

Habitat use of Bornean Orangutans (*Pongo pygmaeus morio*) in an Industrial Forestry Plantation in East Kalimantan, Indonesia



Stephanie N. Spehar^{1,2} · Yaya Rayadin^{3,4}

Received: 23 June 2016 / Accepted: 2 February 2017
© Springer Science+Business Media New York 2017

Abstract Many primates now live in anthropogenic landscapes dominated by human activity such as agriculture. Conserving primates in such contexts requires detailed information about habitat use, including landscape features that may influence population viability. We studied Northeast Bornean orangutan (*Pongo pygmaeus morio*) habitat use in a forestry plantation in East Kalimantan, Indonesia. We conducted camera trapping and nest surveys at 13 locations across three habitat types in the plantation (planted acacia stands, planted eucalyptus stands, and secondary forest patches left uncut or allowed to regenerate) September 2012–March 2013, and calculated four measures of orangutan abundance for each location (independent photo captures/100 camera trap days, or RAI_2 ; nest encounter rate; nest density; and orangutan density). Orangutans are relatively common in the plantation; they used all three habitat types and exhibited a higher RAI_2 than 70% of other mammal species detected. A logistic regression found that proximity to natural forest areas best predicted orangutan abundance calculated using camera trap data (RAI_2) but that habitat type combined with distance to natural forest best predicted orangutan abundance calculated using nest counts. This suggests that orangutans use planted areas for movement and feeding, but rely on patches of natural forest for resting and access to key resources. Our study and others indicate that orangutans can coexist with some human activities if

Handling Editor: Matthew McLennan

✉ Stephanie N. Spehar
spehars@uwosh.edu

¹ Anthropology Program, University of Wisconsin Oshkosh, Oshkosh, WI 54901, USA

² Borneo Futures, Bandar Seri Begawan BS8811, Brunei Darussalam

³ School of Biodiversity and Wildlife Conservation Laboratory, Forestry Faculty of Mulawarman University, Samarinda, East Kalimantan 75123, Indonesia

⁴ Ecology and Conservation Center for Tropical Studies (Ecositrop), Samarinda, East Kalimantan 75118, Indonesia

provided with sufficient access to natural forest. However, we must conduct further research to facilitate effective conservation planning, including gathering additional details about habitat and resource use and possible long-term population impacts.

Keywords Anthropogenic landscapes · Camera trapping · Conservation · Habitat use · Nest surveys · *Pongo pygmaeus morio*

Introduction

A growing number of primates live in anthropogenic landscapes that are significantly modified by human activities. Anthropogenic landscapes are characterized by a matrix of altered areas interspersed with fragments of native habitat, and include agroforestry systems, mixed agricultural landscapes, plantations, regenerating forests, logging concessions, and human settlements (Estrada *et al.* 2012; Hockings *et al.* 2015; McKinney 2015). Given the accelerating rate of human impact on the environment, and the fact that most primates live outside protected areas, researchers and conservation practitioners are increasingly recognizing that anthropogenic landscapes must be incorporated into conservation strategy (Koh and Gardner 2010; Meijaard 2016; Sodhi *et al.* 2010). Doing so requires that we understand how primates respond to the altered ecological challenges presented by such habitats. Studies have documented how some primates adjust their diets, activity budgets, habitat use, group size, and other aspects of behavior in anthropogenic landscapes (Estrada *et al.* 2012; Hockings *et al.* 2012, 2015; McCarthy *et al.* 2016; McKinney 2015; McLennan 2013). An important aspect of this behavioral adaptation often involves the incorporation of human crops into the diet (Hockings and McLennan 2012; McLennan and Hockings 2014; Saj *et al.* 1999; Warren *et al.* 2011), which can lead to primate–human conflict, the categorization of primates as “pests,” and, sometimes, the killing of primates (Hill 2005; Hockings and Humle 2009; Hockings and McLennan 2016). However, responses to anthropogenic change can vary considerably based on land-use type, e.g., industrial plantation, agroforestry system, regenerating forest, and species-specific variables, e.g., body size, dietary and locomotor plasticity, behavioral flexibility, and reproductive rate (Cardillo *et al.* 2005; Isaac and Cowlshaw 2004; Kamilar and Paciulli 2008; Purvis *et al.* 2000; Sih *et al.* 2011). We must therefore generalize with caution and recognize that taxa- and landscape-specific studies may be necessary to understand if and when anthropogenic change can be tolerated.

Orangutans (*Pongo* spp.) present an interesting and important case study. Both Bornean (*P. pygmaeus*) and Sumatran (*P. abelii*) orangutans are Critically Endangered, as their populations have declined by 50–80% over the last 60–75 years (IUCN 2016). These declines are attributed primarily to forest loss, fragmentation, and hunting (Marshall and Nardiyono 2006; Meijaard *et al.* 2012; Wich *et al.* 2012a). Forest conversion continues at a rapid pace in both Borneo and Sumatra, driven by agriculture, mining, and especially the expansion of industrial forestry and oil palm plantations (Gibbs *et al.* 2010; Gilbert 2012; Koh 2007; Koh and Wilcove 2008; Margono *et al.* 2014; Wich *et al.* 2012a). As a result, the orangutan’s range is becoming increasingly characterized by a matrix of heavily altered, human-dominated areas interspersed with patches of natural forest of varying size and shape (Ancrenaz *et al.* 2015; Wich *et al.*

2008, 2012a). Such conversion is likely to continue, at least in the immediate future, owing to the economic importance of oil palm and other plantation crops to the two orangutan range countries, Malaysia and Indonesia; complex bureaucracy and regulatory structures that make it difficult to regulate land-use patterns; and lack of enforcement of existing laws (Meijaard and Sheil 2013; Meijaard *et al.* 2012; Miettinen *et al.* 2012; Nantha and Tisdell 2009). As up to 75% of orangutans live outside protected areas (Wich *et al.* 2008, 2012a), understanding how we can effectively integrate human-dominated landscapes into orangutan conservation strategies is a high priority.

It was long assumed that orangutans, generally regarded as ecological specialists that rely on forest with high connectivity for arboreal travel, could not cope with heavily altered anthropogenic landscapes. For example, recent maps of orangutan distribution eliminated such areas from their potential range (Wich *et al.* 2008) because it was thought that orangutans could not survive there. However, reports of orangutans using plantations and agricultural areas started to surface in the 1990s, and recent research has documented orangutans using and even living in anthropogenic habitats (Table 1). These studies have documented orangutans nesting in oil palms (Ancrenaz *et al.* 2015) and even on the ground (Y. Rayadin and S. Spehar, *unpubl. Data*), engaging in frequent terrestrial movement (Ancrenaz *et al.* 2014, 2015), and regularly exploiting cultivated food sources including garden crops, the cambium of *Acacia magnium* trees, the pith of immature oil palm trees, and oil palm fruits (Ancrenaz *et al.* 2015; Campbell-Smith *et al.* 2011a, 2011b; Meijaard *et al.* 2010). In the one population from

Table 1 Key findings from studies of orangutans in anthropogenic habitats

Site	(Sub)species	Primary habitat type	Behavioral adaptations seen	References
Kutai Landscape, East Kalimantan, Borneo	<i>Pongo pygmaeus morio</i>	Forestry, rubber, and oil palm plantations; coal mining concessions	Frequent terrestriality; nest building, e.g., in acacia and eucalyptus trees, on ground in heavily degraded areas; extensive use of human crops (acacia and rubber tree cambium, oil palm pith)	Meijaard <i>et al.</i> (2010); Rayadin and Spehar (2015); Y. Rayadin and S. Spehar, <i>unpubl. Data</i>
Kinabatangan, Borneo	<i>P. P. morio</i>	Oil palm plantation	Terrestriality; nest building, e.g., in oil palms; extensive use of human crops (oil palm pith, fruits)	Ancrenaz <i>et al.</i> (2015); F. Oram and M. Ancrenaz, <i>unpubl. Data</i>
Central Kalimantan, Borneo	<i>Pongo pygmaeus wurmbii</i>	Oil palm plantation	Some terrestriality; altered ranging patterns, e.g., smaller home ranges; limited use of human crops (oil palm pith)	International Animal Rescue Indonesia and Austindo Nusantara Jaya, <i>unpubl. Data</i>
Batang Serangan, Sumatra	<i>Pongo abelli</i>	Agroforestry	Some terrestriality; altered ranging patterns, e.g., smaller home ranges; extensive use of human crops (fruit cultivars)	Campbell-Smith <i>et al.</i> (2011a, 2011b)

which detailed behavioral data have been published (an agroforestry landscape in Batang Serangan, Sumatra), orangutans differed from those living in natural forest in various aspects of their ranging and activity patterns, exhibiting smaller home ranges, shorter daily path lengths, and more time resting (Campbell-Smith *et al.* 2011a, 2011b). Such flexible responses are likely facilitated by the capacity for behavioral plasticity and innovation present in the great apes (Hockings *et al.* 2015).

Such studies suggest that orangutans can alter their behavior in response to some human activities, and indicate that anthropogenic landscapes should be incorporated into orangutan conservation strategies (Ancrenaz *et al.* 2016). However, the extent to which orangutans can use and move through different parts of the anthropogenic matrix remains unclear. A long-term study of orangutans living in a landscape dominated by oil palm in Sabah, Malaysia, found that most orangutan activity occurred within 50 m of natural forest patches (Ancrenaz *et al.* 2015), and simulations indicate that connectivity is crucial for maintaining genetic diversity (Bruford *et al.* 2010). Also, there may be sex differences in the use of anthropogenic landscapes; specifically, males may be found more frequently or deeper into the interior of plantations and other disturbed habitat than females (Ancrenaz *et al.* 2015) because they use the ground more often (Ashbury *et al.* 2015) and range over larger distances (Singleton and van Schaik 2001). Thus, the ability of females to disperse through heavily disturbed habitat may be more limited. The importance of natural forest and connectivity is reinforced by the fact that orangutans sometimes become “stranded” in small forest patches and must be relocated by government bodies or private companies to larger forest patches or protected areas (Rayadin and Spehar 2015; Russon 2009). Some of these individuals are in very poor body condition at the time of relocation, presumably owing to a lack of resources (Rayadin and Spehar 2015). This underscores the fact that anthropogenic landscapes are complex, composed of different habitat types that may vary in their ability to support viable orangutan populations.

To develop land-use policies that maximize conservation benefits for orangutans, we must understand how orangutans are using different habitats in anthropogenic landscapes, and what landscape features promote or threaten individual and population viability. To help address these questions we performed an initial study of orangutan habitat use in a forestry plantation in East Kalimantan, Indonesia. This 259,400-ha plantation is dominated by stands of planted *Acacia mangium* but also contains patches of *Eucalyptus* spp. and secondary forest. The plantation is part of a larger matrix of forestry and oil palm plantations, coal mining concessions, and natural forest patches, including the degraded Kutai National Park (Dennis and Colfer 2006; Russon *et al.* 2015), which abuts the plantation (Fig. 1). Northeast Bornean orangutans (*Pongo pygmaeus morio*) have been reported as using the plantation since the mid-1990s (Rayadin and Spehar 2015). Previous surveys suggest that this plantation may harbor nearly 1400 orangutans, or possibly 50% of the Northeast Bornean orangutan population in East Kalimantan and 3–4% of the total Bornean orangutan population (Meijaard *et al.* 2010). However, although it is clear that orangutans are using the plantation, their relative use of the different habitat types (secondary forest areas and planted acacia and eucalyptus stands) found throughout the plantation has not been quantified. Orangutans commonly consume the cambium of acacia trees and are often seen traveling and building nests in planted acacia stands, but anecdotal data suggest that they also depend heavily on patches of natural forest as key sites for nests, feeding, and resting (Y.

