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The effect of tropical forest modification on primate population density and richness

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Abstract

Agricultural expansion is increasingly forcing primates to exist within heavily modified landscapes. To assess the long-term viability of these populations, robust monitoring is required, however the cryptic nature of primates and sparse distribution often makes collecting sufficient data to produce precise density estimates challenging, particularly within disturbed areas. Here, I undertook a pilot study assessing the feasibility of using occupancy modelling as a state variable for monitoring six diurnal primate species, the Sabah Grey Langur *(Presbytis sabana),* red leaf monkey *(Presbytis rubicunda),* long tailed macaque *(Macaca fascicularis),* pig tailed macaque *(Macaca nemestrina),* Bornean gibbon *(Hylobates muelleri)* and orangutan *(Pongo pygmaeus morio),* using direct observations within a heavily modified landscape in Borneo. Low detection rates led to high levels of uncertainty and using simulations to extrapolate these results to the maximum survey effort available for a main study, revealed no single study design would provide precise estimates (SE <0.075). Therefore, using indirect nest count methods, I conducted orangutan (*Pongo pygmaeus morio*) surveys across three habitat types (continuous logged forest, recently salvaged, logged forest and remnant forest patches within oil palm estates) and assessed the influence of landscape features and forest structural metrics obtained from LiDAR, on estimates of orangutan abundance. Recent salvage logging activities (2013-2016) appeared to have little effect of orangutan density, with no significant difference between recently salvaged, logged and continuous logged forest. Although orangutans were still present in remnant forest patches within oil palm plantations, they were found at significantly lower densities. Generalised linear models revealed that distance from the nearest continuous logged forest had no significant effect on orangutan density. However, canopy height standard deviation had a significant positive effect on orangutan density. These findings suggest that orangutans can persist, at least in the short term, within human modified landscapes, providing sufficient, good quality forest remains. Further research is needed to assess the long-term viability of populations within heavily modified landscapes, for example resource availability, changes in population demographics and effects of human-orangutan conflicts. Despite these questions, these data add to the growing recognition that human modified landscapes should be included within any orangutan conservation strategies.

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Chapter One

Testing the feasibility of occupancy modelling as a method for surveying primates within a highly modified landscape.

Introduction

With 60% of the World's primate species threatened with extinction on the IUCN Red List of Threatened Species (Estrada *et al*. 2017), effective population monitoring is essential to inform their conservation. However, primates share many characteristics that prove problematic when both designing surveys and for field staff collecting data. Many primate taxa live within tropical forests in which access is difficult and visibility is often poor (Peres 1999). They are also highly mobile and will regularly flee when human observers are detected. These cryptic tendencies and often sparse distributions, can result in primates frequently being undetected, when they are in fact present (false absences). To combat this, analyses should account for detection probability, which can then be used to correct estimates for missed observations (Buckland *et al.* 2005). The most commonly employed survey method for monitoring primates is distance sampling (Buckland *et al*. 2001), where transects are systematically placed within an area of interest and perpendicular distances to all observed primates recorded and observations can be either individual animals or groups. The probability of observing an animal at any given distance can then be calculated and along with total survey effort, used to estimate density (individual or groups per unit area) and abundance for a finite area. However, for accurate density estimates to be produced in this way, between 40 to 60 observations are frequently needed (Marshall, *et al.* 2008). This will often equate to a prohibitively high survey effort, particularly when primates are expected to be in low densities. For instance, Peres (1999) reports that for neotropical primates, even with a cumulative survey effort of >300km, collecting a sufficient number of observations may be unrealistic.

In cases such as these, methods are frequently modified to use indirect observations. For instance, great apes will regularly build nests distinguishable from other species and using distance sampling methods to record nests can produce accurate nest density estimates (Kühl 2008). Similarly, indirect survey techniques are regularly used for gibbons, where teams of observer's record estimated distance and angles of gibbon calls and triangulate their locations and to calculate group densities (Kidney, *et al.* 2016; Höing *et al*. 2013). However, for these estimates to be informative, extra parameters need to be calculated to convert these indirect estimates to absolute primate densities. In the case of orangutans, three parameters need to be obtained, proportion of nest builders within the population, nest production rate and nest decay rate. These parameters can range widely over different habitat types and between populations and as a result, locally produced estimates are needed for confident densities to be established (Spehar *et al.* 2010). Likewise, for gibbons, average local group size must be known if robust densities are to be produced from indirect methods (Höing *et al*. 2013). Therefore, although these survey methods mitigate the problems associated with small sample sizes obtained from direct observations, they still require large amounts of underlying demographic and environmental information and these data are often only available for sites with long term research programmes. As a result, alternative methods for monitoring primates may prove increasingly valuable in providing effective, long term conservation for this threatened taxa.

Occupancy, or the proportion of a given area occupied by one or more species, is increasingly being used as a state variable to monitor temporal trends in wildlife populations (Guillera-Arroita *et al*. 2010). Occupancy modelling has the potential to provide valuable information to inform primate conservation, using fewer resources and without the need of extensive training of field staff or long term observational data (Guillera-Arroita, *et al.* 2010; MacKenzie *et al*. 2002). Generally, occupancy is estimated by repeat visits to multiple sites and recording whether or not the target species is detected within each site. The proportion of sites occupied is then calculated to give a naïve occupancy estimate. By visiting sites on multiple occasions, each sites history of detection or none-detection can be used to calculate a detection probability and the naïve occupancy adjusted to reflect this, thereby producing a more robust estimate (MacKenzie *et al.* 2002; 2003). Although this method may lack the ability to detect subtle changes in density, temporal changes in species occupancy can yield insights into population trends and assess the effects of conservation efforts (MacKenzie, *et al*. 2017).

With ecological studies, designing a survey that will fulfil the desired outcomes under the available resources, is often a challenge (Bailey *et al*. 2007). As occupancy requires repeat visits to multiple sites, this raises logistical constraints with time and resources having to be shared between the total number of sites visited and the number of times each site can be resurveyed. This is often achieved with the use of asymptotic approximations, which extrapolate from existing data or predicted values, based on professional opinion, to assess the most effective allocation of survey effort (Bailey *et al*. 2007; MacKenzie & Royle 2005). However, when sample size is expected to be small, or low probability of detection and occupancy are anticipated, asymptotic approximations are least robust and therefore, not appropriate (Guillera-Arroita *et al.* 2010). In these cases, the use of simulations may be a better approach. Using the same information as asymptotic approximations, simulated surveys can be run on possible data sets and over large numbers of iterations. By assessing the distribution of the simulated results, the bias and precision can be calculated to test possible survey designs (Guillera-Arroita *et al*. 2010, Bailey *et al*. 2007).

Although several authors have offered advice for designing occupancy studies, these methods have rarely been used in surveying primates (Guillera-Arroita *et al*. 2010, Keane *et al.* 2012), therefore, recommendations for designing occupancy studies of primates are limited. Here, I test the feasibility of using occupancy modelling to monitor primates within a highly modified landscape in Borneo. Using data collected over a three month pilot study, I employ simulations to investigate if, given the finite survey effort available, occupancy estimates can be produced at an accuracy from which robust ecological conclusions can be drawn.

Method

Study site

The study was conducted in a mosaic landscape covering approximately 13,000ha in the Malaysian state of Sabah, Borneo and encompasses a disturbance gradient ranging from continuous logged forest, to monoculture oil palm. At the core of the site is the Stability of Altered Forest Ecosystems (SAFE) project (https://safeproject.net/, 4° 33′ N, 117° 16′ E), a large scale (7,200ha) fragmentation experiment, investigating the effects of human modified landscapes on biodiversity and ecosystem function (Ewers *et al.* 2011). The SAFE site had received multiple (≤3) intensive logging rotations from 1978 until 2000 (Struebig *et al.* 2013). Except for six systematically placed replicated fragment blocks, the site has been entirely salvage logged and currently awaiting conversion to oil palm. Each replicated fragment block contains one 100ha fragment, two 10ha fragments and four 1ha fragments (Ewers *et al.* 2011). The wider landscape incorporates two areas of continuous logged forest, the Ulu Segama Forest Reserve covering <1 million ha of twice logged forest (Ancrenaz *et al*. 2010) and the Brantian Tantulit Virgin Jungle Reserve (VJR) covering 2,200 ha. The remainder of the site is made up of relatively mature oil palm (trees aged 8 – 12) estates, that retain remnant forest patches and riparian reserves (See figure 1).

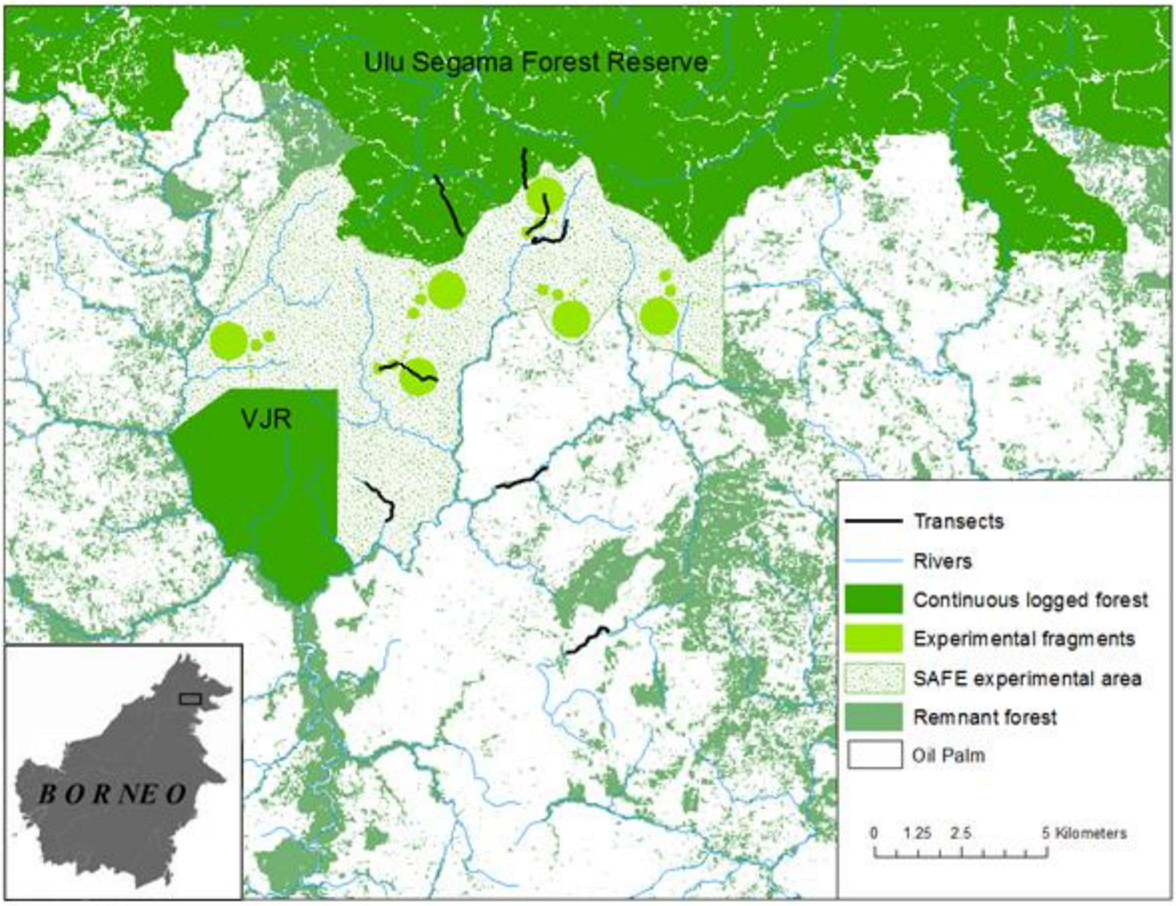

Figure 1. Map of study area, with transect locations for pilot study. Displaying continuous logged forest Ulu Segama Forest Reserve and Brantian Tantulit Virgin Jungle Reserve (VJR).

