understand the ecological factors that limit orangutan populations (Marshall et al., 2009a,b; Wich et al., 2011a). Information on orangutan abundance and density is also crucial for orangutan conservation. Both orangutan species are classified by the IUCN as endangered; the population of the Bornean orangutan has declined over 50% in the last 60 years and the Sumatran orangutan population has declined an estimated 80% over the last 75 years (Ancrenaz et al., 2008; Singleton et al., 2008).

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The causes of this decline are extensive habitat loss and fragmentation due to logging, mining, the expansion of oil palm and acacia plantations, and fire (Marshall et al., 2006; Wich et al., 2011b; Meijaard et al., 2012), and forest conversion continues at a rapid rate on both Borneo and Sumatra (Sodhi et al., 2004; Margono et al., 2014). Hunting, and, increasingly, human–orangutan conflict are also major contributors to this decline (Meijaard et al., 2011; Davis et al., 2013). Conservation action is urgently needed to prevent further population declines, and knowledge of densities and abundance are important for implementing effective conservation policy.

However, it is notoriously difficult to obtain accurate abundance or density estimates for orangutans. They are cryptic, solitary, and generally live at low densities, making direct counts impractical for most studies. Because of these difficulties, researchers generally rely on counts of indirect sign to census their populations (Kühl et al., 2008). To-date the most popular survey method for orangutans are nest count methods, in which the sleeping platforms (nests) that orangutans build each night are used to calculate a density of individuals in an area. In the most popular version of these methods, all nests visible from a line transect or in a plot are counted; nest counts are then converted into nest densities by dividing the number of nests counted by the area surveyed, which is either known (plot surveys; van Schaik et al., 2005) or estimated using a detection function (line transects surveyed using distance sampling methods; Buckland et al., 2001; Thomas et al., 2010). Nest densities are then converted into orangutan density estimates using the following formula:

$$D_{ind} = D_{nest} / p * r * t$$

in which D_{ind} = density of individuals, D_{nest} = density of nests, p = proportion of nest builders in the population, r = number of nests built per individual per day, and t = nest decay time (Hashimoto, 1995; van Schaik et al., 1995).

Nest count methods have been used extensively to assess or monitor orangutan populations (Husson et al., 2009). However, these methods have limitations (Mathewson et al., 2008; Marshall and Meijaard, 2009; Spehar et al., 2010). First, these methods rely on the assumption of perfect detection (in the case of line transects, that all nests above the line are counted; in the case of plot surveys, that all nests in the plot are counted) although studies demonstrate that even teams of experienced observers miss nests (van Schaik et al., 1995, 2005; Johnson et al., 2005). Another major issue lies in the parameters used to convert nest density into orangutan density (p , r , and t). 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, and nest decay rate (t) must also be based on observations of nest longevity in an area, although mathematical modeling (Markov chain analysis) can be used to calculate nest decay from shorter-term observations (Buij et al., 2003; Johnson et al., 2005; Mathewson et al., 2008). Obtaining accurate information for these parameters requires substantial time and effort, so values calculated from a few long-term study sites are often applied in studies across the orangutan range. This can be a concern as some parameters (in particular nest decay, t) exhibit very high variability between sites (Mathewson et al., 2008). As any changes in parameters produce directly proportional changes in the resulting orangutan density estimate, this means that density estimates that do not use precise or locally calculated parameters could be unreliable (Mathewson et al., 2008). Such issues clearly have major implications for our understanding of orangutan ecology and for conservation planning, and finding an alternative to nest surveys should be a high priority. However most studies still calculate densities based on nest surveys, and many of these continue to employ non-local parameters due to limited time and money (Spehar et al., 2010; Meijaard et al., 2012).

A possible alternative for estimating abundance and density are camera trap methods. Camera trapping is becoming a preferred method for studying rare and elusive species (e.g., O'Connell et al., 2010). Recent

advances in statistical techniques, namely spatial capture–recapture modeling or SCR (Borchers and Efford, 2008; Royle and Young, 2008; Efford, 2011; Royle et al., 2013, 2015), allow the calculation of population density from ‘captures’ of individual animals obtained using camera traps. SCR models have an advantage over conventional capture–recapture (CR) models in that they allow for flexible trap arrangement (e.g., grid vs. linear arrangements that do not require even spacing across the study area; Efford and Fewster, 2013; Tobler and Powell, 2013) and can incorporate both individual-level covariates (e.g., sex or age class) as well as station level covariates (e.g., road vs. trail or habitat; Sollmann et al., 2011). This type of flexibility is especially important in Borneo and Sumatra, where field conditions like difficult terrain can make research design a challenge.

SCR modeling relates the encounter history of individuals (when and where they are captured) to activity centers of individuals during the trapping period (calculated as the spatial relationship between individuals and camera traps). Density is estimated as number of individuals occurring within some delineated area (the “state-space”), usually defined by the camera trapping array plus a buffer area (Royle and Gardner, 2011). SCR modeling has now been used to estimate densities for many mammals that are elusive, occur at low densities, and occupy large home ranges (Royle et al., 2009a,b, 2011; Gardner et al., 2010a,b). These methods count the animals themselves and thus do not present problems related to converting indirect sign into animal densities. In addition, if deployed properly camera traps can also provide additional information about habitat use, behavior, and even demography (e.g., Galvis et al., 2014).