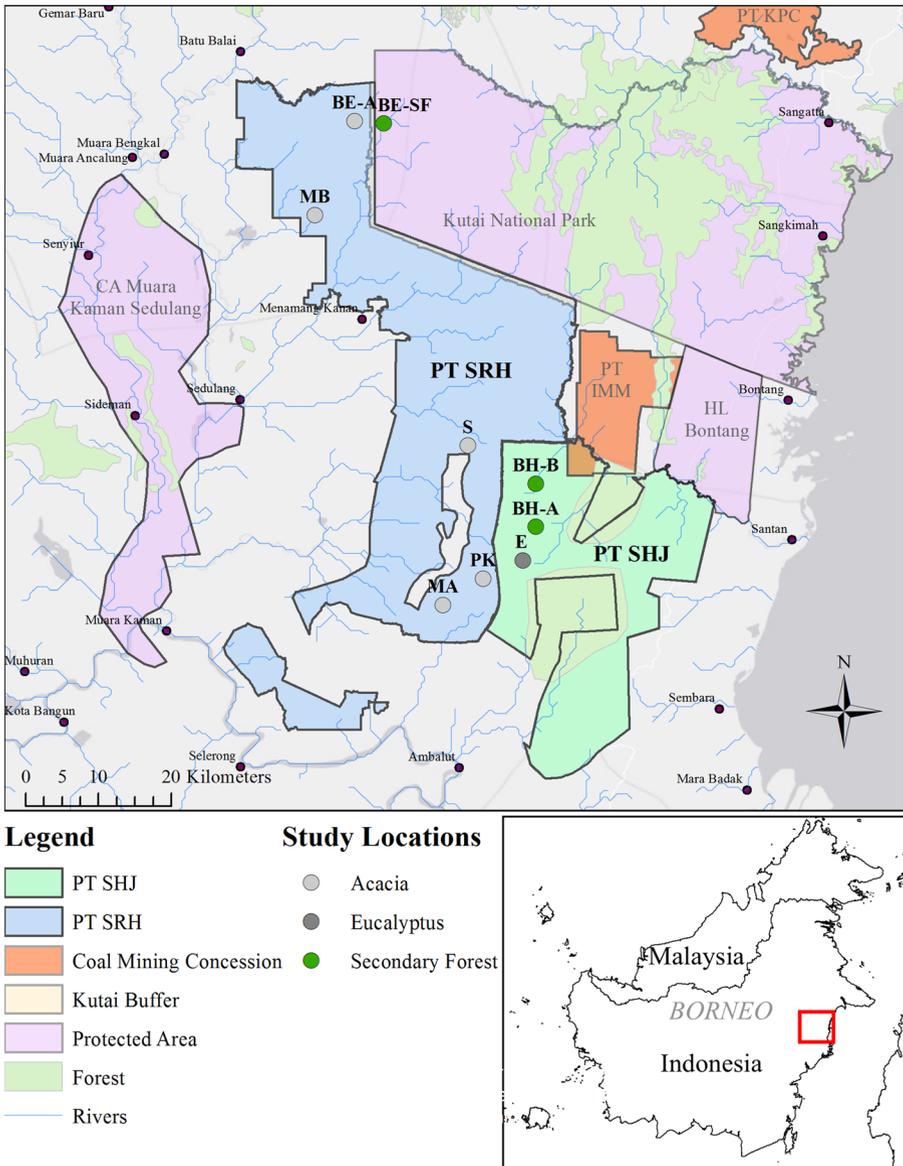


Fig. 1 Map of study area, plantation PT Surya Hutani Jaya (PT SRH) and PT Sumalindo Hutani Jaya (PT SHJ), and location of study sites referenced in Table IV. Other important components of the landscape (protected areas, coal mining concessions) are also included, as is the location of the study area in Borneo.

Rayadin and S. Spehar, *unpubl. Data*). It is also unclear whether the orangutans found in the plantation are migrants from the neighboring Kutai National Park, or if the plantation represents permanent habitat for at least some orangutans (Meijaard *et al.* 2010).

We surveyed orangutans across different habitat types in the plantation to determine how habitat type and proximity to key landscape features (natural forest patches, forest

corridors along waterways, and Kutai National Park) influence orangutan habitat use. Specifically, we collected two types of data that can provide estimates of orangutan abundance and thus indices of relative habitat use: 1) camera trap data, which provided us with a measure of relative abundance (RAI₂) for orangutans as well as other mammalian species; and 2) nest count data, which provided us with three indicators of orangutan abundance: nest encounter rate, nest density, and orangutan density. Camera trapping has gained popularity among wildlife researchers as a method for studying rare and elusive species (O’Connell *et al.* 2010) and is growing in popularity among primatologists as a way of surveying populations and even studying behavior (Galvis *et al.* 2014; Head *et al.* 2012; Kühl *et al.* 2016; Loken *et al.* 2013; Musgrave *et al.* 2016; Nakashima *et al.* 2013; Olson *et al.* 2012). Unlike nest counts, the method traditionally used to survey orangutan populations, camera traps count the animals themselves and thus do not require the application of parameters that can introduce error when converting nest counts into orangutan density estimates (Marshall and Meijaard 2009; Mathewson *et al.* 2008; Spehar *et al.* 2010). However, the small sample sizes obtained in camera trapping studies of orangutans can sometimes make interpretation of results difficult (Spehar *et al.* 2015). Also, comparing terrestrial camera trap captures between habitat types as a measure of relative orangutan abundance and/or habitat use assumes that orangutans are equally likely to use the ground in all habitat types. While previous camera trapping studies indicate that orangutans do use the ground in all habitat types, including primary forest (Ancrenaz *et al.* 2014; Ashbury *et al.* 2015; Loken *et al.* 2013), rates are sometimes higher in disturbed areas (Ancrenaz *et al.* 2014). This is one of the reasons we chose to employ both camera trapping and nest counts as measures of relative habitat use. Each method has different strengths and weaknesses, and when combined can potentially provide a fuller picture of orangutan abundance and habitat use than can either method alone (Spehar *et al.* 2015). Finally, camera trapping also provides us with data on wildlife other than orangutans, and here we compare the relative presence of orangutans in different habitats to other wildlife as a rough measure of orangutan adaptability relative to other primate and nonprimate species.

Methods

Study Area

The plantation that comprised our study area is managed by two companies [PT Surya Hutani Jaya (SRH) and PT Sumalindo Hutani Jaya (SHJ)] and was first cleared for planting in 1993. It consists of 259,400 ha (PT SRH: 183,300 ha; PT SHJ: 76,100 ha) of stands of fast-growing *Acacia mangium* (70% of plantation land cover) and *Eucalyptus* spp. (20% of plantation land cover) of varying age, interspersed with patches of secondary forest (10% of plantation land cover). These patches of secondary forest were left uncleared or allowed to regenerate by plantation management to comply with Indonesian law that $\geq 10\%$ of all concessions must be natural forest. They range 100–4000 ha in size and comprise areas set aside and protected by plantation management for the purposes of forest and wildlife conservation (“conservation areas”), corridors of forest along larger rivers, and the buffer zone with Kutai National Park (Y. Rayadin,

unpubl. Data). Orangutans were first reported in the plantation in 1996, and surveys by Rayadin (*unpubl. Data*) and Meijaard *et al.* (2010) found that a sizable population of orangutans uses and likely resides in the plantation. Kutai National Park (ca. 200,000 ha) abuts the plantation and may serve as a local source and refuge for orangutan populations in areas near the park (Fig. 1).

Human activity in the plantation is very regular, although its distribution and intensity can vary depending on whether an area is being harvested. Human activity takes the form of harvesting, planting, and tending crops; transporting personnel and materials via truck, car, or motorbike on the extensive road network in the plantation; and habitation (there are several employee camps and two or three small villages in the plantation). Orangutans regularly eat the inner bark of planted acacia trees and consume crops, e.g., tree fruits, from the gardens of villagers, and plantation workers and villagers encounter orangutans in planted areas, along roads, and when orangutans pass near or through human habituation sites. To minimize orangutan–human conflict and/or the harassment of orangutans, plantation management has established an Orangutan Rescue and Management Team trained in orangutan ecology, behavior, and relocation by Y. Rayadin that can respond in situations when orangutans are threatened or when orangutan–human conflict arises.

Data Collection

To document the relative use of different habitat types in the plantation by orangutans and other wildlife, we placed arrays of camera traps and nest transects at eight study sites distributed across the three different habitat types (acacia, eucalyptus, and secondary forest) (Fig. 1). When possible, we employed a stratified random study design, but as the study area is a working plantation, our ability to access different habitats and the need to comply with safety restrictions also determined study site placement. This means that eucalyptus study sites are underrepresented relative to acacia study sites in our data; we have accounted for this by reporting relative as well as absolute measures of abundance for each habitat type. Each study site ($N = 8$) contained at least one survey location, each of which consisted of a camera trap array and a set of nest transects. Some survey sites were large, in which case we placed more than one location in that survey area for a total of $N = 13$ locations surveyed for this study. We always situated locations ≥ 0.5 km apart, and thus consider them independent for the purposes of analysis.

We collected camera trap and nest data September 2012–March 2013. Each camera trap array consisted of 6–11 Bushnell Trophy Cams placed in a grid with cameras 500 m apart. We fixed each camera to a tree at a height of ca. 50 cm from the ground and set them to take three pictures per trigger, with a reset time of 1 s. We baited each camera with one or two durian fruits placed on the ground directly in front of the camera to maximize the chance that an orangutan would walk in front of the camera if it was in the area. Given the olfactory capabilities of orangutans, we felt confident that the durian bait would not draw orangutans to the camera unless they were already in the immediate vicinity. We left cameras at each study site for ca. 30 days, and then moved them to a new site. We surveyed nest transects at the same time that camera traps were placed at each location. Nest transects at each location consisted of three 1-km transects cut perpendicular to a single midline and placed 500 m apart except at the Bhirawa site,

where the smaller size and shape of the study site necessitated single transects 1 km in length. Each transect was surveyed by a team of two or three experienced observers who walked slowly while searching the trees and recorded the presence of orangutan nests, the perpendicular distance from the transect to each nest (m), and the decay state of each nest using 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 (following Spehar *et al.* 2010). We surveyed each transect once in each direction to minimize the likelihood that observers missed nests.