Pervious primate surveys had been carried out at the site by between 2011 and 2012, before the salvage logging had commenced (Bernard *et al*. 2016). This revealed a high level of primate species richness at the site, with nine of the 10 species known from Sabah recorded at the site. Although the SAFE experimental area had received a higher intensity of logging than surrounding continuous forest, there was little variation in primate species across the site.

Site selection

Sites were chosen to maximise the number of repeat visits, given the logistical constraints, whilst still providing as representative sample of the site as possible. In total, eight sites were selected, these included two 100ha forest fragments, two continuous logged forest sites, two riparian reserves within the SAFE experimental area and two riparian reserves within established oil palm estates. A single transect was placed at each site ranging between 1.5 to 2km in length. With the exception of one logged forest site, transects were placed using existing trails to minimise disturbance within an area of active research, that includes several permanent vegetation plots. Although other researchers were present at the project during this study, no work was being carried at any of the chosen sites, therefore human disturbance was minimal.

Data collection

Transects were walked by teams of at least two observers and surveys started between 6:00 and 6:30am in order to coincide with the highest primate activity. Observers walked at a slow pace, roughly ½ km/hr and all direct primate observations were recorded. When primates were encountered the species was noted and if possible, group size, when more than one animal was present. Distance from observer to where the animal was first encountered was also recorded, as well as angle from the transect line. When more than one primate was encountered, the distance to the nearest animal was measured.

Primate occupancy

I considered each transect an individual site and using the pivot table function in Microsoft Excel, I produced detection histories for each species, where each replicate survey was given 1 if the species was observed or 0 if the species was not detected through direct observation. Calls were not included within the models, as the distance from the observer to animal could not be calculated accurately and this may have resulted in sites being recorded as occupied when in fact the species was absent. Similarly, I excluded nests from the analysis, as the long periods of time nests can remain visible for may again lead to an over estimation of occupancy. A simple single-season occupancy model was then fitted to each species detection history using the 'occu' function in the R package 'unmarked' (Fiske & Chandler, 2011) using R version 3.4.2 statistical software (R Core Team, 2017). As the sample size was exceptionally small, we were only able to fit one model where occupancy and detection probabilities were fixed and we made no attempt to fit models containing covariates.

Survey design feasibility

Two parameters are estimated with single-season occupancy models, detection probability (*p*) and occupancy (ψ). We used these parameters to test the feasibility of different study designs for monitoring primates within the SAFE study area given our maximum available survey effort (E_{max}) of 120 days. For each study design E_{max} remained constant but was allocated in different quantities between number of sites S and repeat visits K. This allowed us to investigate the trade-offs between maximising the number of sites versus repeat visits. For each study design, 50,000 simulations were run, using potential datasets generated, based on the survey design, as well as the detection probability and occupancy estimate produced by our pilot study. These simulations produce maximum likelihood estimates and the distribution of these are used to predict estimator (detection probability and occupancy) bias and variance, given each design scenario. We deemed a survey design feasible if the Root Mean Square Error (RMSE) for the occupancy estimator was below 0.075 (analogous to Standard Error SE), therefore indicating if the survey were to be carried out, occupancy would be produced with high precision (Guillera-Arroita *et al.* 2010). Only the RMSE of occupancy was considered when evaluating each survey design, as this is the state variable of most interest in our eventual study. Simulations were run using the 'evaldesign' and 'loglikf' functions and plotted using the plotMLEdist function coded by

Guillera-Arroita *et al*. (2010: available from: https://www.kent.ac.uk/smsas/personal/msr/webfiles/soda/occdesign1sp.R) in R version 3.4.2 statistical software (R Core Team, 2017). Although software to automatically evaluate all possible survey designs based on these parameters is available (SODA available from: https://www.kent.ac.uk/smsas/personal/msr/soda.html), here we are interested in surveying multiple species simultaneously. Therefore, I manually ran simulations for each species, in order to compare outputs and ascertain if there is a single suitable survey design.

Results

Between September and December 2016, the eight sites were each visited four times, giving a total survey effort of 32 repeat visits. During the study period, we encountered six of the nine primate species previously recorded at the site (Bernard *et al.* 2016). The most common being the Bornean gibbon *(Hylobates muelleri)* with six observations. Orangutans *(Pongo pygmaeus)* and red leaf monkeys *(Presbytis rubicunda)* were both observed on five occasions, long tailed macaques *(Macaca fascicularis)* and pig tailed macaques *(Macaca nemestrina)* were both observed on three surveys and the Sabah grey langur *(Presbytis sabana)* was only observed on a single survey (See Table 1). Detection histories were created for all species, with the exception of the Sabah grey langur, due to this species only being observed once. Interestingly, the continuous logged forest and riparian reserves within oil palm estates had a comparable number of direct primate observations (N = 10 vs N = 11) and species richness (N = 4 vs N = 5). However, the species composition was different between habitat types, with both macaque species only being observed in riparian reserves within oil palm and higher observations of orangutan and langur species within continuous logged forest (See Table 1).

Table 1 Primate detection histories across habitat types

Species		IUCN Status	Habitat type Logged forest	Forest fragment	Exp riparian	Oil palm riparian
Long-tailed macaque	*Macaca fascicularis*	LC	0	0	0	3
Pig-tailed macaque	*Macaca nemestrina*	VU	0	0	0	3
Bornean orangutan	*Pongo pygmaeus*	CR	4	0	0	1
Bornean gibbon	*Hylobates muelleri*	EN	2	0	1	3
Red leaf monkey	*Presbytis rubicunda*	LC	3	1	0	1
Sabah gery langur	*Presbytis sabana*	VU	1	0	0	0
		Total No. of Observations	10	1	1	11
		Total No. of Species	4	1	1	5

IUCN status: LC = Least concern, VU = Vulnerable, EN = Endangered and CR = Critically endangered

Primate occupancy

Occupancy models for gibbons and red leaf monkeys produced low detection probabilities but extremely high occupancy estimates (gibbon $p = 0.19$, $\psi = 1$, red leaf monkey $p = 0.16$, $\psi = 0.99$). Simulations by MacKenzie *et al.* (2002) have shown that small sample size with low detection probabilities can lead to overestimations of occupancy, inflated to or close to one and this appears to be the case here. Therefore, gibbons and red leaf monkeys were excluded from further analyses. Orangutans had a relatively low detection probability $p = 0.34 \pm 0.17$ SE and an occupancy estimate of $\psi = 0.47 \pm 0.24$ SE. Pig-tailed macaques had a similar pattern with detection probability of $p = 0.27 \pm 0.21$ SE and an occupancy estimate of $\psi = 0.35 \pm 0.27$ SE. Long-tailed macaques had a relatively high detection probability $p = 0.75 \pm 0.22$ SE but a low occupancy estimate $\psi = 0.13 \pm 0.12$ SE.

Survey design feasibility

Five study designs were evaluated for three species, orangutan, long-tailed macaques and pig-tailed macaques (see Table 2). For all species, both bias and variance generally decreased as the number of replicates increased. The percentage of boundary estimates, where ψ is inflated to/or close to 1, also decreased when repeated visits where prioritised, indicating improved performance of the estimators (See Figure 2). However, for one species, the long-tailed macaques, a study design was deemed feasible where S was 20 and K was 6 giving an RMSE value of 0.074, although bias did increase slightly to 0.010.

Table 2 Simulation results

		S/K				
$E_{max} = 120$		60/2	40/3	30/4	24/5	20/6
Orangutan						
(ψ=0.46 p=0.34)	bias ψ	0.083	0.047	0.030	0.021	0.016
	RMSE ψ	0.241	0.177	0.148	0.133	0.131
	Boundary estimates	10.7%	2.9%	0.8%	0.3%	0.1%
Long-tailed Macaque (ψ=0.13 p=0.75)						
	bias ψ	0.015	0.008	0.007	0.007	0.010
	RMSE ψ	0.098	0.082	0.080	0.075	0.074
	Boundary estimates	0.9%	0.5%	0.4%	0.2%	0.0%
Pig-tailed Macaque (ψ=0.35 p=0.27)						
	bias ψ	0.156	0.101	0.073	0.055	0.044
	RMSE ψ	0.345	0.264	0.169	0.192	0.175
	Boundary estimates	22.3%	9.3%	4.9%	3.0%	2.2%

Simulation results for the occupancy estimator for three species under different allocations of survey effort E_{max} between number of sites S and number of repeat visits K. For each survey design estimates of occupancy bias (bias ψ), the Root Mean Square Error (RMSE ψ) and percentage of boundary estimates (where $\psi = 1$) are shown.

For both orangutans and pig-tailed macaques, bias and precision both improved when the number of repeat visits increased. However, none of the possible survey designs were deemed feasible as for both species the RMSE was above the 0.075 limit (orangutan RMSE = 0.131, pig-tailed macaque = 0.175).

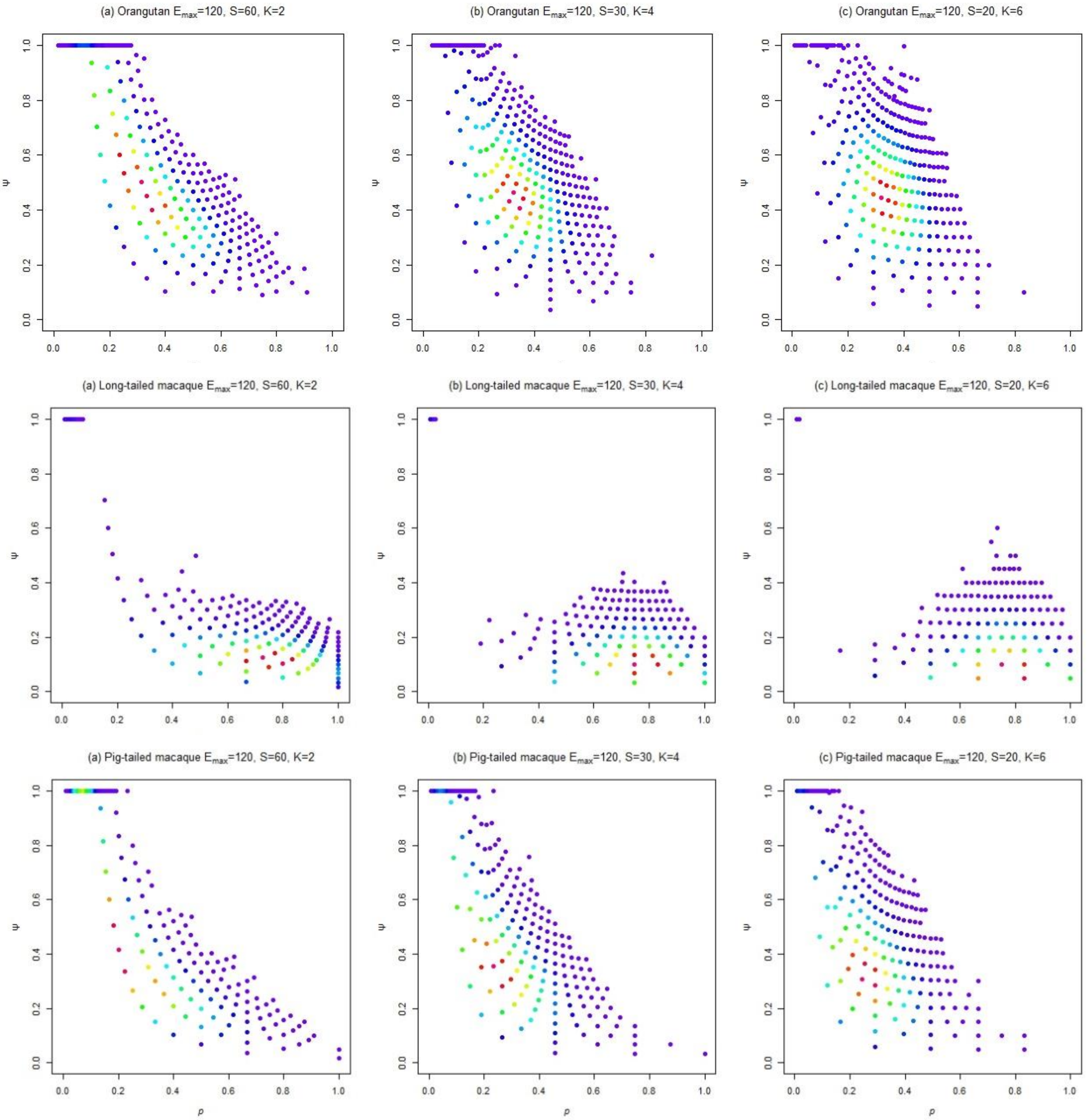

Figure 2. Distribution of simulated estimates of occupancy and detection probability, with red/orange colours indicating the most likely outcomes. For all three species, estimator performance improves for each survey design when the number of repeat visits increases, from (a) $S = 60$, $K = 2$, to (b) $S = 30$, $K = 4$ and (c) $S = 20$, $K = 6$. Although bias increases slightly for long-tailed macaque for survey design c. Boundary estimates, far right corner, also reduces as the number of repeat visits increases.