Despite its promise and wide application in wildlife studies, camera trapping has only recently been embraced by primatologists (Head et al., 2012; Olson et al., 2012; Tan et al., 2013; Loken et al., 2013, 2015; Galvis et al., 2014; Gregory et al., 2014). Most notably, a recent study simultaneously used nest surveys and camera trapping to estimate the relative abundance and distribution of chimpanzees (*Pan troglodytes troglodytes*) and gorillas (*Gorilla gorilla gorilla*) across different habitat types in West Africa, and found that the two methods produced roughly comparable results (Nakashima et al., 2013). However, this study was only able to use mean camera trap capture rate to calculate a relative abundance index for each species. The “next step” that would allow the calculation of absolute abundance and density is the use of new statistical techniques like SCR modeling, which have not yet been applied to primate populations. For camera traps to be used to estimate abundance and population density using SCR modeling or similar techniques, animals must be individually identifiable from photographs and individuals need to be captured and recaptured by camera traps, which are most easily placed on the ground. These criteria may be difficult to meet for some primates, but recent research suggests that this method may be appropriate for use with orangutans. Orangutans do not have unique stripe patterns or markings, but individuals are identifiable based on facial characteristics and other features that can be recognized from photographs. Secondly, recent studies indicate that Bornean orangutans may move on the ground more than previously thought, although Sumatran orangutans seem to engage in terrestrial behavior less often, perhaps because of the presence of a potential terrestrial predator, the tiger (Loken et al., 2013, 2015; Anczenaz et al., 2014). This increases the likelihood of capture by camera traps for at least Bornean orangutans.

Given their extensive use to estimate densities for other elusive animals, we were interested in examining the applicability of camera trapping and SCR modeling to orangutan populations. The purpose of this study was three-fold: 1) to evaluate the feasibility of using of camera traps and SCR modeling to estimate orangutan densities, using a population of Northeast Bornean orangutans (*P.p. morio*) as a case study; 2) to compare results obtained using camera trapping and SCR modeling to those obtained using an established method (nest surveys); and 3) to assess the advantages and disadvantages of both methods to make general recommendations for researchers wishing to estimate population parameters for orangutans and other elusive animals.

2. Methods

2.1. Study site

This study was carried out in the Wehea Forest in East Kutai District, East Kalimantan, Indonesia. Wehea (01°32'46"N, 116°46'43"E) contains 38,000 ha of mostly undisturbed forest bordered by large tracts of primary and secondary forests currently classified as logging concessions. Logging ceased in the mid-1990s and Wehea has been protected by an agreement between a local community and the local government since 2004. Wehea Forest contains lowland Dipterocarp, sub-montane and montane forests, with mean annual rainfall of 3000 mm and a mean temperature of 27 °C. The site's topography is characterized by steep ravines, ridges and runoff streams and elevations range from 250–1750 masl. Ten species of nonhuman primate have been reported from the site (Meijaard and Nijman, 2003; Loken et al., 2013). The eastern part of Wehea contains a network of old logging roads that have not been used since logging ceased and is now heavily overgrown and more like trails. These roads were utilized for camera trapping and nest surveys.

2.2. Camera trapping: data collection and analysis

In March 2012, 68 non-baited cameras were set in pairs at ~500 m intervals along old logging roads and trails and one camera trap was set at a natural salt lick (small sepan). This design was used to maximize capture rates (Tobler and Powell, 2013) and the station array covered an approximate area of 70 km² (Fig. 1). The cameras used were Bushnell Trophy Cams ($n = 61$) and Reconyx HC500 ($n = 8$) cameras. In May, an additional Bushnell Trophy Cam was added at a second natural salt lick (large sepan), bringing the total number to 70 cameras set and resulting in a sampling effort of 7320 trap days. All cameras remained at the same locations until this study concluded in October 2012. We chose a 6-month study length in order to obtain the greatest number

of orangutan photos while still assuming population closure. Each camera was placed ~50 cm from the ground and set to take three pictures per trigger, with a reset time of one second. Cameras were checked a total of three times, in the middle of May, the beginning of July and again in October at the conclusion of the camera trapping study. At each visit, non-functioning cameras were replaced with new cameras, batteries were changed and the SD card storing the photos was removed from the camera and replaced by a new card.

A total of 658 photographs of orangutans were collected during this study, many of which were repeat photos of the same individual or group of individuals due to the fact that cameras were set to take 3 photos per trigger, with a reset time of 1 s. All photographs were visually examined to determine 1) the number of individuals represented, and 2) the number of times each individual was recorded at different camera trap stations, using the following process: photos were first divided by camera trap station and then into age–sex class categories (flanged adult male, unflanged adult male, adult female, adult of indeterminate sex, juvenile) based on external genitalia if visible, secondary sexual characteristics (cheek flanges, throat pouch, cape of hair on back, elongated nipples), and body size and shape. Photographs were then examined for cues to individual identity, noting characteristics for each of the following categories: body size; hair color and quality (e.g., thick, thin, any bald patches); facial features (prominence of brow ridges; prognathism; angle and size of nostrils and mouth; overall shape of face), shape of hair on head, and any other identifying features (e.g., elongated nipples, marks or scars, distinctive body posture). If the individual's face and/or some other clear identifying mark (e.g., a distinctive injury) were not visible in a photograph, we did not attempt to identify that individual. After this initial assessment was performed, photographs were placed side-by-side for comparison to determine if the same individual had been captured at multiple stations and to ensure that no individual was counted more than once. This process was completed in its entirety from the beginning two separate times