Camera Trapping Data Analysis

For camera trapping data, we considered photos to be independent captures of a species if they were taken at different camera traps, or on separate days at the same camera trap. We employed this conservative criterion of separate days between captures at the same camera trap to minimize the possibility of recaptures of the same individual or group owing to animals remaining in the area as a result of camera trap baiting, or to species traveling in groups (O'Brien *et al.* 2003; O'Connell *et al.* 2010; Tobler *et al.* 2008; Treves *et al.* 2010). For orangutans, we also examined photos for indications of the age–sex class of captured individuals and categorized individuals as adult females with offspring, females without offspring, flanged adult males, unflanged males, and age–sex class unknown, using features such as body size, coat length, the presence or absence of cheek flanges, the presence or absence of dependent offspring, and other relevant characteristics. For the purposes of this analysis, dependent offspring traveling with their mothers were not considered captures independent from their mothers.

We report camera trap results for each survey location, and also sum results across locations within habitat types to provide overall results for each habitat type (secondary forest, acacia, and eucalyptus). We calculated the number of camera trap days for each location by summing the number of days each camera trap was operational in each array (camera traps sometimes failed because of battery issues, weather, or human or animal tampering). We report observed mammalian species richness (the number of different species captured) and proportional mammalian species richness (the percentage of the total mammalian species inventory for the plantation captured in this study) for each location and habitat type. We calculate independent captures per 100 camera trap days, a version of the relative abundance index (RAI_2), following O'Brien *et al.* (2003) and Treves *et al.* (2010), as a measure of relative abundance of different mammalian species, including orangutans, in different locations and habitat types. We calculated this for all mammalian species captured (Overall RAI_2), and separately for each individual mammal species found in the plantation, including orangutans (*Pongo* RAI_2). We also report the number of habitat types at which a species was photographed as an index of relative distribution across habitat types.

Nest Survey Data Analysis

For nest survey data, we calculated three measures that allow us to compare relative orangutan abundance in each survey location/habitat type, and therefore provide some indication of relative habitat use: nest encounter rate, nest density, and orangutan

density. We report each measure for each survey location (although small sample sizes for some locations mean results should be interpreted with caution), and we also summed nest counts across locations within habitat types to provide overall results for each habitat type (secondary forest, acacia, and eucalyptus). We calculated nest encounter rate by dividing nest count by survey effort (km of transect). Unlike nest density and orangutan density estimates, nest encounter rate does not require the application of parameters such as nest decay time that can introduce error. However, direct comparison of nest encounter rates is not advisable if there is variation in nest detection distance and nest decay rate between habitat types. To examine whether such variation was an issue for our dataset, we compared the distribution of nest detection distance between secondary forest ($N = 152$ nests) and acacia ($N = 133$ nests) and found no significant difference in distribution of nest detection distance (secondary forest: mean = $11.24 \pm \text{SD } 8.36$ m; acacia: mean = $11.11 \pm \text{SD } 7.75$ m; Kolmogorov–Smirnov two-sample test, $D = 0.0977$, $P = 0.486$). Eucalyptus sites did not have a sufficient sample size of nests to be included in analysis ($N = 7$). We also compared the distribution of nest decay states for nests counted in each habitat type (Table II). When comparing the two habitat types for which there were sufficient sample sizes of nests (secondary forest and acacia), we found no significant difference between habitat types in the distribution of nest decay states ($\text{df} = 4$, $\chi^2 = 7.01$, $P = 0.14$).

Although these tests suggest that direct comparisons of nest encounter rates between habitat types may be acceptable, we also calculated nest density and orangutan density because these measures provide additional correction for the possible effects of differences in nest detection and decay rate between habitat types. Nest density is calculated using the formula $D_{\text{nest}} = N / L \times 2w$, where N is the number of nests counted from a transect, L is the length of the transect (km), and w is the estimated strip width (km), or the perpendicular distance on either side of the transect from which all nests are assumed to be sighted. The application of w effectively corrects for possible differences in nest detection. Orangutan density can then be calculated using the formula $D_{\text{OU}} = D_{\text{nest}} / p \times r \times t$, 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 (Hashimoto 1995; van Schaik *et al.* 1995). These parameters are often difficult to estimate accurately, and as any changes in parameters p , r , or t produce directly

Table II Number of orangutan nests found in each decay state in different habitat types in the plantation September 2012–March 2013, pooled across survey locations

Habitat type (no. of survey locations)	Nest decay state					Total
	A	B	C	D	E	
Secondary forest ($N = 3$)	5	1	39	41	66	152
Acacia ($N = 8$)	4	8	31	38	52	133
Eucalyptus ($N = 2$)	1	0	0	4	2	7
Total	10	9	70	83	120	292

The decay state of each nest was assessed using 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

proportional changes in the resulting orangutan density estimate, orangutan density estimates must be interpreted with caution (Buij *et al.* 2003; Marshall and Meijaard 2009; Mathewson *et al.* 2008; Spehar *et al.* 2010; van Schaik *et al.* 1995). However, calculating orangutan density using a locally derived decay time (t) potentially allows us to correct for the influence of different nest decay times between habitats, so we have carried out such an analysis here.

Calculation of Parameters w , p , r , and t

We used DISTANCE 6.2 (Thomas *et al.* 2010) to calculate the estimated strip width (w) for secondary forest and acacia habitats. We pooled all nests across locations for each habitat type ($N = 3$ locations for secondary forest; $N = 8$ locations for acacia), as the small number of nests found at some locations made calculation of w for all individual locations impossible, and we had no reason to think that detection distance varied between locations for the same habitat type. Sample size for eucalyptus sites were too small ($N = 7$ nests total) to calculate w , so the w for acacia sites were applied to calculate nest densities for eucalyptus locations. We selected models to fit the detection function for calculating w in DISTANCE 6.2 following Buij *et al.* (2003). 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. We used a P value of 0.88 and an r value of 1.12, the mean of values obtained from four long-term study sites in Borneo (Husson *et al.* 2009). These parameters were calculated using data from less disturbed sites (with the exception of Kinabatangan in Sabah, which consists of a mosaic of oil palm plantations and natural forest). It is possible that r , in particular, is different in highly altered plantation habitat because of differing rates of nest reuse and the construction of day nests (Meijaard *et al.* 2010), which should be taken into account when interpreting our results.

Nest decay time can vary widely between sites, so calculating a local decay time is particularly important (Marshall and Meijaard 2009; Mathewson *et al.* 2008). We calculated habitat-specific decay times for the two major habitat types in the plantation (secondary forest and acacia) from nest monitoring data collected in the plantation March–September 2007. A team of two or three experienced observers walked a set of transects ($N = 9500$ m or 1 km transects each in secondary forest and acacia) in March 2007 and recorded the location and decay state (A, B, C, D, E) of each nest found. The team resurveyed each transect at regular intervals (every 20 days for $N = 11$ intervals in secondary forest; every 10 days for $N = 14$ intervals for acacia), reassessing the decay state of each marked nest and incorporating new nests produced since the previous survey to increase sample size. As most nests were not monitored from the freshest decay stage to disappearance, we used a Markov chain analysis (following Mathewson *et al.* 2008) to calculate nest decay rate for secondary forest ($t = 320.33$ days, based on $N = 251$ nests) and acacia ($t = 117.5$ days, based on $N = 89$ nests).

Quantifying Orangutan Density Estimate Precision

The indices of orangutan abundance (nest encounter rate, nest density, and orangutan density) provided for each location are meant to compare relative use of different habitat types by orangutans, not to provide an estimate of overall orangutan abundance in each habitat type in the plantation. However, orangutan density estimates for each

habitat type may be useful for assessing the conservation value of different habitat types, so we wanted to provide some measure of precision for these estimates. We used the delta method to calculate the coefficient of variation (CV) and confidence intervals (CIs) for our orangutan density estimates for each habitat type. The delta method accounts for variation in nest encounter rate and parameters p , r , and t to obtain the CV for orangutan density using the formula $CV^2(D_{OU}) = CV^2(N) + CV^2(p) + CV^2(r) + CV^2(t)$. The CV for nest encounter (N) is provided by DISTANCE 6.2 and includes the probability density function evaluated at distance 0. This CV was calculated for each habitat type (secondary forest and acacia) based on the analysis of all nests found in each habitat type. The CVs for p and r were calculated based on site-specific studies of these parameters (Husson *et al.* 2009). Because a Markov chain analysis was used to obtain a nest decay rate and very few nests were followed from the freshest decay stage to disappearance, we could not calculate a CV for t and thus it was not incorporated into the calculation. This should be taken into account when considering the precision of our density estimates, as incorporation of nest decay rate error into the calculation would almost certainly have broadened the 95% CI for our orangutan density estimates. We used the calculated CVs to determine 95% CIs for our orangutan density estimates following Ancrenaz *et al.* (2004, equations 3 and 4).

GIS Analysis

We obtained Landsat maps of the plantation and surrounding areas in 2014 which, along with groundtruthing carried out 2012–2014, allowed us to determine the location of key landscape features that were potentially important in influencing orangutan use of an area: 1) the closest boundary with Kutai National Park (Boundary Kutai NP); 2) the closest natural forest patch outside the plantation (Forest patch outside); 3) the closest secondary forest patch inside the plantation (Forest patch inside); and 4) the closest riparian corridor, or waterway with significant natural forest cover that could potentially act as a natural forest corridor inside the plantation (riparian corridor). We used ArcMAP 10.2 (ESRI 2014, <http://www.esri.com/>) to calculate the straight-line distance from each study location to the closest boundary of these key landscape features. When the study location was a secondary forest patch, we set the distance to SFP to 0 for that location (Table III).

Statistical Tests

The relationship between habitat type and our measures of orangutan abundance (*Pongo* RAI₂ and nest count measures, including nest encounter rate, nest density, and orangutan density), as well as the relationship between habitat type and more general indicators of wildlife abundance (relative species richness and overall RAI₂), were tested using a chi-square goodness-of-fit test. Logistic regression was used to model measures of orangutan abundance (*Pongo* RAI₂ and nest count measures, including nest encounter rate, nest density, and orangutan density) as a function of predictor variables, including survey location habitat type (secondary forest, acacia, and eucalyptus) and/or distance to potentially important landscape features: the boundary with Kutai National Park (Boundary Kutai NP), the closest natural forest areas outside the plantation (Forest patch outside), the closest secondary forest patches inside the

Table III Shortest distance (km) from survey locations in the plantation to landscape features that may influence orangutan habitat use: Natural forest areas inside the plantation (Forest patch inside and Riparian corridor) and outside the plantation (Boundary Kutai NP and Forest patch outside)

Site	Locations	Forest patch inside	Riparian corridor	Boundary Kutai NP	Forest patch outside
Secondary Forest					
Beliwit 1	BE-SF	0	14.4	0.55	16.4
Bhirawa	BH-SFA	0	12.26	31.11	4.12
	BH-SFB	0	12.78	31.39	4.09
Acacia					
Beliwit 2	BE-A	3.3	14.43	2.15	18.78
Muara	MB-A19	15.29	7.47	8	20.81
Bengkal	MB-A20	15.78	6.47	7.34	21.09
Sebulu	S-A	10.35	12.74	23.89	16.93
Padat Kayra	PK-AA	11.5	23.5	41	7.22
	PK-AB	9.82	21.9	39.52	5.96
Menara Api	MA-AA	17	28.2	44.75	12.95
	MA-AB	16.37	28.14	48.84	11.63
Eucalyptus					
Eucalyptus	Plot A	2.94	15.79	34.5	3.91
	Plot B	4.47	17.27	35.73	2.85

plantation (Forest patch inside), and the closest riparian corridor, or waterway with significant forest cover that could potentially act as a natural forest corridor inside the plantation (Riparian corridor) (Table III). In total, we compared support for 26 models of each measure of orangutan abundance, including a null (intercept-only) model for each analysis. The relative support for each model was compared in an information-theoretic framework using an information criterion corrected for small sample size (AICc, Burnham and Anderson 2002). Analyses and plots were coded in R 3.3.1 (The R Foundation for Statistical Computing 2016, <http://www.r-project.org>). Before logistic regression analyses, all data sets were checked for outliers, and as a result all nest count measures (nest encounter rate, nest density, and orangutan or *Pongo* density) were log-transformed to reduce skew in these data. As it is possible that male and female orangutans use disturbed habitat differently, we examined the relationship between the number of males and females captured at each study location (using the $N = 12$ independent captures that could be assigned to sex) and distance to nearest natural forest area (for which Boundary Kutai NP, Forest patch outside, Forest patch inside, and Riparian corridor were all considered) using a nonparametric Spearman rank correlation.

