Influences of Forest Structure on the density and habitat preference of two sympatric gibbons (*Symphalangus syndactylus* and *Hylobates lar*).

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Abstract

Forest structure, defined as the three-dimensional vertical and horizontal distribution of canopy vegetation, has great influence on the distribution patterns and abundance of forest primates. The complexity of this structural canopy produces a diverse range of microhabitats and distinct ecological niches, allowing ecologically similar species to co-exist. Degradation of forests through anthropogenic factors significantly alters forest structure, and arboreal species such as gibbons are particularly vulnerable to these changes due to their reliance on canopy for survival. We investigated how forest structural variables influenced the density of two sympatric gibbon species (siamangs *Symphalangus syndactylus* and lar gibbons *Hylobates lar*) in Sikundur, a historically disturbed tropical lowland forest in north Sumatra. We used auditory sampling to establish group density in 10 locations and assessed structural characteristics of forest within 4-6 vegetation plots in each location. Lar gibbon group densities were 0.53-3.10 groups/km2 and siamang group densities were lower, with 0.0-1.0 groups/km2. The densities of both species were positively influenced by median height of first bole and the percentage of canopy connectivity. Lar gibbon group density was positively related to large (DBH 30-100 cm), tall (20-25 m) trees with a large crown area (100-300m2), while siamang group density showed no significant relationships with these variables. These findings show canopy connectivity and height to first bole are significant structural variables for the continued presence of both gibbon species although, ecologically similar species can be influenced by different levels of structural disturbance. This canopy structural variation between sympatric species existing in the same ecosystem allows for home range overlap, low interspecies competition and co-existence.

Keywords: small ape, rainforest, primate abundance, conservation

Introduction

Tropical rainforests are highly complex, spatially heterogeneous ecosystems, with a multifaceted, three-dimensional structure. Thus, it is not surprising that they are one of the world's most biodiverse ecosystems, containing two-thirds of the earth's terrestrial wildlife (Gardner et al. 2009) and almost 90% of the world's primate species (Estrada et al. 2017; Gross 2017). The evolutionary history of many forest species is closely linked to the canopy structure of tropical forests (Fleagle 2013), and numerous species have evolved specific morphological and behavioural adaptions for an exclusive arboreal lifestyle (Fleagle & Lieberman 2015). This structural complexity creates a diversity of microhabitats and distinctive ecological niches, allowing ecologically similar species to co-exist with limited interspecific competition. These sympatric species co-exist by using different canopy strata (Morrogh-Bernard et al. 2014; Fenosoa et al. 2018), exhibiting distinctive forms of locomotion (Garber 2011), dietary variation (Dew 2005; Zhou et al. 2014), and temporal portioning of daytime behaviours (Kronfeld-Schor & Dayan 2003; Snodderly et al. 2019).

Tropical rainforest is being lost and degraded at unsustainable rates across the world due to the continued escalation and expansion of agriculture and urbanisation (Gaveau et al. 2009; Turubanova et al. 2018), resulting in fragmentation and canopy disruption. Habitat destruction and degradation are the most serious threats to species worldwide (Tabarelli & Gascon 2005), and have already resulted in high levels of plant and animal extinctions (Wilcove et al. 2013). Degradation and fragmentation decrease habitat quality, and change the complex structure of the forest canopy, narrowing the available ecological niches and potentially leading to an increase in interspecies competition (Chesson 2000). Arboreal species, such as many primate species, are sensitive to forest structural disturbance resulting from habitat degradation, owing to their reliance on canopy structure for movement (Pozo-Montuy et al. 2011; Cheyne et al. 2013). A frugivorous diet, large home range size and slow life histories also increase a species sensitivity to habitat alteration (Boyle & Smith 2010). However, the negative impacts of habitat degradation on many forest dwelling species such as primates are difficult to quantify, especially where long-term population data are unavailable (Phoonjampa et al. 2011).

Primate responses to habitat changes vary. Some primate species exhibit morphological adaptations and behavioural plasticity that allow them to subsist in degraded and structurally modified forest habitats, such as the Angolan black and white colobus monkey *Colobus angolensis* and the mantled howler monkey *Alouatta palliata* (Duckworth et al. 1999; Bicca-Marques 2003; Anderson et al. 2007), whereas others appear to be more vulnerable due to greater specialisation both morphologically and behaviourally (Schwitzer et al. 2011), such as the Bornean orangutan *Pongo pygmeaus* (Engstrom 2000), the saki monkey *Chiropotes satanas* (Boyle & Smith 2010), the southern gentle lemur *Hapalemur meridionalis* (Eppley et al. 2011), and the brown spider monkey *Ateles hybridus* (Marsh et al. 2016).