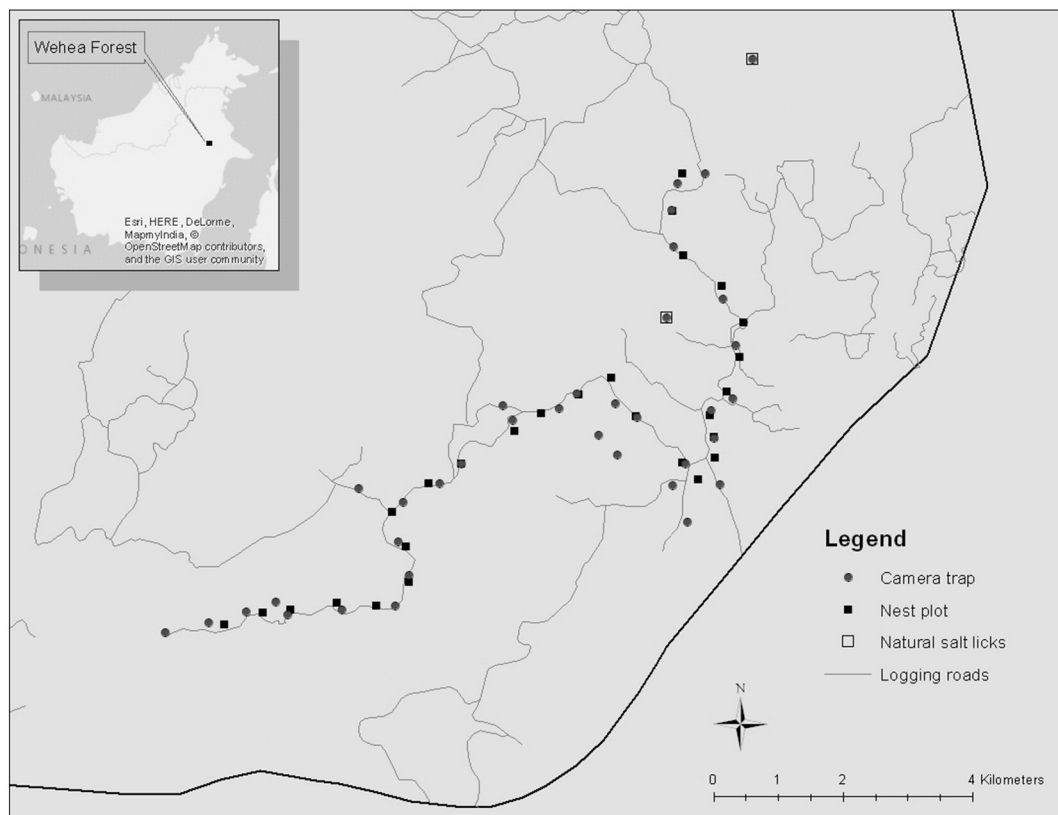


Fig. 1. Map of study area, indicating placement of camera traps and nest plots.

to maximize confidence in the assessment. After this process was completed, only series of photos taken with >1 h interval between photos of different individuals at each station were categorized as separate records ($n = 112$ series of photos that constituted separate records). Of these records, $n = 67$ contained images of sufficient quality or appropriate composition to allow for the successful identification of individuals in subsequent photographs (Fig. 2).

These $n = 67$ individually identifiable records were then converted into individual encounter histories appropriate for SCR modeling by first discarding any records of the same individual taken at the same trap on the same day, leaving us with 64 individually identifiable captures. Using the date and location of captures of each individual we produced a record of when and where each individual was captured (“individual encounter histories”) $y_{i,j,k}$ for individual $i = 1, 2, \dots, n$; traps $j = 1, 2, \dots, J$; and sample periods $k = 1, 2, \dots, K$.

2.3. Spatial capture–recapture model

Spatial capture–recapture (SCR) models describe the spatial pattern of individual encounters using a parametric model for detection probability in which the probability (Pr) of encounter at a location x is a function of distance between x and an individual's home range center s . In SCR models, the home range centers are regarded as unknown random effects (Borchers and Efford, 2008; Royle and Young, 2008). In our analysis we used the half-normal model:

$$\text{Pr}(\text{encounter at location } x) = p_0 \exp\left(-\text{dist}(x, s)^2 / 2\sigma^2\right)$$

where p_0 is the baseline encounter probability (the probability of an individual being encountered at its home range center) and σ is a scale parameter of the encounter probability model which determines the relative change in encounter probability as distance from the sample location to home range center increases. Since male and female orangutans