Ethical Note

This research complied with protocols approved by the Institutional Animal Care and Use Committee of the University of Wisconsin Oshkosh (protocol 0026–000255-R1–01–06–15), was approved by the State Ministry of Research and Technology of

Indonesia (permit number 242/SIP/FRP/SM/VII/2012), and adhered to the legal requirements of Indonesia. None of our data collection methods endangered our study animals. This includes the baiting of camera traps, which can be a concern at sites where human–wildlife conflict is high because humans can use bait as an opportunity to poison or kill animals (Hockings and Humle 2009; Hockings and McLennan 2016). Given the active commitment of plantation management to orangutan conservation and the low observed rates of human–orangutan conflict in the plantation we felt confident that baiting did not endanger orangutans.

Results

Camera Trapping

Over 2065 total camera trap days across all habitat types we collected 5641 identifiable photos of mammal species, 417 of which were independent photo captures taken one day apart (Table IV). These photos documented 23 different mammal species across the plantation, including three primate species (Table V). Orangutans accounted for 3% of total identifiable photos and 4% of total independent photo captures during this study (Table V). All age–sex classes of orangutan were captured via camera trap in the plantation (Table VI), and there was no correlation between the number of females or males captured at a location and the distance to the nearest forested area (Spearman rank correlation; males: $r_s = -0.45$, $P = 0.26$; females: $r_s = 0.10$, $P = 0.80$). When we examined the distribution of orangutan captures over time (using a data set of $N = 17$ captures because a reliable time of day was not recorded for one capture) we found that overall the majority of captures occurred in the morning, 06:00–12:00 h ($N = 10$, 58%). When we examined capture time by habitat type, we found that for planted areas (acacia and eucalyptus combined, $N = 9$ captures), $N = 7$ captures were recorded 06:00–12:00 h, $N = 2$ captures were recorded 12:00–15:00 h, and no captures were recorded after 15:00 h. For secondary forest areas ($N = 8$ captures), $N = 3$ captures were recorded 06:00–12:00 h, $N = 4$ captures were recorded 12:00–19:00 h, and one capture was recorded in the middle of the night at ca. 01:46 h.

Habitat types (secondary forest, acacia, and eucalyptus) differed in the number of species detected/100 camera trap days (chi-square goodness-of-fit test: $df = 2$, $\chi^2 = 10.10$, $P = 0.006$) and RAI_2 , or the number of independent photo captures of species/100 camera trap days ($df = 2$, $\chi^2 = 23.62$, $P < 0.001$), with secondary forest exhibiting the highest values (Table IV). This difference remained significant when we attempted to account for the small number of eucalyptus locations ($N = 2$) by lumping eucalyptus locations with acacia locations (species detected/100 camera trap days: $df = 1$, $\chi^2 = 7.32$, $P = 0.007$; RAI_2 : $df = 1$, $\chi^2 = 21.83$, $P < 0.001$) or eliminating eucalyptus locations from the analysis (species detected/100 camera trap days: $df = 1$, $\chi^2 = 6.81$, $P = 0.009$; RAI_2 : $df = 1$, $\chi^2 = 16.43$, $P < 0.001$), and after we performed a Bonferroni correction for multiple tests.

Species richness was roughly similar across habitat types, ranging 65–78% of total species detected in the plantation, although there was a great deal of variation in species richness between study locations (Table IV). Our data indicate that some mammalian species were more widely distributed and abundant across the plantation relative to

Table IV Camera trapping and orangutan nest survey data for survey locations in each habitat type (secondary forest, acacia, and eucalyptus) in the plantation September 2012–March 2013

Survey information		Camera trapping				Nest surveys						
Site	Locations	Camera trap days	Independent photos (captures)	Species richness	Species richness as % total	Overall RAI ₂	Pongo RAI ₂	Transect length (km)	Nest count	Nest encounter rate (nests/km)	Nest density (nests/km ²)	Pongo density (indiv/km ²)
Secondary forest												
Beliwit 1	BE-SF	160	96	16	0.70	60	0.63	3	60	20	613.53	1.95
Bhirawa	BH-SFA	137	40	8	0.35	28.47	2.19	1	52	52	1595.19	5.07
	BH-SFB	107	28	6	0.26	26.17	2.80	1	40	40	1227.07	3.90
Overall		404	164	16	0.70	40.35	1.98	5	152	30.4	895.74	2.85
Acacia												
Beliwit 2	BE-A	153	10	5	0.22	6.54	0.65	3	18	6	168.15	1.46
Muara Bengkal	MB-A19	72	4	3	0.13	5.56	0	3	1	0.33	9.34	0.08
	MB-A20	65	1	1	0.04	1.54	0	3	1	0.33	9.34	0.08
Sebulu	S-A	177	21	7	0.30	11.86	1.13	3	49	16.33	457.75	3.96
Padat Karya	PK-AA	208	43	6	0.26	20.67	0	3	12	4	112.10	0.97
	PK-AB	179	23	6	0.26	12.85	0.56	3	22	7.33	205.52	1.78
Menara Api	MA-AA	88	8	8	0.35	31.82	0	3	17	5.67	158.81	1.38
	MA-AB	183	50	14	0.61	27.32	0.55	3	13	4.33	121.44	1.05
Overall		1125	180	18	0.78	16.00	0.44	24	133	5.54	205.52	1.78
Eucalyptus												
Eucalyptus	Plot A	293	57	9	0.39	19.45	1.71	3	5	1.67	46.71	0.40
	Plot B	243	16	8	0.35	6.58	0	3	2	0.67	18.68	0.16
Overall		536	73	15	0.65	13.62	0.93	6	7	1.17	102.94	0.85

Camera trapping data includes data for all mammal species captured via camera trap, including orangutans. RAI₂ is the number of independent photo captures/camera trap days × 100. Overall RAI₂ includes captures of all mammal species; Pongo RAI₂ includes only orangutan captures

Table V Mammalian species detected via camera trap, indices of relative abundance for each species (RAI₂, or no. of independent captures/camera trap days × 100), and distribution across the landscape for each species (habitat types and no. of locations in which each species was detected) in the plantation September 2012–March 2013

Species	Common name	Habitat types	No. of locations	Total photos	Ind photos (captures)	RAI ₂
Primates						
<i>Macaca fascicularis</i>	Long-tailed macaque	SF, A, E	3	137	12	0.58
<i>Macaca nemestrina</i>	Pig-tailed macaque	SF, A, E	10	1854	113	5.47
<i>Pongo pygmaeus</i>	Bornean orangutan	SF, A, E	8	158	18	0.87
Carnivora						
<i>Paguma larvata</i>	Masked palm civet	SF, A, E	6	72	10	0.48
<i>Herpestes semitorquatus</i>	Collared mongoose	SF, E	2	7	2	0.10
<i>Hemigalus derbyanus</i>	Banded civet	SF, E	2	9	3	0.15
<i>Viverra zangalunga</i>	Malay civet	A, E	7	118	24	1.16
<i>Arctogalidia trivirgata</i>	Small-toothed palm civet	E	1	3	1	0.05
<i>Prionailurus bengalensis</i>	Leopard cat	SF, A	3	15	6	0.29
<i>Prionailurus planiceps</i>	Flat-headed cat	SF	1	3	1	0.05
<i>Helarctos malayanus</i>	Sun bear	A	1	6	1	0.05
Scandentia						
<i>Tupaia picta</i>	Painted treeshrew	SF, A	3	144	23	1.11
<i>Tupaia tana</i>	Large treeshrew	A	2	24	4	0.19
<i>Tupaia minor</i>	Lesser treeshrew	A	1	3	1	0.05
<i>Tupaia glis</i>	Common treeshrew	A	2	48	10	0.48
Rodentia						
<i>Callosciurus notatus</i>	Plantain squirrel	SF, A, E	3	82	16	0.77
<i>Exilisciurus</i> spp.	Pygmy squirrel	E	1	5	2	0.10
<i>Rattus</i> spp.	Field rat	SF, A, E	4	70	13	0.63
<i>Hystrix brachyura</i>	Malayan porcupine	SF, A, E	8	859	36	1.74
Artiodactyla						
<i>Rusa unicolor</i>	Sambar deer	SF, A	3	136	7	0.34
<i>Muntiacus muntjak</i>	Southern red muntjak	SF, A, E	13	933	45	2.18
<i>Tragulus napu</i>	Greater mouse deer	SF, A, E	5	656	55	2.66
<i>Sus barbatus</i>	Bearded pig	SF, A, E	8	299	14	0.68

We surveyed 13 locations across three habitat types including secondary forest (SF), acacia (A), and eucalyptus (E)

others, with variation between species in the number of total photos (mean: 245, range: 3–1854), the number of independent photo captures (mean: 18, range: 1–113), the number of locations at which the species was detected (mean: 4, range: 1–13), and RAI₂ (mean: 0.88, range: 0.05–5.47) (Table V). The RAI₂ of the three primate species fall within the top 50% of all species detected, with pig-tailed macaques (*Macaca nemestrina*) exhibiting the highest overall number of captures and highest RAI₂ of any species, and orangutans exhibiting a RAI₂ higher than 70% of the species detected

Table VI Age–sex class of orangutan individuals captured via camera trap across survey locations in the plantation September 2012–March 2013

Site	Location	Adult female w/ infant	Female w/out infant	Flanged adult male	Unflanged male	Unknown
Secondary forest						
Beliwit 1	BE-SF	1	0	0	0	0
Bhirawa	BH-SFA	1	0	2	0	1
Bhirawa	BH-SFB	0	0	0	1	2
Total		2	0	2	1	3
Acacia						
Beliwit 2	BE-A	0	0	0	0	1
Sebulu	S-A	0	0	1	0	1
Padat Karya	PK-AB	0	1	0	0	0
Menara Api	MA-AB	1	0	0	0	0
Total		1	1	1	0	2
Eucalyptus						
Eucalyptus	Plot A	3 ^a	1	0	0	1
Total		3	1	0	0	1
Grand total		6	2	3	1	6

Individuals were classified as “Unknown” if age–sex class could not be confidently assessed from camera trap photos

^a These three captures likely represent recaptures of the same mother–infant pair

(Table V). Orangutans were also one of only 44% of species that were detected in all three habitat types in the plantation (Table V), and the RAI_2 for orangutans ($Pongo$ RAI_2) did not differ significantly between habitat types (chi-square goodness-of-fit test: $df = 2$, $\chi^2 = 1.62$, $P = 0.44$), even when we lumped eucalyptus locations with acacia locations ($df = 1$, $\chi^2 = 1.46$, $P = 0.23$) or eliminated from the analysis ($df = 1$, $\chi^2 = 1.97$, $P = 0.16$). However, $Pongo$ RAI_2 showed a great deal of variation between locations within habitat types, ranging 0.63–2.80 in secondary forest, 0–1.13 in acacia, and 0–1.17 in eucalyptus (Table IV).