Discussion

The purpose of this study was to determine the feasibility of a wider study, some interesting anecdotal patterns are worth mentioning, though the sample size is too small to draw statistical conclusions. The lowest primate detections and species richness were recorded in the SAFE experimental area, suggesting the recent salvage logging has had a negative effect on the local populations since the pervious study by Bernard *et al.* (2016). The continuous logged forest and riparian reserves within oil palm estates had a comparable number of primate detections and species richness but there was a difference in the community composition. As may be expected, more generalist species, such as macaques, were observed within the oil palm estates and higher detections of forest dependant species such as langurs were confined largely to the continuous forest. One surprising finding was the number of gibbon detections in riparian reserves within oil palm estates. Although gibbons are capable of terrestrial movement, their brachiating form of locomotion makes them largely dependent on forested areas (Cheyne, 2011). All gibbon detections were of age diverse groups (Per, Obs) and it is likely that these animals were displaced by the recent salvage logging and are now confined to remnant forest patches within the modified landscape. This raises several questions, for instance, are these displaced individuals or resident animals, are there sufficient resources to maintain the population in the long term and what is the dispersal capability for gibbons within this highly modified landscape. Although the highest number of direct observations were from continuous logged forest, orangutan nests were observed on 100% of surveys, suggesting that although not encountered, orangutans were present across the site.

Here we aimed to determine the potential of occupancy modelling as a feasible option for monitoring primate populations within a human modified landscape. Simulations revealed that for all species, estimator performance increased when repeat visits were prioritised over the total number of sites. For long-tailed macaques this is somewhat surprising, as their high detection probability but low occupancy would intuitively suggest that increasing the number of repeat visits would quickly lead to minimal improvement in estimator performance. This illustrates the need for using simulation as opposed to asymptotic approximations when either detection or occupancy estimates are low, as they are likely to underestimate variance in these cases (Guillera-Arroita *et al*. 2010). For both orangutans and pig-tailed macaques, estimator performance also increased when the number of repeat visits were prioritised, with bias and variance decreasing. Despite this, both species failed to fall below our target level of precision of SE <0.075. Therefore, no survey design fulfils all our requirements of simultaneously surveying all primate species while minimising variance surrounding occupancy estimates and for our purposes, occupancy modelling does not appear to be a viable option.

There are however, several caveats that need to be considered when interpreting these results. The simulations performed here are highly simplistic, failing to take into account certain nuances that would be encountered within a real large scale survey. For instance, occupancy and detectability were fixed but in reality, these are unlikely to remain constant across the landscape, particularly within a highly modified area such as SAFE and surrounding oil palm estates. Similarly, site closure was assumed, where if a site was occupied on one survey, this does not change between surveys and this can lead to an over estimation of occupancy (Rota, *et al.* 2009). These models also allocated survey effort equally between the number of sites and repeat visits. Under real circumstances, site logistics and other constraints, such as bad weather or vehicle failures are likely to lead to some sites being visited more than others. Similarly, due to the small sample size of our pilot study there are large uncertainties surrounding our single-season occupancy estimates. If the true values of occupancy or detectability are at the upper or lower limits, this may have a large effect on the actual survey effort required. Nevertheless, as the estimates produced from this pilot study appear to make biological sense, we feel this analysis provides a good indication that given our potential resources, we should not continue with a larger occupancy study.

Although we have deemed the current survey unfeasible, there are several options which may be considered if we wished to continue the study. One possibility would be to relax our target level of precision, to allow the project to go ahead with the best performing survey design (Guillera-Arroita, *et al*. 2010). While this would be the easiest option, it would be rather undesirable as this would reduce our ability to demonstrate with statistical confidence the effects of human disturbance on local primate populations. Similarly, if future surveys were to be performed, the power to detect changes in occupancy would also be reduced. A better option would be to increase the survey effort and run simulations again to see if additional resources would make the project viable. However, here I ran simulations using the maximum possible survey effort so therefore, this is not an option I have at my disposal.

While our study has shown that for our purposes, the use of occupancy modelling would not be viable, this does not rule out the method as a tool for monitoring primates in all cases. Guillera-Arroita, *et al.* (2010) successfully used occupancy modelling for monitoring a Critically Endangered lemur species. However, their study took place in an area known to have high densities of the species (Mutschler, *et al.* 2001) and a local ecotourism program has led to the lemurs being habituated to human observers (Rendigs, *et al*. 2015). As a result, the occupancy and detection probabilities for the species are high, which likely contributed to occupancy modelling proving successful for their objectives. Instead, we have highlighted some of the difficulties faced when surveying a rare, cryptic and sparsely dispersed taxa such as primates. Each case should be considered on its own merits, using simulations to test possible survey designs, ideally with pilot study data, in order to prevent finite resources being wasted which could be put to better use elsewhere.

Occupancy modelling is a rapidly evolving field, with constant innovations, leading to the methods increasing flexibility. Recent advances have shown that occupancy modelling can be used to survey rare and highly dispersed species through indirect observations using spatial replicates (Whittington, *et al*. 2015). In this case, rather than repeat visits, detection histories are derived from dividing existing transects into segments and recording detection/none detection within each segment. So far, this method has had limited use but has already proven successful within tropical forests in Sumatra for surveying tigers (Hines, *et al*. 2010). This method has the advantage that only a single visit to each site is needed and by using indirect observations, larger sample sizes can be obtained. Although this would not be applicable to all primate species, orangutans have several ecological features which may make this a viable option. Like tigers, orangutans are largely solitary, have large home ranges and are sparsely distributed within the landscape (Delgado & Van Schaik, 2000). They will also regularly build nests, which can easily be identified and are a clear indication of their presence (Ancrenaz, *et al.* 2004). Therefore, this method may be worth considering for surveying orangutans in areas where the necessary long term data needed to produce density estimates is lacking.

Conclusion

Here we have shown that although occupancy modelling has the potential to be a useful tool for monitoring primates, in our case at least, their cryptic nature and sparse distribution would require a prohibitively high survey effort. This highlights how the use of freely available software, used to test the feasibility of an ecological survey, can prevent large amounts of resource being wasted. We have also identified a contemporary occupancy modelling method which could possibly be used for surveying orangutans, where prior knowledge required to produce extra parameters needed for traditional methods is lacking.

Chapter Two

The effects of habitat modification on orangutan populations, across a gradient of disturbed habitats.

Introduction

Agriculture has historically been the leading cause of global deforestation (Sandker, *et al*. 2017) with an estimated 49.1 million km^2 of the Earths land already under some form of agricultural production (Zabel, *et al.* 2014). Although improvements in farming technologies and the genetic modification of crops have improved yields and reduced pressure on forests (Byerlee, *et al.* 2014; Qaim & Zilberman, 2003), increasing demands for food, cosmetics and biofuels still make agriculture the largest cause of deforestation (Sandker, *et al*. 2017). Inevitably, deforestation leads to losses of biodiversity and ecosystem services (Chapin Iii, *et al*. 2000) and with naturally high levels of biodiversity, nowhere are these losses felt more than tropical regions (Pimm & Raven, 2000). On top of this, tropical regions are predicted to see the largest increase in agriculture expansion, owing to continued growth in the human population and higher per-capita income leading to higher consumption (Fitzherbert, *et al.* 2008). This presents a huge challenge for environmental conservation, in balancing the needs of developing nations whilst protecting biodiversity and the valuable ecosystem services they provide. A prime example of this is Southeast Asia, which encompasses several biodiversity hotspots (Myers, *et al.* 2000) and has experienced high deforestation rates in recent decades (Miettinen, *et al.* 2011). In recent years, deforestation has been particularly severe in Sumatra, Borneo and peninsula Malaysia, which by 2010 had lost roughly 70% of original lowland forests and 60% of peat swamp forest (Miettinen, *et al*. 2011). Forests in the region have been cleared for commercial plantations, such as rubber, timber and fast growing trees for the pulp and paper industry but clearance for oil palm has been particularly extensive over the last 20 years (Fitzherbert, *et al.* 2008). With very few exceptions, forest conversion to oil palm has a negative effect on biodiversity. On average, across taxa, plantations support only

15% of species observed in undisturbed forest (Fitzherbert, at el. 2008), however, within plantations not all species are at equal risk of extinction, with specialist and rare species being most vulnerable (Turner, 1996).

Orangutans (*Pongo* spp) are the only non-human great ape found outside of Africa and historically ranged across much of Southeast Asia (Delgado & Van Schaik, 2000). Today, populations are restricted to the islands of Sumatra and Borneo. These currently represent three species, the Sumatran orangutan (*Pongo abelii*) and the recently described Tapanuli orangutan *(Pongo tapanuliensis*) (Nater, *et al.* 2017) from Sumatra and the Bornean orangutan (*Pongo pygmaeus*) found only on Borneo. Despite being heralded as conservation icons, regularly attracting large amounts of funding for conservation ($75million between 1990 and 2011 Meijaard, *et al*. 2012) and boasting strict legal protection, all three species are considered Critically Endangered on the IUCN Red List of Threatened Species (Nowak, *et al.* 2017; Singleton, *et al*. 2016; Ancrenaz*, at el.* 2016). Orangutan populations face a multitude of threats including hunting, forest fires and climate change. However, habitat loss and fragmentation continues to be the leading cause of population decline for all orangutan taxa (Nowak, *et al.* 2017; Singleton, *et al.* 2016; Ancrenaz*, at el.* 2016) and could have particularly catastrophic consequences in combination with climate change (Struebig *et al*. 2015). On the island of Borneo, habitat loss and fragmentation has led to increased instances of human-orangutan conflict and as a result, hunting is emerging as potentially a more acute cause of population decline than habitat loss and fragmentation alone (Meijaard, *et al*. 2011). While orangutans are observed at elevations of up to 1500 m.a.s.l, they appear to favour lowland forest areas, being found at highest densities below 500 m.a.s.l (Meijaard & Wich, 2007). However, these low-lying areas are often the most suitable for agricultural production, leading to high levels of deforestation and forest degradation within the orangutans range. Further forest conversion is expected, and estimates of future orangutan habitat loss range from 9,000km^2 (Struebig, *et al* 2015) to as much as 57,000km^2 by the 2020s (Wich, *et al*. 2012). The current orangutan population is already fragmented (Santika, *et al*. 2017), however the high rates of deforestation will increase the level of fragmentation and further limit dispersal between isolated populations. Previous population viability analysis has shown that fragmented orangutan populations, numbering 250 or less, have a high probability of extinction without management intervention (Marshall, *et al*. 2009). In addition, fragmentation also limits movement across landscapes. Models projecting changes to forest suitability in response to anthropogenic climate change have shown suitable orangutan habitat will likely shift upslope, meaning that individuals would need to either adapt to adverse conditions or move to higher elevations to track their ideal niche (Struebig, *et al*. 2015). Therefore, maintaining populations within, and allowing movement across human modified landscapes, is important for orangutan conversation and will be vital to ensure the species persists long term (Ancrenaz, *et al*. 2016).