are known to have different ranging patterns (Singleton et al., 2009), we employed models that allowed for population substructuring, specifically sex structuring, to take into account the possibility of differences in space use and encounter rate for males and females (Royle et al., 2015). We considered sex specificity of the parameters σ and p_0 , fitting a set of four models which included: null (no sex effects), $p(\text{sex})$ (sex-specific effects on p_0 , which represents the baseline encounter probability), $\sigma(\text{sex})$ (sex-specific effects on σ , which represents the extent of space use by individuals), and both (sex-specific effects on p_0 and σ). Because our assessment of captures suggested that sepans may have a significant effect on baseline encounter probability (p_0), especially for males, we also assessed the sex-specific effects of the sepans on p_0 , resulting in two models that had an additive effect on p_0 : *sep* (sepan effect with no sex-specific effects) and *sep(sex)* (sex-specific sepan effects). As a result a total of 12 models were fitted. For all models, the parameter N represents the number of individuals in the state-space S , parameter D represents the density of individuals in the state-space S , the parameter ψ_{sex} represents the probability that an individual in the population is male, and $\text{sep}_{\text{female}}$ and sep_{male} represent the additive influence of sepan captures on baseline encounter probability (p_0) for males and females.

We estimated SCR model parameters using Maximum Likelihood Estimation (MLE). To obtain the MLEs of the SCR model parameters it is necessary to prescribe a 2-dimensional region within which individual home range centers may exist. This region is called the state-space (S), and the population size parameter N corresponds to the number of individuals having home range centers within this region. While the population size is sensitive to the size and configuration of the state-space, the density of individuals, D , defined as N divided by the area of the state-space S , is invariant to the size of the state-space under standard SCR models (Royle et al., 2013; p. 132). For our analysis we defined the state-space by buffering the minimum area rectangle containing the sample locations by 7.5 km. The total area of this state-space is 568.8 km². This buffer around the sample locations is at least 4 times the estimated value of σ .



Figure 2a (top) and 2b (bottom). Two photos from one record of unflanged male.

Figure 2c (top) and 2d (bottom). Two photos from one record of adult female.

Figure 2e (top) and 2f (bottom). Two photos from one record of flanged male.

Fig. 2. Examples of series of high-quality photographs (records) used for individual identification.

We carried out all modeling using the program R as described in Royle et al. (2015). All code and scripts used are available as supplemental material to that paper at *Ecological Archives*, <http://dx.doi.org/10.1890/ES14-00148.1.sm>.

2.4. Nest surveys: data collection and analysis

Nest surveys were carried out in June–August 2013. We used the plot method, developed by van Schaik et al. (2005), to survey for orangutan nests. The plot method is more effective than line transects in extremely difficult terrain like that at Wehea. We established 50×50 m plots at ~500 m intervals (following van Schaik et al., 2005) along the same routes on which camera traps were placed in order to survey the same area (Fig. 1). Plots were placed at least 100 m from roads to ensure that edge effects did not influence nest counts. Each nest plot was surveyed by a team of 4–5 trained observers. Observers “swept” the plot by spacing themselves out at ~10 m intervals along one of the plot boundaries and then walking slowly, searching the trees for orangutan nests. This was done once in each direction for all plots to ensure no nests were missed. When orangutan nests were spotted on the first sweep, the location of the nest was marked so the same nest would not be counted again on the return sweep.

Individual densities were then calculated using the following formula (van Schaik et al., 2005):

$$D_{ind} = N_{count} / s * p * r * t$$

where N_{count} = the total number of nests counted, s = the total survey area, p = proportion of nest builders in the population, r = number of nests built per individual per day, and t = nest decay time. No significant variation in the proportion of nest builders has been found between Bornean populations (Ancrenaz et al., 2004a; Johnson et al., 2005; van Schaik et al., 2005; Husson et al., 2009), so we used the commonly cited p value of 0.89. The rate at which nests are produced does seem to differ between populations, with Bornean nest building rates ranging from 1.00 in Kinabatangan in Sabah (Ancrenaz et al., 2004a) to 1.15–1.17 at other Bornean sites (Johnson et al., 2005; van Schaik et al., 2005; Husson et al., 2009). As the orangutans at Kinabatangan live in highly disturbed forest, which may influence their nest building and reuse rates, we chose to use an average Borneo-specific r value of 1.16. As nest decay varies substantially between sites, even within Borneo (Mathewson et al., 2008; Husson et al., 2009), we used a t value from a neighboring site (<40 km), Lesan, of 604 days (Mathewson et al., 2008). This site was close enough to Wehea, and the forest structure and climatic conditions so similar, that we believe this can be considered a local decay time. We employed the Delta Method (following Buckland et al., 2001; Mathewson et al., 2008; Ancrenaz et al., 2004b), which incorporates error from all parameters and values used to obtain a density estimate, to obtain a confidence interval for our final orangutan density estimate.

3. Results

3.1. Camera trapping and SCR analysis

From March 21 to October 18, 2012, we obtained a total of 112 distinct camera trap records of orangutans. Photos were high-quality enough to allow us to clearly identify individuals in 67 of these 112 records (60%) (Fig. 2); the remaining records in which photos were not of sufficient quality or composition to facilitate identification of an individual ($n = 45$) were discarded. Adult males accounted for $n = 23$ or 51% of discarded records; adult females for $n = 9$ or 20% of discarded records; and individuals of unknown age/sex for $n = 13$ or 29% of discarded records. Of these 67 individually identifiable records, 3 cases consisted of an individual captured at the same trap in the same day, so these were discarded, leaving us with 64 individual captures that could be used to create individual encounter histories for the SCR analysis. These 64 captures consisted of 16

Table 1

Individually identifiable records across age–sex classes for orangutans in the Wehea Forest from Mar–Oct 2012.