Nest Surveys

We surveyed a total of 35 km of transect across all habitat types, and counted 292 orangutan nests. There was a wide range of variation in nest encounter rate, nest density, and orangutan density between locations within habitat type, e.g., at acacia locations nest encounter rate ranged 0.33–6.00 nests/km, nest density ranged 9.34–457.75 nests/km², and orangutan density ranged 0.08–3.96 indiv/km²) (Table IV). When we pooled results across locations within habitat types, the difference between habitat types was significant for nest encounter rate (chi-square goodness-of-fit test: $df = 2$, $\chi^2 = 65.46$, $P < 0.001$) and nest density ($df = 2$, $\chi^2 = 926.31$, $P < 0.001$), and remained significant when we lumped eucalyptus and acacia locations (nest encounter rate: $df = 2$, $\chi^2 = 59.94$, $P < 0.001$; nest density: $df = 2$, $\chi^2 = 761.00$, $P < 0.001$), when we excluded eucalyptus locations from the analysis (nest encounter rate: $df = 2$,

$\chi^2 = 44.93$, $P < 0.001$; nest density: $df = 2$, $\chi^2 = 432.60$, $P < 0.001$), and after we performed a Bonferroni correction for multiple tests. There was no significant difference between habitat types in orangutan density ($df = 2$, $\chi^2 = 1.09$, $P = 0.58$). The orangutan density estimates for each habitat type, pooled across locations within habitat types, was 2.85 indiv/km² (95% CI: 1.71–4.75) for secondary forest, 1.78 indiv/km² (95% CI: 1.22–2.60) for acacia, and 0.85 indiv/km² (95% CI: 0.61–1.18) for eucalyptus.

Factors Influencing Orangutan Habitat use

Nest encounter rate and nest density were significantly higher in secondary forest, but *Pongo* RAI₂ and orangutan density were not. In addition, all measures showed a great deal of variation between locations within each habitat type (Table IV). Using a logistic regression, the best supported model for *Pongo* RAI₂ had distance to the nearest secondary forest patch as the only predictor (Table VII), meaning that *Pongo* RAI₂ decreased as distance to the nearest secondary forest patch increased. The support for this model was particularly strong, with the evidence ratio suggesting that this model was more than 6.5 times more likely to explain *Pongo* RAI₂ than the next best model, which had habitat type as the only predictor. The best supported model for all the log transformed nest count measures (nest encounter rate, nest density, and orangutan density) combined habitat type and distance to the nearest area of natural forest (including the nearest secondary forest patch, the nearest natural forest area outside the plantation, and Kutai National Park) (Table VII), although support for this model was not as strong as the support for the best for model for *Pongo* RAI₂.

Discussion

Our data suggest that orangutans are more common than many other mammals in the plantation, as the RAI₂ for orangutans (*Pongo* RAI₂) was higher than the RAI₂ for 70% of the other mammal species detected during this study, and orangutans were one of 44% of mammalian species detected in all three plantation habitat types (secondary forest, acacia, and eucalyptus). However, the presence of natural forest seems to play a key role in orangutan use of different areas. Two of our measures of orangutan abundance (nest encounter rate and nest density) were significantly higher in secondary forest, while two were not (orangutan density and *Pongo* RAI₂). A logistic regression indicates that it is not just the habitat type of the survey location but also (and in the case of *Pongo* RAI₂, primarily) proximity to natural forest areas that influences orangutan abundance. We must interpret these results with caution given our small sample sizes for some survey locations and habitat types. However, these data do allow us to make observations about orangutan use of an anthropogenic landscape that can provide guidance for further research and conservation.

Our comparisons of RAI₂ across species indicate that orangutans fall in a category of high-to-intermediate RAI₂ along with several other species that are known to be relatively flexible in the face of human habitat alteration, e.g., the bearded pig (*Sus barbatus*), greater mouse deer (*Tragulus napu*), Malay porcupine (*Hystrix brachyuran*), and Malay civet (*Viverra zibetha*). Our relatively high *Pongo* RAI₂ may be due not

Table VII Relative support for selected models of orangutan abundance in the plantation September 2012–March 2013

Model	Log likelihood	<i>K</i>	AICc	Δ AICc	AICcWt	Cumulativeweight	Evidence ratio
<i>Pongo</i> RAI ₂							
FPI	-12.822	3	34.311	0	0.668	0.668	1.000
Habitat type	-12.538	4	38.076	3.766	0.102	0.769	6.572
FPO	-15.113	3	38.892	4.582	0.068	0.837	9.884
Null	-16.894	2	38.988	4.677	0.064	0.901	10.366
Log nest encounter rate							
Habitat type + FPI + KNP + FPO	-4.507	7	45.413	0	0.690	0.690	1.000
Habitat type + FPI + KNP	-11.071	6	48.142	2.729	0.176	0.866	3.913
Habitat type	-19.555	4	52.110	6.696	0.024	0.891	28.451
Habitat type + FPI + RC	-13.126	6	52.252	6.838	0.023	0.913	30.546
Log nest density							
Habitat type + FPI + KNP + FPO	-4.506	7	45.412	0	0.687	0.687	1.000
Habitat type + FPI + KNP	-11.043	6	48.086	2.674	0.181	0.868	3.808
Habitat type	-19.519	4	52.038	6.626	0.025	0.893	27.465
Habitat type + FPI + RC	-13.108	6	52.216	6.804	0.023	0.916	30.021
Log orangutan density							
Habitat type + FPI + KNP + FPO	-4.506	7	45.412	0	0.598	0.598	1.000
Habitat type + FPI + KNP	-11.043	6	48.086	2.674	0.157	0.755	3.808
Null	-22.439	2	50.078	4.667	0.058	0.813	10.311
FPI	-21.036	3	50.738	5.327	0.042	0.854	14.344

Models are ranked in order of increasing AICc values (Akaike's information criterion, adjusted for small sample size). *K* is the number of fitted parameters and Δ AICc is the difference between the indicated model and the best model (the model with the lowest AICc). Only the top four models (models with Δ AICc > 7) are shown, as the explanatory power of models declined significantly after this. The generalized Akaike weight of each model (AICcWt) indicates the relative strength of evidence in support of each model; it ranges from 0 to 1. Evidence ratio is the AICcWt of that model divided by the AICcWt of the model with the lowest AICc; lower numbers indicate greater support. Habitat type = habitat of survey location; FPI = distance to nearest secondary forest patch inside the plantation; KNP = distance to boundary with Kutai National Park; FPO = distance to closest natural forest patch outside plantation; and RC = distance to nearest riparian corridor inside plantation. Please see Methods for further description of model predictors

to a higher relative abundance of orangutans, but to the higher detectability of orangutans relative to other species. Detectability can vary based on features such as body size, diurnality, terrestriality, and gregariousness (O'Brien *et al.* 2003; O'Connell *et al.* 2010; Tobler *et al.* 2008; Treves *et al.* 2010). For example, this may be one reason for the very high RAI₂ for pig-tailed macaques in this study, as they are a large-bodied terrestrial species that lives in large social groups. However, we do not think detectability was an issue for *Pongo* RAI₂ in our study for two reasons. First, we employed a very conservative criterion for independent photo captures, requiring that they be taken at different camera traps or spaced at the same camera trap by at least 1 day. We did this

to minimize the possibility that we would “re-count” captures of the same individual or group on the same day because of gregariousness or the fact that individuals were spending extended time near the camera because of the presence of bait (durian) (following Treves *et al.* 2010). Second, while orangutans are large-bodied they are also largely arboreal and live at low densities, and prior studies have found that terrestrial camera trapping may underestimate orangutan density (Spehar *et al.* 2015). Therefore, it is unlikely that the *Pongo* RAI₂ reported here is an overestimate.

We found that two of our measures of orangutan abundance (nest encounter rate and nest density) were significantly higher in secondary forest locations, while two other measures (orangutan density and *Pongo* RAI₂) were not. The difference in magnitude between nest encounter rate and nest density on one hand, and orangutan density on the other, may have been influenced by the application of nest decay rates to calculate orangutan density from nest counts. Secondary forest habitat had a much longer decay time than acacia ($t = 320.33$ days vs. $t = 117.5$ days), which, when applied in the orangutan density calculation, reduced the effect of the large difference in nest counts between secondary forest and acacia and eucalyptus locations. This illustrates the effect that nest decay rates can have on estimates of orangutan abundance and underscores the importance of calculating local nest decay rates (Marshall and Meijaard 2009; Mathewson *et al.* 2008). Also, the rough correspondence between our camera trapping and nest density results, in terms of the relative difference in orangutan abundance between habitat types, e.g., higher in secondary forest and lower in planted areas, suggests that both methods seem to be measuring the same kinds of difference. Orangutan ground use in different habitat types may be similar enough, at least in this setting, to use camera trapping data to assess relative use of different habitats. However, different use of the ground by orangutans in different habitats could affect capture rates (Ancrenaz *et al.* 2014) and may have influenced our camera trapping results.