Orangutans have remained poorly studied until relatively recently, with only four sites of active orangutan research taking place until the start of the millennium (Delgado & Van Schaik, 2000). As a result, unlike the African great apes, with the exception of bonobos (*Pan paniscus*), much of the orangutans' natural history and behavioural ecology has largely remained a mystery (Delgado & Van Schaik, 2000). Recent efforts have been made to fill this knowledge gap, yielding information on distributions (Husson, *et al*. 2009, Wich, *et al*. 2012), population trends (Santika, *et al*. 2017; Meijaard & Wich, 2007), responses to future human and climate driven land cover changes (Struebig *et al*. 2015; Wich *et al*. 2016) and the effects of habitat disturbance (Spehar & Rayadin. 2017; Ancrenaz, *et al*. 2015, 2010; Meijaard, *et al*. 2010; Marshall, *at el*. 2006). Conventionally, orangutans were thought to be dependent on pristine old growth forest, but recent research is changing these long-held views and it is now generally recognised that orangutans can persist in forests with low levels of disturbance. For instance, Marshall, *et al.* (2006) reported that low logging intensity (<5 stems / ha) has minimal effects on orangutan population density and several studies have found orangutan density may even increase within areas of low disturbance (Husson, *et al*. 2009), however this may be attributed to a compression effect, where animals from surrounding areas of high disturbance are displaced into areas of low disturbance (Mathewson, *et al.* 2008). High levels of disturbance have been shown to have a deleterious effect on local orangutan populations, with meta-analyses revealing a significant reduction in population density within heavily logged areas (Husson, *et al*. 2009). Additionally, high levels of forest degradation can impair movement across areas that were previously connected. Ancrenaz *et al.* (2010) found orangutan densities differed on opposite sides of major rivers within heavily disturbed areas of the Ulu Segama Forest Reserve. Orangutans will use large trees to cross rivers, and after these are removed during logging, rivers which were previously navigable, may become barriers to dispersal (Ancrenaz *et al.* 2010). Despite the increasing number of studies investigating orangutan densities within disturbed forests, there is only limited research investigating how orangutans respond to forest conversion for agriculture. The few recent studies have found orangutans to be surprisingly resilient to habitat modification. For instance, Meijaard *et al.* (2010) found orangutans at relatively high densities (1.24 - 1.75 individuals/km^2) within two pulp and paper plantations of *Acacia mangium* and *Eucalyptus* spp. in East Kalimantan, Indonesia. More recently, Spehar & Rayadin (2017) found that the relative abundance of orangutans within the same plantations, were higher than 70% of other mammal species recorded. Despite these potentially positive results, further research is needed to fully understand the long term viability of this population. Orangutans have been regularly observed within oil palm plantations and occasionally nest in palms, although typically within 50m of forest (Ancrenaz, *et al*. 2015). This unexpected resilience to even high levels of anthropogenic disturbance, may have implications for orangutan conservation strategies. This is particularly true on Borneo, where an estimated 78% of the island’s orangutan population is currently found outside of protected areas and conservative estimates suggest close to half this area will be deforested (Wich *et al.* 2012*)*. Although on Sumatra, roughly 91% of the current orangutans range is within the protected Leuser Ecosystem (Wich, *et al.* 2008), illegal habitat conversion, primarily for oil palm, is still a major threat to the species (Singleton, *et al.* 2015). Thus, in order to effectively converse the species, understanding how orangutans respond to habitat conversion will be of increasing importance.

Orangutans dietary and behavioural ecology makes these species highly adapted to tropical forests, being predominantly arboreal, feeding mainly on fruit and nesting within the canopy (Marshall *et al*. 2009). The forest canopy also buffers against external environmental conditions, retaining moisture and protecting against extreme temperature changes and solar radiation (Hardwick *et al*. 2015). Therefore, dimensional structural features of the canopy are likely to be important determinants of orangutan presence. Light Detection and Ranging (LiDAR) is a remote sensing technology which is becoming increasingly popular and accessible within ecological studies (Davies & Asner, 2014). Airborne LiDAR can scan large areas of forest at high resolution, enabling detailed forest structural data to be measured. LiDAR has been used to measure tropical forest carbon and more recently linked with ecological data to predict species movement (McLean *et al*. 2016, Davies *et al*. 2017) and species richness (Gouveia *et al.* 2014, Goetz *et al.* 2007). LiDAR has revealed horizontal connectivity within the canopy is of more importance in influencing orangutan movement than vertical structures such as number of contiguous layers (Davies *et al*. 2017).

Using a landscape currently undergoing a planned conversion to oil palm, I investigate the effects of habitat modification on orangutan populations. I use commonly employed orangutan nest survey methods, to determine orangutan population density across a gradient of modified forest habitats and investigate if landscape feature and forest structural data, can be used to predict orangutan density across modified landscapes. Orangutans are known from the site and nests have been observed in heavily degraded forest and forest remnants in the surrounding oil palm estates. Similarly, Ancrenaz *et al.* (2015) has shown that orangutans are commonly observed within mature (>5 years) oil palm plantations by workers. What is less clear is how these animals are moving across these agro-industrial landscapes, weather moving directly between forest patches or taking less direct routes in order to maximize the amount of time spent in forested areas. If the latter is true we would expect to see significantly higher densities with the least isolated forest fragments and riparian reserves, closest to continuous forests. However if orangutans will readily move over large distances of heavily degraded areas, such as oil palm, there should be little difference in density and increased patch isolation.

Methods

Study site

The study was conducted at the Stability of Altered Forest Ecosystems project (SAFE: https://www.safeproject.net), part of the Kalabakan Forest Reserve (4° 33′ N, 117° 16′ E) and surrounding oil palm estates covering an area of approximately 13,000 ha, in the Malaysian state of Sabah, Borneo. The SAFE project covers an area of 7200ha which has experienced multiple logging rotations since 1978 and is currently in the process of being converted to oil palm plantation (Struebig *et al*. 2013, Ewers *et al*. 2011). Between 2013 and 2016, the SAFE site was salvage logged, with the exception of a network of replicated forest fragments and riparian reserves ranging from 1ha to 100ha and 5 m to 120 m respectively (See figure 3). At the time of this study no further development had taken place and clearance for plantation was delayed, leaving a soft matrix of regenerating scrubland with a network of logging roads

(Deere *et al*. 2017). The northern extent of the site includes the Ulu Segama Forest Reserve, a twice logged continuous forest block of >1 million ha that connects the pristine conservation areas Danum Valley, Maliau Basin and Imbak Canyon (Ewers *et al*. 2011). Ulu Segama contains one of the largest unfragmented populations of orangutans within Malaysia, consisting of 2,300 individuals (95%CI = 1,744 and 3,657), which is thought to have remained relatively stable since initial surveys in 2002 (Ancrenaz *et al*. 2010). The wider land scape also contains a substantial block of old growth forest, the Brantian-Tatulit Virgin Jungle Reserve (VJR) which covers 2200 ha, although logging encroachment has caused considerable degradation across much of the reserve (Deere *et al.* 2017). The remainder of the site comprises established oil palm plantations managed by Benta Wawasan Sdn. Bhd. and Sabah Softwoods Sdn Bhd., with trees ranging in age from 8 to 12 years. The estates contain remnant logged forest patches and riparian reserves, which can varying in width from 15 to 500 metres, although 30 metres is typical (Mitchell, *et al.* in press). Between 2002 and 2003 and again in 2007, Ancrenaz *et al* (2010) conducted aerial orangutan nest surveys of the area but as far as I am aware, I am the first to conduct ground surveys at the site.

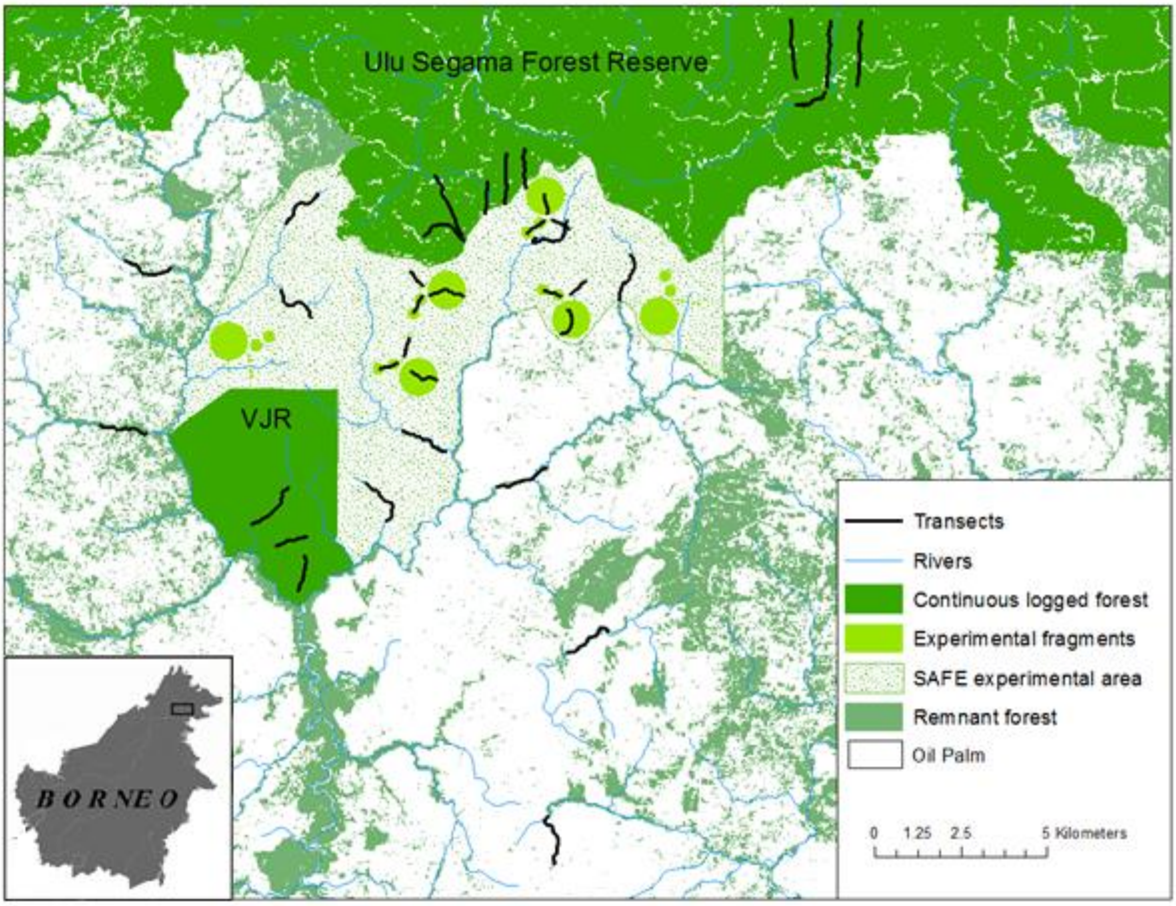

Figure 3. Transect location across study landscape. Transects within forest areas were made as straight as possible, however the complex terrain meant it was not always possible. Within riparian areas, transects followed the rivers natural course to ensure the matrix was not over sampled.