	# Individ	# Records	% Total records
Flanged adult males	5	22	34%
Unflanged adult males	3	14	22%
Adult females	6	24	38%
Unknown	2	4	6%

unique orangutan individuals: 8 adult males, 6 adult females and 2 individuals of unknown sex. Adult males (flanged and unflanged) represented 56% of all captures, compared to 38% for females (Table 1) and also had the highest number of individual captures during the study (Table 2). Further investigation revealed that the reason for this difference was largely due to captures obtained from the two sepan (natural salt licks), which were entirely of males ($n = 19$ captures, or 30% of male captures). We modeled this heterogeneity in capture probability by including parameters that accounted for sex-specific effects of the sepan on baseline encounter probability, as described in the Methods.

The 12 models fitted consisted of different combinations of the four basic models: $p(\text{sex})$ (sex-specific effects on p_0 , or encounter probability), $\sigma(\text{sex})$ (sex-specific effects on σ , or the extent of space use by individuals), Both (sex-specific effects on p and σ), and Null (no sex-specific effects); plus the two sepan effect models: $\text{sep}(\text{sex})$ (sex-specific effects of sepan on p_0) and sep (non-sex-specific effects of sepan on p_0) (Table 3). The top three models all include the sex-specific sepan effect indicating that sepan had an important sex-specific effect on encounter probability. Indeed, the results indicate that near sepan, encounter probability for males (sep_{male}) was nearly 1 but for females ($\text{sep}_{\text{female}}$) was near 0 (the effects are modeled on the $\log \text{it}(p_0)$ scale and so large negative values indicate p_0 near 0 whereas large positive values indicate p_0 near 1). However, the sepan effect did not appear to influence overall population (N) and density (D) estimates (for example, compare results of models Both and Both + $\text{sep}(\text{sex})$). The favored model was Both + $\text{sep}(\text{sex})$, indicating that there is a difference in baseline (p_0) and sepan encounter probability for males and females, and that males have larger home ranges than females (σ), consistent with what was observed in our data and what is

Table 2

Individual frequencies of capture for orangutans in the Wehea forest from Mar–Oct 2012. Rows represent unique trap frequencies and columns represent total number of captures (e.g., we captured 2 males 1 time, by default in only 1 trap; and we captured 1 female 4 times in 3 different traps).

Adult males (flanged and unflanged)						
# Traps	# Captures					
	1	2	3	7	8	11
1	2	0	0	0	1	1
2	0	1	1	0	0	0
3	0	0	1	0	0	0
4	0	0	0	1	0	0

Adult females			
# Traps	# Captures		
	3	4	8
1	2	0	0
2	1	0	0
3	1	1	0
4	0	0	1

Unknown		
# Traps	# Captures	
	1	3
1	1	0
2	0	1

Table 3
Results of fitting sex-specific and null models to orangutan data set. # parm refers to the number of parameters used for each model. All values are real values except for the sep_{female} and sep_{male} parameters, where effects are modeled on the log it(p_0) scale and large negative values indicate p_0 near 0 and large positive values indicate p_0 near 1. Please see text for further explanation of model parameters.

Model	# parm	p_{female}	p_{male}	σ_{female}	σ_{male}	N	D	ψ_{sex}	sep_{female}	sep_{male}	AIC
Both + $sep(sex)$	7	0.0055	0.0027	0.9259	1.6636	89.186	0.1568	0.3150	−12.041	18.853	375.876
$\sigma(sex)$ + $sep(sex)$	6	0.0037	0.0037	1.0523	1.6586	87.450	0.1537	0.3053	−12.128	18.842	375.917
$p(sex)$ + $sep(sex)$	6	0.0034	0.0028	1.4903	1.4903	72.149	0.1268	0.4287	−11.23	18.749	379.527
Both + sep	6	0.0076	0.0027	0.7741	1.660	78.803	0.1385	0.3631	18.324	18.324	386.486
$\sigma(sex)$ + sep	5	0.0050	0.0050	0.8253	1.6736	76.099	0.1338	0.3466	18.131	18.131	389.478
$p(sex)$ + sep	5	0.0070	0.0029	1.3539	1.3539	62.479	0.1098	0.6061	18.423	18.423	400.945
Null + sep	4	0.0044	0.0044	1.3165	1.3165	64.521	0.1134	0.5715	18.455	18.455	401.714
Null + $sep(sex)$	5	0.0041	0.0041	1.3485	1.3485	65.501	0.1152	0.5941	18.455	5.078	403.095
$\sigma(sex)$	4	0.0057	0.0057	0.9130	1.7914	90.889	0.1598	0.3766	N/A	N/A	446.146
Both	5	0.0055	0.0060	0.9222	1.7878	90.739	0.1595	0.3745	N/A	N/A	448.127
$p(sex)$	4	0.0035	0.0070	1.4638	1.4638	79.498	0.1398	0.5038	N/A	N/A	452.357
Null	3	0.0053	0.0053	1.4814	1.4814	76.643	0.1347	0.5715	N/A	N/A	452.533

known about orangutan ranging patterns (Singleton et al., 2009). Under this model the probability that an individual in the population is male (ψ_{sex}) is 0.315 (CI: 0.128–0.590), and orangutan density is estimated at 0.16 indiv/km² (95% CI: 0.0912–0.2909 indiv/km²) within the state-space (568.8 km²).