Our data on orangutan abundance provide some information about how orangutans use different habitats within the plantation. A logistic regression indicates that proximity to natural forest areas best predicts orangutan abundance calculated using camera trap data (RAI₂), but that habitat type combined with distance to natural forest best predicts orangutan abundance calculated using nest counts (nest encounter rate, nest density, and orangutan density). This difference in results between methods may be due to the fact that camera trapping and nest counts sample somewhat different types of habitat use, providing clues into the role that natural forest areas play for orangutans in the plantation. First, natural forest patches may be important nest sites. Our data and anecdotal observations suggest that orangutans prefer to build their nests for resting and sleeping in natural forest patches, perhaps because the denser canopy cover means they are less exposed (Y. Rayadin and S. Spehar, *unpubl. Data*). Second, natural forest areas are almost certainly a source of nutritionally or seasonally important foods. The inner cambium of young acacia trees is commonly eaten by orangutans in the plantation (Meijaard *et al.* 2010; Y. Rayadin, *unpubl. Data*); indeed, such feeding destroys a significant percentage of the plantation management’s acacia crop each year (Y. Rayadin, *unpubl. Data*). However, a diet that relies entirely on acacia cambium is probably nutritionally and perhaps calorically insufficient over the long term (Wich *et al.* 2012a). We have seen orangutans travel relatively long distances to feed at trees fruiting in secondary forest patches, and have seen up to four individuals feeding in a single fruiting fig (*Ficus* spp.) tree in one of these patches (S. Spehar and Y. Rayadin,

unpubl. Data). A recent study of patterns of chimpanzee food availability across an anthropogenic landscape in Bossou, Guinea, West Africa, found that natural forest areas contained the highest densities of chimpanzee food tree species (Bryson-Morrison *et al.* 2016). We suspect a similar pattern would be found in our study area, indicating that habitat types in anthropogenic landscapes vary in temporal and spatial resource availability and that remnant natural forest areas provide crucially important resources for resident primates. Finally, natural forest patches may be important for thermoregulation. The challenge of maintaining homeostasis in different climactic conditions constrains activity and influences primate distribution and density (Dunbar *et al.* 2009), and modeling indicates that mean daily temperature range is one of the major predictors of Bornean orangutan distribution (Wich *et al.* 2012a). Daytime temperatures in planted areas of the plantation are often well above 32 °C, hotter than daytime temperature in closed-canopy natural forest in the same region (Wich *et al.* 2012a), and are frequently highest in the early afternoon 12:00–15:00 h (Y. Rayadin and S. Spehar, *pers. obs.*). The fact that we found more captures in planted areas 06:00–12:00 h (77%), when temperatures are cooler, compared to secondary forest locations where captures were more evenly distributed across all times of day (38% 06:00–12:00 h and 50% 12:00–19:00 h), provides some preliminary support for this hypothesis. Orangutans living in the plantation may need to retreat to natural forest patches to rest and escape the heat in the middle of the day.

If orangutans use planted areas primarily for feeding or movement, but prefer to build nests in natural forest, we would expect that measures of abundance based on nest counts would be most strongly influenced by the habitat type of the survey location, while this would not necessarily be true of camera trap data. Proximity to natural forest should be important for both, as orangutans may return to natural forest to rest or take advantage of important food sources even if they move through or forage in planted areas nearby (Ancrenaz *et al.* 2015). This is the pattern we see in our data. Overall, our data suggest that orangutans use all the major habitat types found in the plantation, but that their activities are concentrated near natural forest areas that they may use as a “home base” for sleeping, resting, and accessing key resources. This echoes the findings of Ancrenaz *et al.* (2015) that most orangutan activity in plantations is concentrated near natural forest, as well as similar results for chimpanzees living in anthropogenic landscapes (Blanco and Waltert 2013). However, researchers must confirm this pattern with further data collection, in particular direct behavioral observations (cf. Russon *et al.* 2015). Furthermore, it is possible that additional factors, e.g., intensity of human activity, influence habitat use (Campbell-Smith *et al.* 2011b), but unfortunately we were not able to measure such variables in our study; future studies should employ a design that allows them to take such variables into account.

Another insight that our data provide is that the plantation landscape almost certainly harbors a significant population of resident orangutans. A previous survey (Meijaard *et al.* 2010) calculated that the SRH/SHJ plantation contained, conservatively, 1361 individuals (95% CI: 1004–2304), but stated it was “still too early to know whether these populations are transient individuals in search of new forest habitat, or whether this area is part of a recolonization process from nearby over-degraded forests” (p. e12813). Many of the results from Meijaard *et al.* (2010) and our study are not directly comparable, due to changes in the forest cover of the two plantations and differences in how survey effort was allocated. Also, unlike Meijaard *et al.* (2010) we do not calculate

an overall orangutan population estimate for our study area, as there are too many unknowns about the overall forest cover in the plantation to do this reliably. However, for those results that are comparable (Table VIII), it seems that the population of orangutans in the plantation has remained similar since the Meijaard *et al.* (2010) study or perhaps even increased. We must be cautious in directly comparing results within habitat type from each study because the locations surveyed in each habitat type were not necessarily the same between studies. However, this comparison does seem to indicate that a significant population of orangutans continues to live in the plantation. Furthermore, the mean distance from our study locations to the nearest boundary with Kutai National Park, the only protected area that abuts the plantation, was 26.83 km (range 0.55–48.84 km). Proximity to Kutai National Park, while a predictor of orangutan abundance measured using nest counts, was not the strongest single predictor of any measure of abundance. Distances to other natural forests areas outside the plantation were also large (mean 11.29 km, range 2.85–21.09 km). It therefore seems highly unlikely that individuals are regularly moving in and out of the plantation from Kutai National Park or other nearby forested or protected areas. The SRH/SHJ plantation is likely, for better or worse, primary habitat for a large population of Bornean orangutans.

According to our camera trap capture data (Table VI) the population of orangutans in the SRH/SHJ plantation includes both males and females, including females with dependent offspring. Although previous studies suggested that males may be found more frequently or deeper into the interior of disturbed habitats than females (Ancrenaz *et al.* 2015), our limited data do not indicate that this is the case in our study area. Both males and females appear to live in the plantation and use all habitat types there. However, our sample size is very small and we need long-term camera trapping and behavioral data to determine if there are significant sex differences in orangutan use of plantations.

Although the data from our study are limited, when combined with a growing body of evidence from other sites (Table I), they have significant implications for Bornean orangutan conservation. They indicate that, like other great apes (Hockings *et al.* 2015)

Table VIII Comparison between results of a previous orangutan nest survey in the plantation (Meijaard *et al.* 2010) and this study (September 2012–March 2013)

	Planted areas		Buffer zone		Conservation areas	
	Encounter rate (nests/km)	<i>Pongo</i> density (indiv/km ²)	Encounter rate (nests/km)	<i>Pongo</i> density (indiv/km ²)	Encounter rate (nests/km)	<i>Pongo</i> density (indiv/km ²)
Meijaard <i>et al.</i> (2010) PT SRH	5.3	1.45 (1.24–1.75)	12	n/a	9.2	1.76 (1.11–4.5)
Meijaard <i>et al.</i> (2010) PT SHJ	13.8	n/a	n/a	n/a	25.7	n/a
This study	5.54	1.78 (1.22–2.60)	20	1.95 (1.17–3.24)	46	3.99 (3.00–5.30)

The 95% CI for orangutan density estimates is provided in parentheses

and some other primate species (Estrada *et al.* 2012; McKinney 2015), Bornean orangutans are flexible enough to coexist with many human activities—provided they have sufficient access to natural forest (Ancrenaz *et al.* 2015) and that killing, which can quickly decimate orangutan populations (Davis *et al.* 2013; Marshall and Nardiyono 2006; Marshall *et al.* 2009; Meijaard *et al.* 2011; Wich *et al.* 2012b), is prevented. This suggests that a pivot or at least broadening in Bornean orangutan conservation strategy should occur, from the current dominant strategy that focuses largely on establishing and maintaining protected areas, to a landscape approach that recognizes the conservation value of habitat outside protected areas and focuses on how we can promote orangutan coexistence with humans across different land-use types (Meijaard 2016; Meijaard *et al.* 2012; Sayer *et al.* 2013). Such a shift in strategy is further supported by modeling that indicates that protected areas alone are not sufficient to preserve biodiversity in Southeast Asia, especially in the face of advancing climate change (Brun *et al.* 2015; Gregory *et al.* 2012; Scriven *et al.* 2015; Struebig *et al.* 2015). Such a landscape approach is relevant for other primate species as well. However, the conservation value of anthropogenic landscapes depends on proper management. If such landscapes are to support orangutans and other primate populations over the long term, killing must be minimized, animals must have access to natural forest, and metapopulation dynamics such as gene flow must be supported by maintaining sufficient connectivity (Lindenmayer *et al.* 2006; Meijaard 2016). This requires working with a broad range of stakeholders (including local and national government, private companies, nongovernmental organizations (NGOs), and local communities) to coordinate land-use practices, develop strategies to mitigate primate–human conflict, and enforce existing laws banning the killing of orangutans and other primates (Sayer *et al.* 2013).

Working with private companies that manage industrial plantations and extractive activities is especially important in orangutan range countries (Indonesia and Malaysia), as these stakeholders often have the largest on-the-ground impact on orangutan habitat. Enforcement of existing laws, e.g., Indonesia’s requirement that 10% of all plantations remain forested, and targeted incentives for wildlife-friendly behavior are vitally important, and must come from the government as well as the international community in the form of consumer pressure and certification schemes (Meijaard *et al.* 2012; Wilcove and Koh 2010). Also crucial, however, is training and support for plantation management in wildlife-friendly land-use planning and orangutan-human conflict mitigation strategies. This is an area in which NGOs and scientists can make a real impact. For example, one of the authors (Y. Rayadin) has worked with multiple companies in East Kalimantan, including the management of the SRH/SHJ plantation, to create Orangutan Management and Rescue Teams made up of carefully selected company employees who receive training in orangutan ecology, behavior, and relocation. These teams increase the company’s ability to effectively manage the orangutan population in its concession and to respond to orangutan–human conflict. Larger-scale coordination between stakeholders, e.g., between different companies and with local communities, to carry out broad land-use planning is also needed. NGOs and scientists, together with local government, can encourage this by acting as links between important stakeholders and providing support for the coordination process.

Researchers must gather additional information to fine-tune an approach that incorporates anthropogenic landscapes into conservation strategy for orangutans and other primates. We still have limited understanding of how orangutans use different anthropogenic landscapes and the resources in them, especially their relative reliance on different food sources (including human crops) and their ability to move through different parts of the anthropogenic matrix. Such information is crucial to effective land-use planning. We also do not yet understand the possible long-term impacts of habitat fragmentation, altered diets, and increased human contact on the health and reproduction of orangutans and other primates (Chapman *et al.* 2005). Orangutans are long-lived animals and there is potentially a long “lag time” between events that negatively impact populations and extinction (Marshall *et al.* 2009). It is thus possible that orangutans and perhaps other primates currently living in anthropogenic habitats represent declining remnants rather than viable populations that will persist long term (Meijaard 2016). Only careful long-term monitoring, combined with genetic, behavioral, and hormonal data to assess health and demography, will help us discern which is the case and how we might maximize the likelihood of long-term persistence.