Transect design

To investigate the effects of habitat modification on orangutan densities, I placed transects within three distinct habitat types representative of the wider landscape. These included:

- 13 Transects in the continuous logged forest of Ulu Segama Forest Reserve and Brantian-Tatulit Virgin Jungle Reserve;
- 19 Transects in the salvaged logged SAFE experimental area, where transects were placed within the newly isolated fragments and riparian reserves, surrounded by a matrix of recently salvage logged forest;

- 12 Transects in forest remnants (hillside fragments and riparian reserves) within established oil palm estates, surrounded by palms aged 8-12 years.

In the continuous logged forest, to maintain randomisation and ensure spatial independence, initial transects were placed based on randomly generated points, produced by the SAFE project or LOMBOK consortium (http://lombok.hmtf.info/), who were working at the site and subsequent transects were placed at 500m intervals. Within the SAFE experimental area, I ensured transects were randomly placed by nesting them within the existing network of trails which form part of the SAFE project design (Ewers *et al*. 2011). Average transects length was 1.6km and ranged between 0.6km and 2km. Using a Garmin eTrex 10 handheld GPS, waypoints were taken at the start, finish and every 100 metres along each transect to delineate survey effort. Within riparian areas, transects were not straight but followed the river's natural course to ensure the transect line remained within the forest buffer and avoid biases from over sampling the surrounding oil palm plantations. In total, 44 transects were surveyed, each transect was surveyed once with a combined survey effort of 51.3km.

Orangutan nest surveys

Orangutans will build nests daily to rest for short periods during the day and to sleep in overnight. These nests are more complex than other great apes species (Prasetyo *et al*. 2009) and have characteristics that make them easily distinguishable from those made by other sympatric species, such as sun bear (*Helarctos malayanus*), giant squirrel (*Ratufa affinis*) or raptors. Using standard distance sampling methods (Buckland *et al*. 2001) along a network of systematically placed transects to record orangutan nests, will usually provide sufficient data >40 (Marshall *et al*. 2008) to produce precise nest density estimates.

I conducted orangutan nest surveys between April and August 2017, using the standing crop methods described by (Spehar *et al*. 2010) as this allowed the need of only a single survey to be conducted on each transect. Prior to the study, I received 5 days training in orangutan survey methods by the highly experienced staff at the HUTAN – Kinabatangan Orangutan Conservation Programme in the Lower Kinabatangan floodplain. Research staff at SAFE were then trained in the method. However to maintain continuity I was present during all orangutan surveys. Transects were walked at a steady pace and stopping at regular intervals to scan every direction for nests. When a nest was encountered, it was confirmed as orangutan using nest characteristics, such as bent or broken branches woven together in a relatively neat and structured fashion. Once confirmed as orangutan, perpendicular distance from directly under the nest to the transect line was measured using a Stanley (0-34-297) 30 metre tape measure. Each nest was assigned a decay rank, from A to E: where A = new nest, solid structure and leaves still green, B = leaves have started to dry out and discolour, C = nest structure still intact, leaves starting to disappear, D = most leaves gone, nest structure starting to disintegrate and E = all leaves gone, structure visible but heavily degraded. The height of each nest within the host tree and DBH of the host tree were also recorded.

Parameters in the orangutan density model

To convert nest density to orangutan density three parameters are needed: proportion of nest builders within the population (p), nest production rate (r) and the nest decay rate (t). These can vary both spatially and temporally and therefore would ideally be would derived from direct observations. However, this requires long term observational research, usually over many years and is rarely possible. As this study was conducted over too short a period to produce site-specific parameter estimates, I incorporated parameters from the published literature, in a similar fashion to Husson, *et al.* (2009). I employed a conservative estimate of proportion of nest producers (p) at 0.85, reported from a long-term study in the Lower Kinabatangan (Ancrenaz *et al.* 2004). Although this is lower than those reported from other sites within Borneo (0.88 - 0.89, Van Schaik, *et al.* 2005; Johnson, *et al.* 2005), the Lower

Kinabatangan has been heavily disturbed and is therefore likely to be more representative of the SAFE landscape. We used a nest production rate (r) value of 1.0, again reported from the same long-term study from the Lower Kinabatangan (Ancrenaz *et al.* 2004). Similarly, this is lower than other sites within Borneo (1.15 – 1.17, Van Schaik, *et al.* 1995, 2005; Husson, *et al*. 2009). As nest decay rate (t) shows the highest variation across sites, we calculated orangutan density using a t value of 259 days, reported from Gunung Palung (Johnson *et al*. 2005). Although decay rates calculated by Ancrenaz *et al.* (2004) were also available, estimates by Johnsons *et al* (2005) were more conservative, produced over an extended period of time (February 1997 – January 2002) and through monitoring a large sample size of nests (1568), therefore I opted to use this estimate. Other published decay rates are often calculated over shorter periods, or by means of Markov chain analysis and are therefore considered more prone to error (Mathewson *et al.* 2008). Changes in environmental conditions associated with habitat disturbance has been reported to influence decay rate (Mathewson *et al.* 2008) and therefore, comparing estimates from across a disturbance gradient using a consistent decay rate may not always be appropriate. However, I found no significant difference in the frequencies of nest decay rank between the three habitat types ($X^2 = 13.051$, df = 8, $P = 0.110$, See Table 3). Although this is not definitive proof that decay rate does not differ across the habitat types and our results should be interpreted as such, it does give us confidence that comparing density estimates using the same decay rate is suitable here.

Table 3. Number of orangutan nests observed in each of the 5 decay classes across the 3 habitat types used in this study.

	Decay class					
Habitat type	A	B	C	D	E	Total
Continuous logged forest	6	13	35	99	141	294
Salvaged logged forest	3	18	38	97	137	293
Remnant forest within oil palm	5	5	4	28	47	89
Total	14	36	77	224	325	676

A = new nest with solid structure green leaves, B = leaves started to dry and discolour, C = nest structure still intact, few leaves remaining, D = most leaves gone, nest structure degrading and E = all leaves gone, structure barely visible.

Calculating nest density

The SAFE study design consists of six systematically placed fragment blocks, with each block containing one 100ha, two 10ha and four 1ha fragments. To account for difference in sampling effort, data from transects within each fragment block were pooled to increase survey effort and transects <1km were excluded from density estimates. Transects <1km were excluded as short transects may result in bias density estimates, particularly if nests are patchily distributed across the landscape (Nomani, *et al.* 2012). Nest encounter rate was calculated by dividing the number of nests recorded along each transect by the total survey effort. There was no difference in the distribution of perpendicular distances across the three habitat sites ($X^2 = 1.0798$, df = 2, $P = 0.583$), and therefore comparing nest encounter rates between habitat types is appropriate.

Nest density was obtained using the formula:

$$D_{nest} = N / (L * 2w)$$

Where N is the number of nests observed along each transect, L is the length of each transect and w is the effective strip width. Effective strip width was calculated using Distance software 7.1 (Thomas *et al.* 2010), as is common practice with orangutan nest count data. Histogram examination suggested the data were slightly spiked at zero, therefore, following methods described by Buckland *et al.* (2003), data were aggregated into distance classes at 4m intervals. Similarly, to avoid biases from outliers, data were truncated at 40m. Six models were fitted to the data, these were uniform key with either cosine or simple polynomial adjustments, half-normal key with either cosine or hermite polynomial adjustments and hazard-rate key with cosine and simple polynomial adjustments. Model fit was assessed using the Chi-Square goodness of fit test (X^2). We obtained estimates of w from the best preforming model, using Akaike Information Criterion (AIC) values. As sufficient numbers of nests were observed within each habitat type, (>40 : Marshall *et al.* 2008), detection functions were fitted to pooled data from each habitat type separately (See Appendix II for plotted detection function and model details).

Nest densities were then converted to orangutan density using the formula:

$D_{orang} = D_{nest} / (p * r * t)$

Where p is the proportion of nest builders within the population, r is nest production rate and t is nest decay rate. In order to assess possible associations between orangutan density and environmental correlates, we calculated orangutan densities individually for each transect or fragment block and produced estimates of error around the mean density of each habitat type.

Determinants of orangutan density

Measures of three dimensional forest structure have been shown to predict habitat used in arboreal primates (Gouveia *et al.* 2014) and orangutan movement (Davies *et al.* 2017). To assess if similar features can explain variations in orangutan density across the study landscape, we employed comparable forest structural metrics obtained from airborne LiDAR data. Data were collected between September and October 2014 by the NERC's Airborne

Research Facility (ARF) (Jucker *et al.* in press). LiDAR produced georeferenced point cloud data from returned laser pluses, which were then divided into vertical strata. Forest structural metrics were then produced based on pixel density or counts from each strata (Jucker *et al.* in press). As distance data were truncated at 40m, LiDAR data were extracted as mean values across a 40m buffer around each transect. Landscape feature have similarly been shown to influence orangutan density, such as level of disturbance or distance from continuous forest (Spehar & Rayadin 2017)Therefore, several landscape variables were derived in ArcGIS software (ESRI 2011), using layers produced by (Deere *et al*. 2017) from Landsat 8 and SPOT5 satellite images originating from 2012–2014 (See Table 4).

Table 4. Predictor variables for Generalized Linear Models

Predictor variables	Measure	Description
Mean canopy height	LiDAR	Number of contiguous layers within the vertical forest strata cross a 40meter buffer
Canopy height SD	LiDAR	Standard deviation of canopy height across a 40metre buffed around each transect, taken as a measure of heterogeneity in the canopy
No. of contiguous layers	LiDAR	Number of contiguous layers within the vertical forest strata cross a 40meter buffer
Shannon	LiDAR	Index of diversity in the distribution of material within define vertical strata
Shape	LiDAR	A metric of canopy morphology, which defines the distribution material throughout the canopy
Distance	Landscape	Distance to the nearest continuous logged forest, measured from the midpoint of each transect to the closest border with either Ulu Segama Forest Reserve or the VJR.
Forest cover 40m	Landscape	Percentage of forest cover within a 40m buffer around each transect
forest cover 1km	Landscape	Percentage of forest cover within a 1km buffer around each transect
Habitat type	Landscape	The habitat type in which the transect is embedded

Predictor variables were examined for collinearity using the Pearson product-moment correlation coefficient (*r*) and generalized variance inflation factors (GVIF), with variables considered highly collinear if $r \geq 7$ or GVIF ≥5 (Zuur *et al.* 2010), I found high levels of collinearity among predictor variables therefore, to avoid bias and reduce error around parameter estimates, several variables were excluded from the analysis. In total, four variables were retained for statistical analysis: habitat type, distance to nearest continuous logged forest, mean number of contiguous layers and the canopy height standard deviation.

Statistical analysis

To assess differences in nest encounter rate and orangutan density between habitat types I employed One Way ANOVA tests. Generalized Linear Models (GLM) were used to assess relationships between nest encounter rate and orangutan density, relative to several landscape and forest structural predictor variables. GLMs with a Gaussian error structure and identity link function were applied to the data, as both nest encounter rate and orangutan density estimates were approximately normally distributed (Shapiro-Wilk test, $W = 0.964$, $P = 0.539$ and $W = 0.973$, $P = 0.769$, respectively). GLMs were specified with an effects parameterisation, designating continuous logged forest as the fixed intercept and reference habitat class from which to assess deviations in the response variable. Using methods delineated by Grueber *et al*. (2011), a global model was fitted to the data which included all predictor variables. Variables were standardised with the R package *arm* (Gelman *et al*. 2009), to have a mean of 0 and a standard deviation of 0.5, as this enables the direct comparison of the effect size of parameter estimates derived from model averages (Schielzeth 2010). The dredge function was then applied to the global model using the *MuMIn* package (Barton 2009), which produces a set of all possible model outcomes, including an intercept only model. Models were ranked based on corrected Akaike Information Criterion (AICc) scores, which compensate for small sample size. From this set of candidate models, a subset was extracted with a maximum delta ΔAICc (the difference between the AICc of each model and the best preforming model) of <2, as models with an ΔAICc values of <2 explain the data equally well (Burnham & Anderson 2004). Across the subset of top performing models, parameter estimates were averaged and parameters weighted based on the proportion of models in which each was included. Residual diagnostics were inspected to determine influences of curvature and heteroscedasticity, considered indicative of poor model fit. Model validation identified a single outlier with high leverage (Cook's Distance > 1), subsequent removal and reanalysis found no significant effect on the parameter estimates, therefore I present findings for models including the outlying data point. All analysis was performed using R version 3.4.2 statistical software (R Core Team, 2017).