3.2. Nest surveys

A total of 27 plots were surveyed during this study. We counted 44 nests total in all plots, with a mean of 1.63 ± 0.32 nests per plot and a nest encounter rate of 6.52 ± 1.28 nests/ha. The calculated density of individuals from this survey, using the parameters outlined in Table 4, is 1.05 indiv/km² (95% CI 0.18–6.01 indiv/km²).

4. Discussion

This study is the first to use camera traps and SCR modeling to estimate the densities of orangutans, or indeed, any primate. Below, we compare camera trapping and SCR modeling to nest counts and discuss the implications for decision making when choosing a method to assess the populations of orangutans or other elusive primates.

4.1. Comparing results obtained using the two methods

The two methods produced density estimates that differ considerably (Table 5). A possible explanation for this difference that must be considered up-front is that there was an actual change in orangutan density in the Wehea Forest between October 2012 (when camera trapping ended) and June 2013 (when nest surveys commenced). Orangutans may engage in large-scale movements between areas in response to changes in resource availability (MacKinnon, 1974; Singleton and van Schaik, 2001; Buij et al., 2002), which presents a challenge for any survey method that is deployed over a relatively short time frame. However, we believe this is not the primary cause of differences between our estimates because we used all visible nests (the standing crop method), rather than only newly built nests (the marked nest count method), to calculate density estimates using the nest count method. The standing

Table 4
Parameters used to calculate orangutan densities from nest counts.

Parameters	Values
N_{count} (nest number) for all 27 plots	44 (mean 1.63 ± 0.32)
s (survey area, in km ²)	0.0675
p (proportion of nest builders in population) ^a	0.89
r (number of nests built per day) ^a	1.16
t (nest decay time, in days) ^b	604

^a Borneo-specific values (Buij et al., 2002; Johnson et al., 2005).

^b Decay time from nearby site (Lesan) (Mathewson et al., 2008).

crop method incorporates nests built in the past and thus provides an estimate of the average orangutan population in an area over a wider timeframe (Spehar et al., 2010). Given the longevity of nests in this part of East Kalimantan (Mathewson et al., 2008), our nest surveys almost certainly incorporated nests built during the camera trapping period and provide an average density for orangutans in the area during the timeframe covered by this study.

Assuming that a substantial change in actual densities did not occur between survey periods allows us to focus on the possible methodological reasons for the difference in density estimates. The 95% confidence interval for the nest count method is very wide, indicating the imprecision and therefore high uncertainty of the density estimate calculated using this method. This wide confidence interval is likely due to high variance in nest encounter rates between plots (mean: 6.52 nest/ha, 95% CI 3.95–9.09; range: 0–7 nests per 0.25 ha plot). This highlights the need for sufficient sample sizes (in the form of a sufficient number of plots or transects to address the issue of high variation in nest encounter rate; van Schaik et al., 2005) when calculating density estimates from nest surveys. This can take a long period of time and a great deal of effort to achieve in areas with low orangutan densities like the Wehea Forest. Thus, rather than being a relatively quick and easy method, nest surveys can require a substantial investment of time and effort if they are to produce reasonably reliable density results, even when locally derived parameters are available (Plumptre, 2000; Mathewson et al., 2008; Marshall and Meijaard, 2009; Spehar et al., 2010).

The density estimate provided by camera trapping/SCR modeling (0.16 indiv/km²) is much lower than most densities reported for other relatively undisturbed sites in Borneo (Husson et al., 2009). Although a comparison of the precision of two estimates calculated using different methods and parameters should be done with caution, both estimates reference orangutan density and it is worth noting that the narrower 95% confidence interval for the camera trapping/SCR density estimate indicates that this estimate is somewhat more precise than the nest survey density estimate. However, the CI of the camera trapping estimate is still fairly wide. We can identify three issues that may have influenced these results. First, this method may have underestimated density due to unmodeled heterogeneity in the camera trap data. We did model sex-specificity of model parameters and trap effects (specifically, sepan

Table 5

Comparisons of orangutan density estimates and extrapolated population size of orangutans in the 38,000 ha² Wehea Forest, assuming sampled area is similar to extrapolated area, using camera trapping/SCR modeling and nest surveys. Density and population size are presented not to suggest that these numbers represent true population abundance in the Wehea Forest, but as a means of contrasting the results provided by the two methods.

	Indiv/km ²	95% CI	# Indiv	95% CI
Camera traps/SCR	0.16	0.09–0.29	60.80	34.66–110.542
Nest count	1.05	0.18–6.01	397.24	69.20–2283.04

effects), both of which seemed to be important sources of variation in encounter probability. However, other sources of detection heterogeneity, including age class, behavior (e.g., some individuals may stay in the trees) and social structure, are potentially present which, because of limited data ($n = 16$ individuals) and limited precision of estimates we did not feel warranted further model development.