Finally, another issue is potential variation between the different orangutan species and subspecies in the ability to adapt to human activities. The well-documented variation between populations due to different ecological selection pressures (van Schaik *et al.* 2009) may translate into increased flexibility in those orangutans adapted to harsher “natural” habitat conditions, e.g., Northeast Bornean orangutans, and relatively lower flexibility in those adapted to more abundant conditions, e.g., Sumatran orangutans. Indeed, studies to-date indicate that Sumatran orangutans do not respond well to human habitat alteration (Husson *et al.* 2009), which clearly has important implications for the kinds of conservation strategies that should be implemented for the species. Such taxa-specific responses are also relevant to other primate species, as features like the degree of behavioral flexibility, dietary breadth, and reproductive rate all impact the response of a species to anthropogenic change (Cardillo *et al.* 2005; Hockings *et al.* 2015; Isaac and Cowlishaw 2004; Kamilar and Paciulli 2008). Addressing these knowledge gaps requires a comparative approach studying orangutans and other primates in a broad range of contexts, including at relatively undisturbed sites and at sites dominated by planted and secondary vegetation. Such research should be a top priority for orangutan and other primate biologists and conservationists going forward.

Acknowledgments We are very thankful to the management of PT Surya Hutani Jaya, PT Sumalindo Hutani Jaya, and Sinar Mas Forestry Group, especially Robert Siagian, Rudi Sasgo, Supriyono Suparman, and Supriyatno, for facilitating and supporting our research in the plantation. We are also grateful to the State Ministry of Research and Technology of Indonesia for granting us permission to conduct research in Indonesia. We thank Hendra Masrun, Nur Komari, Sugihono Hanggito, Slamet Rohmadi, and Ari Meididit of the Center for the Study of Tropical Ecology and Conservation (Ecositrop) for assistance with data collection and general support; Kara Norby, Katherine Scott, and Nicola Thurley for their assistance with data collection; and Junaedi Samsudin and Paul Mathewson for their work on GIS and remote sensing and statistical analyses. We also thank Erik Meijaard and Marc Ancrenaz for essential support, advice, and comments, and three anonymous reviewers and the editors of this Special Issue for comments and feedback that greatly improved this article. We are very grateful to the Arcus Foundation, UW Oshkosh, and Ecositrop for providing funding to support this work.

Compliance with Ethical Standards

Conflicts of interest S. Spehar declares no conflict of interest. Y. Rayadin has consulted with companies in the Kutai Landscape in East Kalimantan, Indonesia to support orangutan conservation in multi-functional landscapes, including in the forestry plantations of PT Surya Hutani Jaya (SRH) and PT Sumalindo Hutani Jaya (SHJ). These companies have no financial interests in this study and had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

References

- Ancrenaz, M., Goossens, B., Gimenez, O., Sawang, A., & Lackman-Ancrenaz, I. (2004). Determination of ape distribution and population size using ground and aerial surveys: A case study with orang-utans in lower Kinabatangan, Sabah, Malaysia. *Animal Conservation*, *7*, 375–385.
- Ancrenaz, M., Gumal, M., Marshall, A. J., Meijaard, E., Wich, S. A., & Husson, S. (2016). *Pongo pygmaeus*. The IUCN red list of threatened species, e.T17975A17966347. doi:10.2305/IUCN.UK.2016-1.RLTS.T17975A17966347.en
- Ancrenaz, M., Oram, F., Ambu, L., Lackman, I., Ahmad, E., et al (2015). Of *Pongo*, palms and perceptions: A multidisciplinary assessment of Bornean orang-utans (*Pongo pygmaeus*) in an oil palm context. *Oryx*, *49*, 465–472.
- Ancrenaz, M., Sollmann, R., Meijaard, E., Hearn, A. J., Ross, J., Samejima, H., et al (2014). Coming down from the trees: Is terrestrial activity in orangutans natural or disturbance-driven? *Scientific Reports*, *4*, 1–4.
- Ashbury, A. M., Posa, M. R. C., Dunkel, L. P., Spillmann, B., Atmoko, S., et al (2015). Why do orangutans leave the trees? Terrestrial behavior among wild Bornean orangutans (*Pongo pygmaeus wurmbii*) at Tuanan, Central Kalimantan. *American Journal of Primatology*, *77*, 1216–1229.
- Blanco, V., & Waltert, M. (2013). Does the tropical agricultural matrix bear potential for primate conservation? A baseline study from western Uganda. *Journal for Nature Conservation*, *21*, 383–393.
- Bryson-Morrison, N., Matsuzawa, T., & Humle, T. (2016). Chimpanzees in an anthropogenic landscape: Examining food resources across habitat types at Bossou, Guinea, West Africa. *American Journal of Primatology*, *78*, 1237–1249.
- Bruford, M. W., Ancrenaz, M., Chikhi, L., Lackman-Ancrenaz, I., Andau, M., et al (2010). Projecting genetic diversity and population viability for the fragmented orangutan population in the Kinabatangan floodplain, Sabah, Malaysia. *Endangered Species Research*, *12*, 249–261.
- Brun, C., Cook, A. R., Lee, J. S. H., Wich, S. A., Koh, L. P., & Carrasco, L. R. (2015). Analysis of deforestation and protected area effectiveness in Indonesia: A comparison of Bayesian spatial models. *Global Environmental Change*, *31*, 285–295.
- Buij, R., Singleton, I., Krakauer, E., & van Schaik, C. P. (2003). Rapid assessment of orangutan density. *Biological Conservation*, *114*(1), 103–113.
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodal inference*. New York: Springer Science+Business Media.
- Campbell-Smith, G., Campbell-Smith, M., Singleton, I., & Linkie, M. (2011a). Apes in space: Saving an imperilled orangutan population in Sumatra. *PLoS One*, *6*, e17210.
- Campbell-Smith, G., Campbell-Smith, M., Singleton, I., & Linkie, M. (2011b). Raiders of the lost bark: Orangutan foraging strategies in a degraded landscape. *PLoS One*, *6*, e20962.
- Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R. P., et al (2005). Multiple causes of high extinction risk in large mammal species. *Science*, *309*, 1239–1241.
- Chapman, C. A., Gillespie, T. R., & Goldberg, T. L. (2005). Primates and the ecology of their infectious diseases: How will anthropogenic change affect host-parasite interactions? *Evolutionary Anthropology: Issues, News, and Reviews*, *14*, 134–144.
- Davis, J. T., Mengersen, K., Abram, N. K., Ancrenaz, M., Wells, J. A., & Meijaard, E. (2013). It's not just conflict that motivates killing of orangutans. *PLoS One*, *8*, e75373.
- Dennis, R., & Colfer, C. (2006). Impacts of land use and fire on the loss and degradation of lowland forest in 1983–2000 in east Kutai District, East Kalimantan, Indonesia. *Singapore Journal of Tropical Geography*, *27*, 30–48.
- Dunbar, R. I. M., Korstjens, A. H., & Lehmann, J. (2009). Time as an ecological constraint. *Biological Reviews*, *84*, 413–429.

- Estrada, A., Raboy, B. E., & Oliveira, L. C. (2012). Agroecosystems and primate conservation in the tropics: A review. *American Journal of Primatology*, *74*, 696–711.
- Galvis, N., Link, A., & Di Fiore, A. (2014). A novel use of camera traps to study demography and life history in wild animals: A case study of spider monkeys (*Ateles belzebuth*). *International Journal of Primatology*, *35*, 908–918.
- Gibbs, H. K., Ruesch, A. S., Achard, F., Clayton, M. K., Holmgren, P., et al. (2010). Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. *Proceedings of the National Academy of Sciences of the USA*, *107*, 16732–16737.
- Gilbert, D. (2012). *Truth and consequences: Oil palm plantations push unique orangutan population to brink of extinction*. San Francisco: Rainforest Action Network.
- Gregory, S. D., Brook, B. W., Goossens, B., Ancrenaz, M., Alfred, R., et al (2012). Long-term field data and climate-habitat models show that orangutan persistence depends on effective forest management and greenhouse gas mitigation. *PLoS One*, *7*, e43846.
- Hashimoto, C. (1995). Population census of the chimpanzees in the Kalinzu Forest, Uganda: Comparison between methods with nest counts. *Primates*, *36*, 477–488.
- Head, J. S., Robbins, M. M., Mundry, R., Makaga, L., & Boesch, C. (2012). Remote video camera traps measure habitat use and competitive exclusion among sympatric chimpanzee, gorilla and elephant in Loango National Park, Gabon. *Journal of Tropical Ecology*, *28*, 571–583.
- Hill, C. M. (2005). People, crops, and primates: A conflict of interests. In J. D. Paterson & J. Wallis (Eds.), *Commensalism and conflict: The human–primate interface* (pp. 41–59). Norman: American Society of Primatologists.
- Hockings, K. J., Anderson, J. R., & Matsuzawa, T. (2012). Socioecological adaptations by chimpanzees, *Pan troglodytes verus*, inhabiting an anthropogenically impacted habitat. *Animal Behaviour*, *83*, 801–810.
- Hockings, K. J., & Humle, T. (2009). *Best practice guidelines for the prevention and mitigation of conflict between humans and great apes*. Gland: IUCN/SSC Primate Specialist Group.
- Hockings, K. J., & McLennan, M. R. (2012). From forest to farm: Systematic review of cultivar feeding by chimpanzees—management implications for wildlife in anthropogenic landscapes. *PLoS One*, *7*, e33391.
- Hockings, K. J., & McLennan, M. R. (2016). Problematic primate behaviour in agricultural landscapes: Chimpanzees as ‘pests’ and ‘predators’. In M. T. Waller (Ed.), *Ethnoprimatology* (pp. 137–156). Cham: Springer International Publishing.
- Hockings, K. J., McLennan, M. R., Carvalho, S., Ancrenaz, M., Bobe, R., et al (2015). Apes in the Anthropocene: Flexibility and survival. *Trends in Ecology and Evolution*, *30*, 215–222.
- Husson, S. J., Wich, S. A., Marshall, A. J., Dennis, R. A., Ancrenaz, M., et al (2009). Orangutan distribution, density, abundance and impacts of disturbance. In S. A. Wich, S. S. Utami Atmoko, T. M. Setia, & C. P. van Schaik (Eds.), *Orangutans: Geographic variation in behavioral ecology and conservation* (pp. 77–96). Oxford: Oxford University Press.
- Isaac, N. J. B., & Cowlshaw, G. (2004). How species respond to multiple extinction threats. *Proceedings of the Royal Society of London B: Biological Sciences*, *271*, 1135–1141.
- Kamilar, J. M., & Paciulli, L. M. (2008). Examining the extinction risk of specialized folivores: A comparative study of colobine monkeys. *American Journal of Primatology*, *70*, 1–12.
- Koh, L. P. (2007). Impending disaster or sliver of hope for southeast Asian forests? The devil may lie in the details. *Biodiversity and Conservation*, *16*, 3935–3938.
- Koh, L. P., & Gardner, T. A. (2010). Conservation in human-modified landscapes. In N. S. Sodhi & P. R. Ehrlich (Eds.), *Conservation biology for all* (pp. 236–261). Oxford: Oxford University Press.
- Koh, L. P., & Wilcove, D. S. (2008). Is oil palm agriculture really destroying tropical biodiversity? *Conservation Letters*, *1*, 60–64.
- Kühl, H. S., Kalan, A. K., Arandjelovic, M., Aubert, F., D’Auvergne, L., et al (2016). Chimpanzee accumulative stone throwing. *Scientific Reports*, *6*, 22219. doi:10.1038/srep22219.
- Lindenmayer, D. B., Franklin, J. F., & Fischer, J. (2006). General management principles and a checklist of strategies to guide forest biodiversity conservation. *Biological Conservation*, *131*, 433–445.
- Loken, B., Spehar, S. N., & Rayadin, Y. (2013). Terrestriality in the Bornean orangutan (*Pongo pygmaeus morio*) and implications for their ecology and conservation. *American Journal of Primatology*, *75*, 1129–1138.
- Margono, B. A., Potapov, P. V., Turbanova, S., Stolle, F., & Hansen, M. C. (2014). Primary forest cover loss in Indonesia over 2000–2012. *Nature Climate Change*. doi:10.1038/NCLIMATE2277.
- Marshall, A. J., Lacy, R., Ancrenaz, M., Byers, O., Husson, S., et al (2009). Orangutan population biology, life history, and conservation: Perspectives from population viability analysis models. In S. A. Wich, S. S. Utami Atmoko, T. M. Setia, & C. P. van Schaik (Eds.), *Orangutans: Geographic variation in behavioral ecology and conservation* (pp. 311–326). Oxford: Oxford University Press.