Ethical Statement

The study was approved by the University of Kent's Animal Welfare Ethics Review Board and fully complied with the International Code of Best Practice for Field Primatology of the Primatological Society. Field research was authorised by Sabah Biodiversity Council and under access licence No. JKM/MBS.1000-2/2 JLD.4(104))

Results

I observed a total of 678 nests along the 44 transects, after transect <1km were excluded and the data were truncated, 594 nests were left for analyses.

Table 5. Summary of transect survey data

Habitat Type	Site ID	No. of nests	Transect length (km)	Effective strip width (metres)	Nest encounter rate (nests/km)	Orangutan density (Ind/km2)
Continous logged forest						
	LF1	31	1.8	15.5	17.2	2.5
	LF2	23	2	15.5	11.5	1.7
	LF3	25	2	15.5	12.5	1.8
	LFR	15	1	15.5	15.0	2.2
	LFE1	17	2	15.5	8.5	1.3
	LFE2	24	1.53	15.5	15.7	2.3
	LFE3	24	1.2	15.5	20.0	2.9
	LFE4	17	1	15.5	17.0	2.5
	LFER	25	1.6	15.5	15.6	2.3
	VJR_R	25	1.6	15.5	15.6	2.3
	VJR_1	37	1.2	15.5	30.8	4.5
	VJR_2	10	1	15.5	10.0	1.5
Salvaged logged forest						
	RR0	30	1.57	14.3	19.1	3.0
	RR5	26	1.5	14.3	17.3	2.8
	RR15	28	1.6	14.3	17.5	2.8
	RR30	29	1.7	14.3	17.1	2.7
	RR60	11	1.5	14.3	7.3	1.2
	RR120	21	1.6	14.3	13.1	2.1
	Block_B	28	1.92	14.3	14.6	2.3
	Block_C	29	2.1	14.3	13.8	2.2
	Block_D	24	2.43	14.3	9.5	1.5
	Block_E	43	2.25	14.3	19.1	3.0
Forest remnants in oil palm plantations						
	OP02	13	1.6	14.7	8.1	1.3
	OP03	9	1.28	14.7	7.0	1.1
	OP07	1	1.8	14.7	0.6	0.1
	OP12	6	1.79	14.7	3.4	0.5
	OP14	16	1.8	14.7	8.9	1.4
	OP16	7	1.75	14.7	4.0	0.6

Break down of site information showing habitat type, Site ID, number of nest per site and survey effort (km). Effective strip width was calculated in Distance 1.7 software (Thomas, *et al*. 2010) separately for each habitat type. Also showing three measures of orangutan abundance, nest encounter rate, nest density and orangutan density.

Orangutan abundance

Mean nest encounter rate was found to be 13.31 nests/km but demonstrated considerable variation across the landscape (range 0.56 - 30.83). A similar pattern was seen with orangutan density, ranging from 0.09 to 4.52 individuals/km^2 (mean = 2.01. See Table 5 for full details). There was a significant difference in mean nest encounter rate between habitat types, (One Way ANOVA F 2,12 = 15.49, P = <0.001). Tukey post hoc test indicated that nest encounter rate in riparian reserves within oil palm estates (Mean = 5.33 nests/km, SD 3.22) was significantly lower than both the continuous logged forest (mean= 15.79 SD 5.75 P = <0.001), and the recently isolated fragments in the SAFE experimental area (14.84 SD 3.99, P = 0.002). However, there was no significant difference between the continuous logged forest of the SAFE experimental area (P = 0.887).

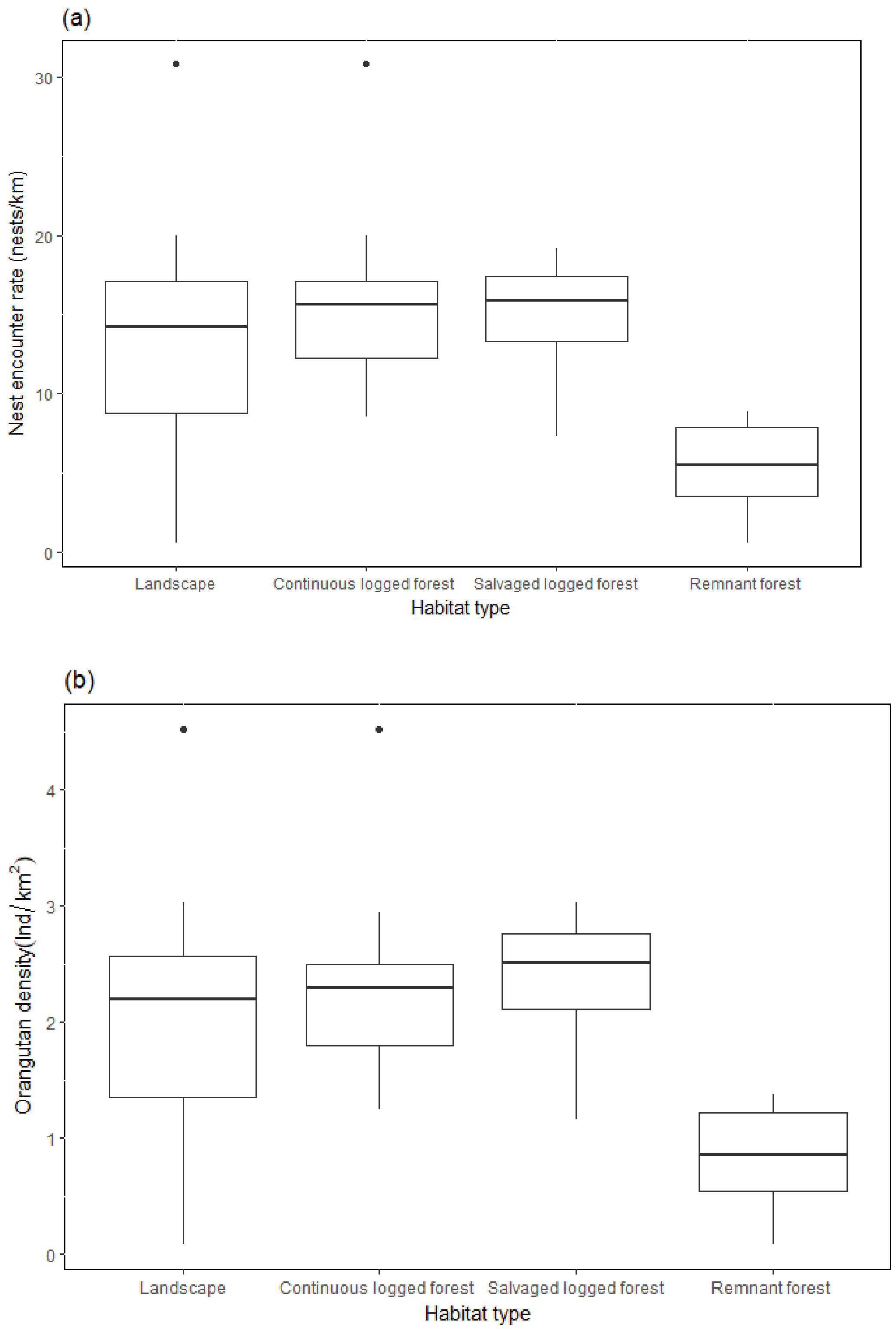

Figure 4. Box plots of (a) nest encounter rate (nest/km) and (b) orangutan density (individuals/km2), for the overall landscape and the three habitat types. The outlaying data point represents transect VJR_1, which had a disproportionately high number of nest recorded compared to other transect.

There was also a significant difference in orangutan density between habitat types (*F* 2,24 = 15.37, *P* = <0.001), with Tukey post hoc test indicated revealing the same pattern, with orangutan density within remnant forest patches (mean = 0.82 ind/km^2, SD 0.45) being significantly lower than both the continuous logged forest (mean = 2.32 SD 0.84, *P* = <0.001), and the salvaged logged SAFE experimental area (mean = 2.35, SD 0.63, *P* = <0.001). Again, there was no significant difference between the continuous logged forest and the SAFE experimental area (*P* = 0.601, See Figure 4).

Figure 6. Subset of top candidate models

Model	K	AICc	ΔAICc	Log-lik	weight
Nest encounter rate ~					
Habitat type + Canopy height SD	5	141.09	0	-63.78	0.52
Habitat type + Canopy height SD + Distance	6	142.4	1.31	-62.58	0.27
Habitat type + Canopy height SD + No. layers	6	142.96	1.87	-62.86	0.21
Orangutan density ~					
Habitat type + Canopy height SD	5	53.84	0	-20.16	0.53
Habitat type + Canopy height SD + Distance	6	55.19	1.34	-18.97	0.27
Habitat type + Canopy height SD + No. layers	6	55.71	1.87	-19.23	0.21

Models are ranked by corrected Akaike's Information Criterion (AICc), a statistical measure of model performance. Models were retained for model averaging based on ΔAICc <2, indicative of relative model performance in comparison to the best preforming model. K indicates the number of parameters used by the model. The log-likelihood value (Log-Lik) is an alternative measure of model performance and denotes the plausibility of the model. Weight representing Akaike's weights.

Determinants of orangutan density

The integrated GLM and information theoretic statistical approach yielded three models with a ΔAICc <2 (See Table 6), from which full model averaged estimates, penalized for parameter redundancy, were produced. For both nest encounter rate and orangutan density the 95% confidence intervals of remnant forest patch did not cross zero (Coefficient β = -14.874, 95%CI = -23.594, -6.155 and β = -2.161, 95%CI = -3.466,-0.857 respectively), suggesting forest conversion to oil palm has a significant negative effect on orangutan abundance (See

Figure 5). Canopy height SD had a significant positive effect for nest encounter rate (β = 7.118, 95%CI = 2.236, 12.000) and orangutan density (β = 1.081, 95%CI = 0.349, 1.813). Remnant forest patch and canopy height were of high and equal importance in predicting orangutan abundance, with both having 100% relative importance, appearing in all models within both subsets of top candidate models. Salvage logged forest had 100% relative importance however, although habitat type is important are predicting orangutan abundance, salvaged logged forest was not significantly different from logged forest. The 95% confidence intervals of all other variable crossed zero and had low <30% relative importance, providing little evidence to suggest that distance from logged forest or number of contiguous layer effects orangutan abundance (See Appendix II).