Second, small sample size (low number of captures and recaptures of individuals) likely influenced the precision of our results. SCR models require that sufficient individuals are captured and that at least some individuals have spatial recaptures (captures at multiple camera trap locations). For some species, this could be accomplished by having an extensive and dense trapping array (Tobler and Powell, 2013; Sollmann et al., 2014). However, we believe that for a wide ranging and mainly arboreal species such as orangutans this design is infeasible, given the logistics and the high costs associated with such an array. We chose instead to pursue a design that covered a larger area and located traps along likely paths of movement. We believe a more important factor contributing to our low sample size was our positioning of camera traps for this study. Given that camera trapping combined with SCR modeling had never been previously attempted for orangutans or any primate, we employed camera trap placement that has been used extensively for capturing the flanks of felids for identification (two camera traps per station set perpendicular to and on opposite sides of the road or trail). The fact that only 67 of 112 orangutan records resulted in individually identifiable photos indicates that this is probably not the most appropriate placement for primates, for whom facial features are much more important for individual identification. Based on our experience studying and identifying wild orangutans, we believe that the low number of individually identifiable photos of orangutans was due to these issues with trap placement, and not because some orangutans are simply not identifiable (meaning that with good photos, all orangutans are in theory identifiable). If a trap arrangement better suited for orangutans had been used, more individuals would have been identified and our sample size (and thus the precision of our estimate) increased. One simple adjustment to increase sample size, while allowing for camera trapping array design similar to the one used in this study, is setting 3–4 camera traps per station and/or adjusting their placement so that more angles are covered to maximize the likelihood that the facial features of each orangutan are captured.

There are also other possible changes to study design that could increase sample size. Setting cameras in the trees is one possibility. Recent studies demonstrate that it is possible to obtain captures of primates with arboreal camera traps (Gregory et al., 2014) and cameras placed in carefully selected arboreal locations could supplement records on the ground. This might be especially useful in areas where there is a sex difference in use of the ground, as may be the case at certain locations in Wehea (e.g., sepans) and has been found at other orangutan study sites (e.g., Manduell et al., 2011). This technique, however, presents many hurdles (e.g., determining placement of cameras, the requirement of specialized expertise and equipment) and may also not be cost-effective in many areas. Sample size could also be increased by setting clusters of camera traps throughout the study area in places where orangutans are more likely to be terrestrial (e.g. canopy gaps, ridges, trails and roads). The flexibility in SCR modeling allows for this type of clustered survey design, which would result in more area covered and fewer cameras used (Efford and Fewster, 2013). Baiting camera traps could increase the likelihood of captures across age–sex classes (Royle et al., 2011; Olson et al., 2012). Lastly, sample sizes could be increased by combining SCR data to estimate shared model parameters from multiple independent camera trapping studies (see Sollmann et al., 2014). Depending on resources, studies could be conducted simultaneously or in successive years and focused in various geographic areas (e.g., within the range of *P.p. morio*). This type of combined information study would yield a large enough data set for more precise and possibly accurate density estimates and also important information how orangutan densities vary across their geographic ranges.

Third, the spacing of camera traps in this study was too close relative to the typical amount of space used by orangutans in this study. Trap spacing of roughly $2 \times \sigma$ has been shown to be nearly optimal from a statistical standpoint based on simulation work (Royle et al., 2013, Section 10.3). In the present study the average trap spacing was about $0.5 \times \sigma$ or less. A wider spacing would have potentially allowed the capture of more individuals, increasing sample size and potentially improving our estimates. However, the likely success of this and other camera placement strategies should be evaluated using simulations before such designs are employed in the field.

4.2. Implications for orangutan survey methods

Our results suggest that with methodological adjustments, camera trapping and SCR modeling could be successfully used to estimate the densities of orangutans and, potentially, other elusive primates. Without applying these methods to a population of known density, it is impossible to determine which method is more accurate, but our results suggest that in at least some settings, camera trapping/SCR modeling may offer more precise results than traditional nest surveys. However, the balance of costs and benefits must be considered carefully before researchers make the decision to use this, or any other, method. We have summarized comparisons of the costs, in both money and effort (Table 6) and overall advantages and disadvantages (Table 7) of the two methods below, acknowledging that this is a simplification and that whether the outcome of the comparison is in favor of one method or another will likely be specific to the study.

Camera trapping does have much higher initial costs than traditional methods like nest surveys. For our camera trapping study, we estimate equipment costs were around \$15,000, and for a study utilizing more stations and more camera traps per station, the estimated cost rose to almost \$38,000 (Table 6) even when using a relatively inexpensive camera trap model (Bushnell TrophyCam HD, \$180/unit, plus costs of batteries and SD card). Because our site was remote, we did not need to use devices for preventing camera trap theft, but at sites closer to human habitation this is often an issue. Such devices are \$20–\$50 per camera, and with this factored in the cost of a study like ours would increase by \$1440–\$3600. This is a substantial investment of resources and not all researchers will have access to this kind of money. However, camera traps can be used for multiple seasons, at many study sites and even shared between researchers, all of which would reduce costs. Camera trapping requires slightly higher effort in the field than nest surveys alone as each trap must be placed and then checked regularly over the course of the study, but when the effort required to calculate a local nest decay time is considered, camera traps actually require about the same or less effort in the field than nest surveys (Table 6).