- Marshall, A. J., & Meijaard, E. (2009). Orangutan nest surveys: The devil is in the details. *Oryx*, *43*, 416–418.
- Marshall, A. J., Nardiyono, Engström, L. M., Pamungkas, B., Palapa, J., et al. (2006). The blowgun is mightier than the chainsaw in determining population density of Bornean orangutans (*Pongo pygmaeus morio*) in the forests of East Kalimantan. *Biological Conservation*, *129*, 566–578.
- Mathewson, P., Spehar, S. N., Meijaard, E., Nardiyono, P., et al. (2008). Evaluating orangutan census techniques using nest decay rates: Implications for population estimates. *Ecological Applications*, *18*, 208–221.
- McCarthy, M. S., Lester, J. D., & Stanford, C. B. (2016). Chimpanzees (*Pan troglodytes*) flexibly use introduced species for nesting and bark feeding in a human-dominated habitat. *International Journal of Primatology*. doi:10.1007/s10764-016-9916-y.
- McKinney, T. (2015). A classification system for describing anthropogenic influence on nonhuman primate populations. *American Journal of Primatology*, *77*, 715–726.
- McLennan, M. R. (2013). Diet and feeding ecology of chimpanzees (*Pan troglodytes*) in Bulindi, Uganda: Foraging strategies at the forest–farm interface. *International Journal of Primatology*, *34*, 585–614.
- McLennan, M. R., & Hockings, K. J. (2014). Wild chimpanzees show group differences in selection of agricultural crops. *Scientific Reports*, *4*, 5956.
- Meijaard, E. (2016). The role of multifunctional landscapes in primate conservation. In S. A. Wich & A. J. Marshall (Eds.), *An introduction to primate conservation* (pp. 205–218). Oxford: Oxford University Press.
- Meijaard, E., Albar, G., Rayadin, Y., Ancrenaz, M., & Spehar, S. N. (2010). Unexpected ecological resilience in Bornean orangutans and implications for pulp and paper plantation management. *PLoS One*, *5*, e12813.
- Meijaard, E., Buchori, D., Hadiprakarsa, Y., Utami-Atmoko, S. S., Nurcahyo, A., et al. (2011). Quantifying killing of orangutans and human-orangutan conflict in Kalimantan, Indonesia. *PLoS One*, *6*, e27491.
- Meijaard, E., & Sheil, D. (2013). Oil-palm plantations in the context of biodiversity conservation. In S. A. Levin (Ed.), *Encyclopedia of biodiversity* (Vol. 5, 2nd ed., pp. 600–612). Waltham: Academic Press.
- Meijaard, E., Wich, S. A., Ancrenaz, M., & Marshall, A. J. (2012). Not by science alone: Why orangutan conservationists must think outside the box. *Annals of the New York Academy of Science*, *1249*, 29–44.
- Miettinen, J., Hooijer, A., Tollenaar, D., Page, S., Malins, C., et al. (2012). *Historical analysis and projection of oil palm plantation expansion on peatland in Southeast Asia*. Washington, DC: International Council on Clean Transportation.
- Musgrave, S., Morgan, D., Lonsdorf, E., Mundry, R., & Sanz, C. (2016). Tool transfers are a form of teaching among chimpanzees. *Scientific Reports*, *6*, 34783. doi:10.1038/srep34783.
- Nakashima, Y., Iwata, Y., Ando, C., Nze Nkogwe, C., Inoue, E., et al. (2013). Assessment of landscape-scale distribution of sympatric great apes in African rainforests: Concurrent use of nest and camera-trap surveys. *American Journal of Primatology*, *75*, 1220–1230.
- Nantha, H. S., & Tisdell, C. (2009). The orangutan–oil palm conflict: Economic constraints and opportunities for conservation. *Biodiversity and Conservation*, *18*, 487–502.
- O'Brien, T. G., Kinnaird, M. F., & Wibisono, H. T. (2003). Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Animal Conservation*, *6*, 131–139.
- O'Connell, A. F., Nichols, J. D., & Karanth, K. U. (2010). *Camera traps in animal ecology: Methods and analyses*. New York: Springer Science+Business Media.
- Olson, E. R., Marsh, R. A., Bovard, B. N., Randrianarimanana, H. L., Ravaloharimanitra, M., et al. (2012). Arboreal camera trapping for the critically endangered greater bamboo lemur *Prolemur simus*. *Oryx*, *46*, 593–597.
- Purvis, A., Gittleman, J. L., Cowlshaw, G., & Mace, G. M. (2000). Predicting extinction risk in declining species. *Proceedings of the Royal Society of London B: Biological Sciences*, *267*, 1947–1952.
- Rayadin, Y., & Spehar, S. N. (2015). Body weights of wild Bornean orangutans living in human-dominated landscapes: Implications for understanding their ecology and conservation. *American Journal of Physical Anthropology*, *157*, 339–346.
- Russon, A. E. (2009). Orangutan rehabilitation and reintroduction. In S. A. Wich, S. S. Utami Atmoko, T. M. Setia, & C. P. van Schaik (Eds.), *Orangutans: Geographic variation in behavioral ecology and conservation* (pp. 327–350). Oxford: Oxford University Press.
- Russon, A. E., Kuncoro, P., & Ferisa, A. (2015). Orangutan behavior in Kutai National Park after drought and fire damage: Adjustments to short-and long-term natural forest regeneration. *American Journal of Primatology*, *77*, 1276–1289.
- Saj, T., Sicotte, P., & Paterson, J. D. (1999). Influence of human food consumption on the time budget of vervets. *International Journal of Primatology*, *20*, 977–994.

- Sayer, J., Sunderland, T., Ghazoul, J., Pfund, J. L., Sheil, D., *et al.* (2013). Ten principles for a landscape approach to reconciling agriculture, conservation, and other competing land uses. *Proceedings of the National Academy of Sciences of the USA*, *110*, 8349–8356.
- Scriven, S. A., Hodgson, J. A., McClean, C. J., & Hill, J. K. (2015). Protected areas in Borneo may fail to conserve tropical forest biodiversity under climate change. *Biological Conservation*, *184*, 414–423.
- Sih, A., Ferrari, M. C., & Harris, D. J. (2011). Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications*, *4*, 367–387.
- Singleton, I., & van Schaik, C. P. (2001). Orangutan home range size and its determinants in a Sumatran swamp forest. *International Journal of Primatology*, *22*, 877–910.
- Sodhi, N. S., Koh, L. P., Clements, R., Wanger, T. C., Hill, J. K., Hamer, K. C., *et al.* (2010). Conserving Southeast Asian forest biodiversity in human-modified landscapes. *Biological Conservation*, *143*(10), 2375–2384.
- Spehar, S. N., Loken, B., Rayadin, Y., & Royle, J. A. (2015). Comparing spatial capture–recapture modeling and nest count methods to estimate orangutan densities in the Wehea Forest, East Kalimantan, Indonesia. *Biological Conservation*, *191*, 185–193.
- Spehar, S. N., Mathewson, P. D., Nuzuar, Wich, S. A., Marshall, A. J., *et al.* (2010). Estimating orangutan densities using the standing crop and marked nest count methods: Lessons learned for conservation. *Biotropica*, *42*, 748–757.
- Struebig, M. J., Fischer, M., Gaveau, D. L. A., Meijaard, E., Wich, S. A., *et al.* (2015). Anticipated climate and land-cover changes reveal refuge areas for Borneo’s orangutans. *Global Change Biology*, *21*, 2891–2904.
- Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., *et al.* (2010). Distance software: Design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology*, *47*, 5–14.
- Tobler, M. W., Carrillo-Percegueiro, S. E., Pitman, R. L., Mares, R., & Powell, G. (2008). An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. *Animal Conservation*, *11*, 169–178.
- Trèves, A., Mwima, P., Plumptre, A. J., & Isoke, S. (2010). Camera-trapping forest–woodland wildlife of western Uganda reveals how gregariousness biases estimates of relative abundance and distribution. *Biological Conservation*, *143*, 521–528.
- van Schaik, C. P., Marshall, A. J., & Wich, S. A. (2009). Geographic variation in orangutan behavior and biology. In S. A. Wich, S. S. Utami Atmoko, T. M. Setia, & C. P. van Schaik (Eds.), *Orangutans: Geographic variation in behavioral ecology and conservation* (pp. 351–362). Oxford: Oxford University Press.
- van Schaik, C. P., Priatna, A., & Priatna, D. (1995). Population estimates and habitat preferences of orangutans based on line transects of nests. In R. D. Nadler, B. F. M. Galdikas, L. K. Sheeran, & N. Rosen (Eds.), *The neglected ape* (pp. 109–116). New York: Plenum Press.
- Warren, Y., Higham, J. P., MacLarnon, A. M., & Ross, C. (2011). Crop-raiding and commensalism in olive baboons: The costs and benefits of living with humans. In V. Sommer & C. Ross (Eds.), *Primates of Gashaka: Socioecology and conservation in Nigeria’s biodiversity hotspot* (pp. 359–384). Developments in primatology: Progress and prospects. New York: Springer science+Business media.
- Wich, S. A., Fredriksson, G. M., Usher, G., Peters, H. H., Priatna, D., *et al.* (2012b). Hunting of Sumatran orangutans and its importance in determining distribution and density. *Biological Conservation*, *146*, 163–169.
- Wich, S. A., Gaveau, D., Abram, N., Ancrenaz, M., Baccini, A., *et al.* (2012a). Understanding the impacts of land-use policies on a threatened species: Is there a future for the Bornean orangutan? *PLoS One*, *7*, e49142.
- Wich, S. A., Meijaard, E., Marshall, A. J., Husson, S., Ancrenaz, M., *et al.* (2008). Distribution and conservation status of the orangutan (*Pongo* spp.) on Borneo and Sumatra: How many remain? *Oryx*, *42*, 329–339.
- Wilcove, D. S., & Koh, L. P. (2010). Addressing the threats to biodiversity from oil-palm agriculture. *Biodiversity and Conservation*, *19*, 999–1007.