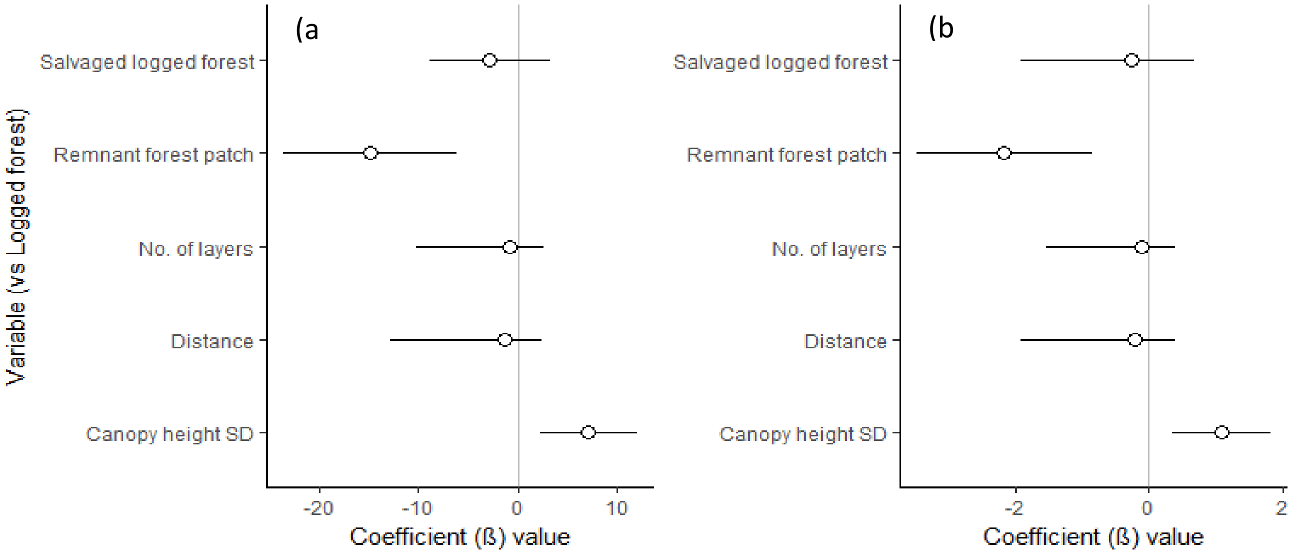

Figure 5. Plotted model averaged coefficients β with 95% confidence intervals for nest encounter rate (a) and orangutan density (b), with logged forest as the fixed intercept. For both abundance indices, the 95% confidence intervals for remnant forest patch and canopy height standard deviation do not cross zero, indicating a significant effect on orangutan abundance.

Discussion

Methodological considerations

Parameter selection

Converting nest density estimates to orangutan density, with the use of demographic and nest visibility parameters, is potentially a significant cause of error (Mathewson *et al*. 2008). Due to the time period of the study, it was not possible to produce site-specific decay rates and therefore, I used a single decay rate taken from published data. This method has been used previously when standardising density estimates across the orangutans range (Husson *et al*. 2009). Like Husson *et al*. (2009), I selected the most appropriate parameters from sites with similar disturbance histories and forest type, however this still raises potential errors. For instance, Spehar and Rayadin (2017) found the use of site-specific decay rates made a difference in the significance of various abundance estimates when compared between habitat types, after the application of site specific decay rates. However, Spehar and Rayadin (2017) compared abundance estimates between natural forested areas and mono-cultured plantations of acacia and eucalyptus and therefore, intrinsic differences in decay rates are to be expected. Here, I conducted nest surveys only in natural forest patches and would not expect the same inherent difference in decay rate between habitat types.

Other factors which have been reported to effect decay rate within Borneo are altitude and rainfall (Mathewson *et al*. 2008, Van Schaik, *et al.* 1995). Altitude range did not differ across my study landscape and therefore is not expected to affect nest decay rate. Although I did not explicitly measure rainfall and cannot guarantee rainfall was homogenous across the site, Mathewson *et al* (2008) found limited support for rainfall affecting decay rate and therefore, I do not feel it is an issue here.

Decay rate has the largest potential to introduce error within density estimates however, demographic factors may also generate biases, particularly in disturbed areas. For instance, increased levels of disturbance may limit nesting opportunities or alter the abundance of tree species orangutans preferentially use for nesting, increasing nest reuse (Ancrenaz *et al*. 2004) and therefore lead to underestimation of orangutan density. Similarly, changes in the demographics of the population will change the proportion of nest builders. Although population demographics are hypothesised to be different within heavily disturbed areas (Marshall *et al*. 2009), long term studies from areas of differing disturbance have showed limited deviation in these two parameters (Mathewson *et al*. 2008). Therefore, using demographic parameters from other studies appears appropriate here, although long term observational studies from areas with high levels of disturbance, such as plantations, are needed to fully understand how the demographics of local orangutan populations are affected.

Distance sampling assumptions

A key assumption of distance sampling is that transects are randomly placed within the study region (Buckland *et al*. 2001). I was able to fulfil this assumption within the logged forest and salvaged logged SAFE experimental area using the existing study design. However, this was difficult to achieve within oil palm estates as riparian reserves are not randomly situated within the landscape, so to overcome this, we employed existing transects located as part of the LOMBOK consortium (http://lombok.hmtf.info/). These were specifically chosen to give a representative sample of riparian reserves for the area. While this approach limits my ability to produce abundance estimates for the landscape, I feel the estimates produced are representative of riparian reserves within the area.

A second assumption is that all nests directly above the transect line are detected with 100% probability (Buckland *et al*. 2001). Particular care was taken during surveys to ensure all nests above the line were recorded however, dense forests can limit visibility and even experienced observers are prone to miss nests (Spehar *et al*. 2010). Histogram plots of perpendicular distances within each habitat type peaked at 0 metres from the transect line and were not significantly different between habitat types, suggesting this assumption was fulfilled across all sites.

Despite the mentioned limitations, density estimates for the Ulu Segama Forest Reserve are within the range of estimates produced by Ancrenaz *et al.* (2010), for the same area by aerial surveys. Therefore, I am confident that the estimates are representative for the landscape.

Comparison of density estimates

Interestingly, the recent salvage logging appeared to have little effect on orangutans, as densities were statistically similar between the salvaged logged SAFE experimental area and the neighbouring secondary logged forest. This is contrary to the prediction that orangutan density would be higher in areas surrounding the recently logged forest, as orangutans are forced to migrate in response to reduced resources and potential nesting opportunities, as has been observed elsewhere (Husson *et al*. 2009). However, our findings may indicate that the decline in orangutan density is not an immediate process but may take time for the full effects of the disturbance to be observed. Orangutans appear to be particularly resilient to food shortages and are able to sustain themselves on fall back foods, such as cambium and bark for relatively long periods of time (Morrogh-Bernard *et al*. 2009). However, the limited food availability within heavily logged landscapes is unlikely to sustain orangutans for extended periods of time and would likely lead to animals eventually having to migrate or face starvation. The salvage logged area is due to be converted to monoculture oil palm, beginning in 2018, although abundance estimates were beyond the scope of this study and no estimates currently exist for the landscape, the area still appears to hold a relatively large number of orangutans. In both Indonesia and Malaysia, the killing of orangutans is illegal (Meijaard *et al*. 2011) but there are currently no legal requirements for the consideration of local orangutan populations during logging. This raises both welfare and conservation concerns for the species, which seemed to have received little attention thus far. During the conversion process, any remaining vegetation will be felled and burnt, before terracing and the planting of oil palm commences, meaning orangutans will either have to migrate to surrounding forested areas, Ulu Segama and the VJR or are likely to be killed. These forested areas appear to already hold relatively high densities of orangutans (2.32 ± SD 0.84), creating increased competition for finite resources. This is particularly true of the VJR, which after the surrounding area is converted to oil palm, will represent a large forest fragment, surrounded by a matrix of oil palm. Any orangutans in the fragment will effectively be trapped, with limited opportunities to disperse and therefore, increased competition from overcrowding is likely to be unsustainable in the long term. A recent integrative trend analysis found orangutan survivorship was lowest in areas of fragmented forest or near to areas of recent forest conversion to agriculture (Santika *et al*. 2017). With increasing areas of orangutan habitat likely to be converted to oil palm, consideration needs to be given to allowing resident animals to either disperse successfully or maintain sufficient forest cover to allow animals to persist.

Both measures of orangutan abundance in remnant forest patches within oil palm estates were significantly lower than those in the continuous logged forest and the salvaged logged SAFE experimental area. As expected, conversion to oil palm has a negative effect on local orangutan populations. Despite this, nests were encountered on all transects within remnant forest patches and riparian reserves in oil palm estates, suggesting orangutans commonly use these areas. Additionally, it is likely at least some of these animals are resident within the estates, as although orangutan home ranges can be difficult to estimate (Singleton & van

Schaik 2001), given the large distances nests were observed from the closest continuous forest (≥12km), it is unlikely these animals are regularly moving between oil palm estates and continuous forested areas. Equally, due to the lack of difference in densities between the salvaged logged and continuous forest, it is doubtful orangutans within oil palm estates are individuals displaced during the salvage logging. As a result, although density is lower, the oil palm landscape appears to still maintain orangutans. The generalised linear models revealed certain nuances in the data which may be important in explaining orangutan persistence within oil palm estates. Although intuitively orangutan distance from logged forests would have a negative effect on orangutan abundance, here there was no evidence that distance from logged forests affected orangutan density. Instead, apart from habitat type, the only other significant variable effecting density was canopy height standard deviation. This suggests that, although remnant forest patches within modified landscapes can support orangutans, this is dependent on forest quality.

Conservation implications

Orangutan populations appear to be relatively robust to forest disturbance but are negatively affected by forest conversion to oil palm however, despite being found at lower densities, orangutans appear to possess sufficient behavioural and dietary plasticity to persist where remnant forest patches remain. Currently, 10% of Borneo's land-cover is under monoculture plantation (Gaveau *et al*. 2014), the majority of which has replaced suitable orangutan habitat. As a result, there is likely to be remnant populations of orangutans already living within human modified landscapes. The lack of quantitative data from these areas has resulted in their exclusion from state or range-wide abundance estimates and distribution models (Wich *et al*. 2012). Excluding these areas may lead to underestimates of population numbers, with a recent report suggesting that in Borneo, as many as 10,000 orangutans are likely to be present within oil palm estates (Meijaard *et al*. 2017).

Previous research on orangutan behavioural ecology suggests orangutans within modified landscapes are likely to be young, subordinate males dispersing, or displaced by, dominant flanged males from more optimal habitat (Ancrenaz *et al*. 2015). Although only anecdotal, during this study, all orangutans observed in remnant forest within oil palm estates were adult females with dependant offspring (Pers, Obs). Similarly, Spehar and Rayadin (2017) also recorded adult females with dependant offspring in timber plantations in East Kalimantan. This can likely be explained by female philopatry, which is common with orangutans (Van Noordwijk, *et al.* 2012) and therefore, females are least likely to disperse in response to disturbance. As a result, remnant forest patches within altered landscapes are likely to hold a significant number of individuals important to the population, which are largely overlooked within conservation strategies.

The continued rate of land cover change across Borneo is expected to be high, through both human modification and anthropogenic climate change (Struebig *et al.* 2015; Wich *et al*. 2012), with a further 50% of the current orangutan range predicted to be deforested (Wich *et al*. 2012). Orangutan populations are already highly fragmented, particularly in Sabah (Santika *et al*. 2017) and further land cover change will increase fragmentation and isolation. This can have deleterious effects, reducing gene flow between isolated populations and leading to inbreeding depression. Modelling the establishment of corridors within the fragmented orangutan population in the Kinabatangan floodplain, is predicted to increase mean population size and reduce inbreeding depression (Bruford *et al*. 2010). Similarly, climate change is likely to shift suitable orangutan habitat up slope, due to changes in temperature, precipitation and seasonality (Struebig *et al.* 2015). In response, orangutan populations will be forced to migrate, in order to track changes in suitable habitat. Until recently, modified landscapes have been thought to be highly impermeable to orangutan movement. However, my data suggests that distance from continuous forest had little effect on orangutan density and that individuals do use riparian areas in oil palm, several kilometres from large forest patches. As mentioned, several of these riparian reserves are relativity large distances from the closest continuous forest and it is therefore plausible that these animals are living exclusively within riparian reserves. Further research is now needed to assess resource availability, the effects of human-orangutan conflict, dispersal abilities and habitat connectivity, in order to fully understand the extent to which these estates can support orangutan populations. For instance, it is unlikely orangutans would be able to travel large distances within oil palm estates without the presence of remnant forest patches. Models by Wich *et al*. (2012) suggest temperature can influence orangutan distributions and increased temperatures recorded in oil palm estates would potentially limit the distance orangutans are able to travel. My data also indicates that forest quality has a significant effect on orangutan density, which may be a result of increased protection against extremes in temperature. Therefore, prolonged travel within oil palm estates would be limited and natural forest patches are likely to be essential to orangutan persistence within these heavily modified landscapes. Designing oil palm estates to maintain sufficient forest cover, in order to facilitate movement between fragmented populations and across human modified landscapes, is likely to have a positive impact on the long term viability of orangutan populations.