Table 6

Cost comparison for camera trapping and nest surveys. Costs are calculated for this study, and for a hypothetical study designed to increase sample size and/or reliability of results.

This study	Camera trapping ^a	Nest survey ^b	Nest survey + nest decay ^c
Equipment (\$)	15,120	900	2000
Field time (hours)	324	135	335
Person hours (field time x personnel)	648	540	940
<i>Hypothetical study</i>			
Equipment (\$)	37,800	900	2000
Field time (hours)	450	200	400
Person hours (field time x personnel)	900	800	1200

^a This study: 36 stations, 70 total cameras; 6 month study, cameras checked twice; and 2 observers needed. Hypothetical study: 45 stations, 4 cameras each; 6 month study, cameras checked twice; and 2 observers needed.

^b This study: 27 plots, checked once; and 4 observers needed. Hypothetical study: 40 plots, checked once; and 4 observers needed.

^c Nest decay for both studies: surveying a set of 40 nests; 1 initial visit and 2 revisits; and 2 observers needed.

Table 7
Comparison of camera trapping (CT) and nest survey (NS) methods as used to calculate animal density, with the overall “winner” in each comparison indicated in the “Outcome” column.

Camera trapping	Nest surveys	Outcome
High equipment cost (Table 6), but camera traps can be reused, reducing average cost across surveys	Low equipment cost (Table 6)	NS
Relatively high effort (field time and person hours) required to obtain sufficient captures and recaptures and maximize ability to ID individuals from photos (Table 6)	Relatively low effort (field time and person hours) required for single surveys, but high effort required to obtain sufficient nest encounter rates and local parameters (Table 6)	Draw
Only appropriate where animals use ground regularly	Appropriate regardless of substrate use by animals	NS
Possible detection heterogeneity (e.g., due to age–sex class, behavior) could influence results	Probability of detection same for all subsets of population	NS
Potential for equipment failure, or theft in areas with high human use	Equipment failure and theft are nonissues	NS
Parameters not needed to obtain density estimates	Must calculate local values for some parameters to obtain reliable density estimates, at additional effort and cost	CT
SCR and other modeling approaches allow flexibility in study design	Little flexibility in study design possible (line transects or plots)	CT
Provide additional info about target population: e.g., demography, movement and activity patterns, behavior, body condition	Provide little additional info about target population	CT
Provides additional info about animal community and biodiversity in study area	Provides no additional info about animal community or biodiversity in study area	CT
Images have multiple uses: education, advocating for conservation	Pictures of nests don't get people excited about conservation	CT

Camera traps offer additional benefits that nest surveys do not (Table 7). First and foremost, camera trapping counts the animals themselves and does not require the application of parameters to obtain density estimates, removing a major potential source of error and providing estimates that may be more reliable in many settings. Camera trapping also provides additional data beyond population abundance or density that can allow researchers to develop a more well-rounded understanding of elusive and difficult-to-study populations. This includes information about population structure, demography, activity and ranging patterns, social interactions, and body condition (Head et al., 2012; Nakashima et al., 2013; Galvis et al., 2014; Gregory et al., 2014). For example, once encounter history data is obtained using camera trapping, more general SCR models for open populations or accommodating non-IDed detections can be developed, allowing researchers to obtain a more detailed understanding of population demographics. Camera traps do not just collect data on the target species but on all animals that pass by, potentially allowing the calculation of general abundance indices for other species and information on the general biodiversity found in a study area. Finally, camera trapping studies provide compelling images that can be used for educational or conservation purposes. The value of these images for raising public awareness and support for conservation should not be underestimated (Hance, 2012).

We believe that nest surveys still have a place in the survey methodology toolbox. Obtaining accurate and precise density estimates from nest counts require a substantial investment of time and effort, but rapid assessments of an area can be done using nest encounter rates or nest densities, which do not require the application of troublesome parameters. Such measures can be used to compare between sites and to get a general sense if the orangutan density in an area is likely to be low or high. If the site seems potentially important, and if camera trapping seems feasible, researchers can conduct a more detailed assessment and study of the population using camera traps or other methods. Nest surveys are also useful for monitoring populations, in which case changes in nest encounter rate or nest density over time can be used. If resources and time permit, a combination of methods (camera trapping and nest counts) to estimate density or abundance could provide even greater confidence in density estimates and a more well-rounded understanding of populations (Nakashima et al., 2013). Finally, there are situations in which camera trapping is not feasible (e.g., when working with study animals for which obtaining a sufficient number of captures and recaptures is very difficult), and in these settings nest surveys may be the best option.

4.3. Conclusions

Overall, we believe that camera trapping and SCR modeling are promising methods that, with some methodological adjustments, could potentially be useful tools for assessing the densities of orangutans as well as other elusive primates. We believe this method warrants

further investigation to determine when and where it is most applicable and what methodological adjustments are needed. In general, we encourage researchers to think carefully about survey goals and to consider the wide range of options available to them before making a decision about methodology. Choosing to employ alternative methods may allow conservationists to allocate more of their limited resources toward the ultimate goal of reducing threats to species survival.

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