This study adds to the increasing recognition that human modified landscapes should be included in conservation strategies. However, several potential negative impacts of maintaining orangutan populations within these landscapes also need to be considered. Orangutans living, or moving, through human dominated landscapes are subject to higher rates of human-orangutan conflict. With orangutans close evolutionary relationship to humans, zoonotic transfer of disease is a significant risk (Russon, 2009). Tuberculosis and hepatitis could have a devastating effect on the population if transfer were to occur (Kilbourn, *et al.* 2003). Although an outbreak has not yet been reported within orangutan populations

(Russon, 2009), fatal transmission of respiratory viruses between human researchers and chimpanzees have been reported (Köndgen *et al*. 2008). Simulation by Carne *et al.* (2014) suggests that unlike chimpanzees, the orangutans largely solitary lifestyle would limit the transmission of even highly infectious diseases, resulting in a limited affect on populations and therefore, the potential negative effects of novel pathogens on orangutan populations remain largely unknown. Hunting is also widespread across much of the orangutans range, particularly in Kalimantan (Meijaard *et al.* 2011) and has been attributed to declines in orangutan populations within degraded habitats (Marshall *et al.* 2006). Orangutans are slow to reproduce, having the largest inter-birth period of any primate (Wich *et al*. 2004) and even just 1% off take from hunting can lead to local extinctions (Marshall *et al*. 2009). Therefore, simply ensuring sufficient habitat remains to allow orangutans to persist will not provide sufficient protection alone. A more holistic approach is needed, not only to conserve the most appropriate forested areas within estates and to ensure connectivity, but also increase public awareness of the laws protecting orangutans and the inherent risk of disease transfer. This would require increased engagement between stakeholders to mitigate problems associated with human-orangutan conflict, such as crop raiding. A large scale approach is needed, to ensure effective landscape planning through co-operation between agricultural corporations. The Round table of Sustainable Palm Oil (RSPO) is an ideal way to facilitate communication between stakeholders.

Integrating modified landscapes into conservation strategies poses significant challenges for conserving orangutans within oil palm estates. For instance, leaving 1,000 ha unconverted can entail annual losses to oil palm producers of over half a million American Dollars (Nantha & Tisdell, 2009). There are limited opportunities for generating economic benefits from eco-tourism with orangutans, particularly within oil palm estates. These areas are often hard for tourists to access, or of limited appeal, therefore offsetting costs of conserving forest will be difficult to achieve (Nantha & Tisdell, 2009). The oil palm industry is increasingly moving towards business models based on corporate social responsibility, in response to consumer demand (Paoli *et al*. 2010) and in Indonesia, RSPO certification reduced deforestation by 33% (Carlson *et al*. 2018), however globally, only an estimated 20% of oil palm was certified by 2017 (Carlson *et al*. 2018). As a result, certification schemes, such as RSPO, have the largest potential to conserve orangutans within oil palm estates (Nantha & Tisdell 2009). However, there may be significantly more orangutans within non-RSPO certified estates (9,300 individuals) than in RSPO certified estates (275 individuals), but relative population decline is higher within non-RSPO estates (Meijaard *et al*. 2017).

The degree to which orangutans can use modified landscapes is to some degree likely to be species specific. Bornean orangutans display higher dietary flexibility than the Sumatran species (Russon, 2009), therefore their ability to cope with the reduced food availability is likely to be greater. Furthermore, this study was conducted on the Northeast Bornean orangutan (*P. p. morio*), which is considered to be the most flexible subspecies, due to the north east of Borneo being particularly prone to the effects of the El Nino Southern Oscillation (Siegert *et al*. 2001). This has led to the subspecies, being particularly adapted to cope with limited fruit availability and to process tough fall back foods, such as bark, due to its robust jaw (Taylor 2006). Sumatran orangutans (*Pongo abelii*) appear to be less resilient to disturbance, being less terrestrial (Delgado, Van Schaik 2000) and having a higher dependency on fruit (Wich *et al*. 2006, Husson *et al*. 2009).

Although these results have been surprising, they should perhaps not have been totally unexpected as orangutans do have several ecological features which may aid them to persist within disturbed habitats. For instance, they are largely solitary and this freedom from competition will allow orangutans to persist in areas with lower resources than other group living species (Delgado & Van Schaik 2000). Despite being adapted for an arboreal lifestyle, orangutans will regularly leave trees and move quadrupedally over ground (Ancrenaz *et al*. 2014). Although this was theorised to be more common among males, which are considerably heavier than females and therefore, less able to utilise small trees for movement (Ashbury *et al*. 2015), increasing evidence suggests terrestrial movement is common among all sex and age classes.

Conclusion

Despite pledges by the Indonesian and Malaysian government to stabilise orangutan populations, they have continued to decline at an alarming rate of 25% over the past 10 years (Santika, *et al.* 2017). Forest conversion to oil palm negatively effects orangutan populations leading to reduced densities, however despite this, orangutans were still present in remnant forest patches within oil palm estates. This increases the recognition that orangutans have greater ecological resilience to disturbance than previously assumed. Not taking into account human modified landscapes within conservation strategies will fail to protect large numbers of orangutans. Although it is unlikely these areas alone can maintain viable populations, if managed appropriately, they may act as important corridors, connecting isolated populations and facilitating migration in response to climate change. This study should not be taken as an endorsement of oil palm. Conversion to oil palm reduces the amount of available resources and increases the risk of human-orangutan conflicts, such as hunting and exposure to novel pathogens. However, with growing demand, further oil palm expansion is inevitable and with orangutan habitat the most suitable for oil palm production, any conservation strategy which fails to include these modified landscapes will hinder orangutan conservation.

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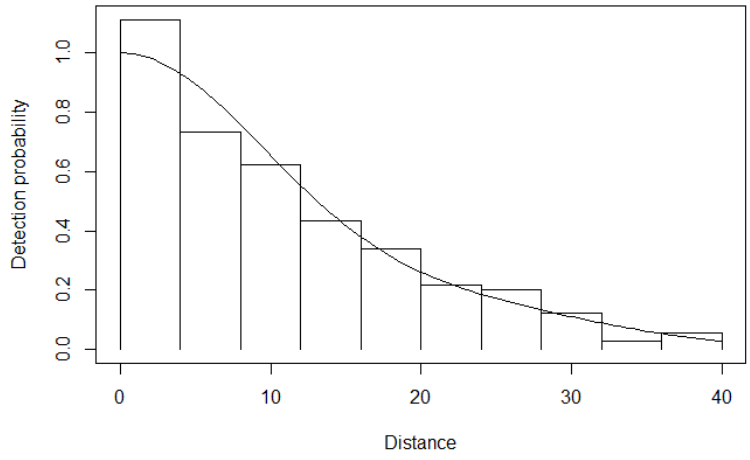
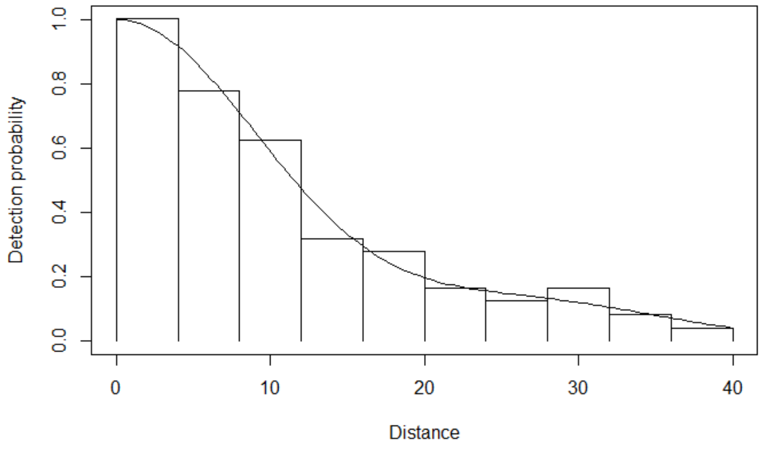
Appendix I

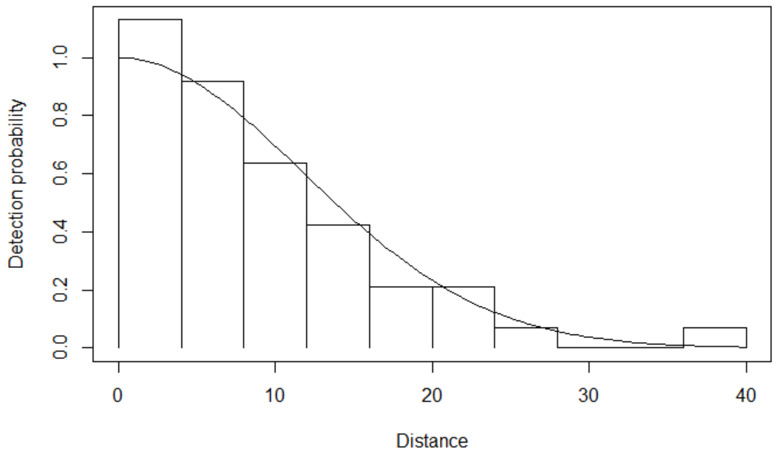
(a) Continuous logged forest - Fitted detection function
Half-normal with Cosine adjustment



(b) salvage logged forest - Fitted detection function
Half-normal with Cosine adjustment



(c) Remnant forest within oil palm - Fitted detection function
Half-normal with Cosine adjustment



Fitted detection functions for the three habitat types continuous logged forest (a), recently salvaged logged forest (b) and remnant forest patches within oil palm estates (c). four models were fitted to the data, Half-normal with both Cosine and simple polynomial adjustment. Models were selected based on Akaike Information Criterion (AIC) values and fit assessed using the Chi-squared goodness of fit test. For each habitat type, half normal with Cosine adjustment performed best and was therefore used to obtain the effective strip width

Goodness of fit tests:

(a) X2 = 6.314, df = 7, p = 0.503

(b) X2 = 3.266, df = 7, p = 0.859

(c) X2 = 12.935, df = 8, p =0.114

Appendix II

Response Variable	Explanatary Variable		β	SE	2.5% CI	97.5% CI	RI
Nest encounter rate	Habitat type (vs Logged forest)	Salvaged logged forest	-2.863	2.975	-8.875	3.250	**1.00**
		Remnant forest	**-14.874**	**4.265**	**-23.594**	**-6.155**	
		Canopy height SD	**7.118**	**2.343**	**2.236**	**12.000**	**1.00**
		Distance	-1.395	2.970	-12.784	2.513	0.27
		No. of layers	-0.772	2.053	-10.167	2.661	0.21
Orangutan Density	Habitat type (vs Logged forest)	Salvaged logged forest	-0.254	0.446	-1.928	0.662	**1.00**
		Remnant forest patch	**-2.161**	**0.446**	**-3.466**	**-0.857**	
		Canopy height SD	**1.081**	**0.351**	**0.349**	**1.813**	**1.00**
		Distance	-0.205	0.442	-1.914	0.383	0.27
		No. of layers	-0.116	0.309	-1.525	0.400	0.21

Model-averaged coefficients (β) for explanatory variables, from the three top preforming models ΔAICc <2, with Logged forest as the fixed intercept. Bold text indicates significant variables, as 95% confidence intervals do not cross zero. Also presented are standard errors and 95% confident interval. RI denotes the sum of Akaike weights for each variable and represents the relative importance of each explanatory variable within the model.