Gibbons exhibit extreme arborealism and have long maturation periods (Reichard & Barelli 2008), reducing the potential for population recovery following disturbance to the forest structure (O'Brien et al. 2003; Phoonjampa et al. 2011). Gibbon species have been the focus of behavioural and ecological studies since the 1930s (Carpenter 1940; Chivers 1984; Mitani 1990; Brockelman & Srikosamatara 1993; Bartlett 2007; Cheyne 2007a; Fan et al. 2009), but the relationship between forest structure and gibbon population densities and their resilience to canopy structural disturbance varies (Geissmann 2007; Lee et al. 2015). Some studies have shown the importance of tall, relatively undisturbed forest with significant canopy coverage for gibbon presence (Traeholt et al. 2006; Hamard et al. 2010; Phoonjampa et al. 2011; Lee et al. 2015; Cheyne et al. 2016), whereas others have found little or no effect of forest structural variables on gibbon densities (Brockelman 2009; Akers et al. 2013; Chandra Ray et al. 2015).

While most gibbon species are allopatric, an exception is the siamang (*Symphalangus syndactylus*), which occurs sympatrically with the lar gibbon (*Hylobates lar*) or agile gibbon (*Hylobates agilis*) on the Thai-Malay Peninsula and the Indonesian island of Sumatra (Gittins & Raemaekers 1980; Reichard & Sommer 1997). Both the lar gibbon and the siamang are classified as Endangered by the IUCN (IUCN 2020) due to Sumatra's high deforestation rates (Miettinen et al. 2012), and hunting for subsistence and the pet trade (Brockelman & Geissmann 2008) both within and outside protected areas (Jepson et al. 2001; Kinnaird et al. 2003; O'Brien et al. 2003). Over the past 70 years, the rainforests of Sumatra have suffered some of the greatest losses recorded (Margono et al. 2014), and much of the island's lowland forests where both species predominantly reside have been exhausted. This has resulted in 54% of lar gibbon habitat and 29% of siamang habitat being lost between 2000 and 2012 (Supriatna et al. 2017). Exact knowledge of both species' current conservation status is limited due to lack of density estimates in Sumatra, especially at the few remaining lowland sites (Yanuar & Sugardjito 1993; Yanuar 2001; O'Brien et al. 2004).

Lar gibbons and siamangs are both highly territorial, pair-living and use loud morning calls or 'duets' for territory defence and strengthening of pair bonds (Chivers 1974; Bartlett 2007). These loud morning calls are highly characteristic of the individual species, and easily differentiated in the field. Duets can be heard up to ~2 km away and can be used for conducting auditory surveys (Brockelman & Ali 1987; Brockelman & Srikosamatara 1993; Cheyne 2007a). Where they occur sympatrically, the species co-ordinate their morning calls, i.e in Peninsular Malaysia siamang duets are heard ~2 hours after those of lar gibbons (Chivers 1974; O'Brien et al. 2004), to avoid competition, though with siamangs being considerably larger than lar gibbons (10-12kg and 5-6kg respectively; Smith & Jungers 1997), they have been known to outcompete lar gibbons for resources both actively and passively (O'Brien and Kinnaird. 2011).

Siamangs and lar gibbons are both extremely arboreal and use brachiation as their main mode of locomotion (Palombit 1997; Fleagle 1980). These species have similar diets and sleeping tree preferences, and depend on tall emergent trees for sleeping and calling, requiring a highly connected, structurally mature canopy for travel, sleep and resource acquisition (Phoonjampa et al. 2010; Cheyne et al. 2012; Lee et al. 2015). Although both the siamang and lar gibbon are classified as frugivores, siamangs are more folivorous than other gibbon species throughout their range in mainland Asia (Chivers 1974; Raemaekers 1984). However, on Sumatra, siamangs are primarily frugivorous, attributed to the increased availability of figs rather than scattered fruit resources (Palombit 1992; 1997), decreasing their daily travel requirements. The siamangs ability to survive on a largely folivorous diet despite being a frugivore may enable this species to be less vulnerable to habitat disturbance (O’Brien et al. 2003), and better able to cope with forest structural change than lar gibbons (Nijman et al. 2020). Range-wide on Sumatra, siamang densities tend to decline from south to north (O’Brien et al. 2004) whereas the lar gibbon is found only in the north of Sumatra and is ‘replaced’ by the ecologically comparable agile gibbon in the centre and south of the island (Brockelman & Geissmann 2020).

We aimed to ascertain how forest structural variation influences the density of the siamang and the lar gibbon in a historically degraded lowland dipterocarp forest. We measured forest structural characteristics and number of gibbon groups in the survey area to investigate these individual species’ habitat requirements and their sensitivity to structural disturbance. We also compared two different methods of density data analysis: the standard triangulation formula and a new acoustic spatial capture-recapture method, to ascertain if results were comparable across these methods.

We hypothesize (H1) that gibbon and siamangs require mature, highly connected forest with sufficient emergent trees to acquire higher group densities. We predicted that group densities were positively related to the average values and/or frequency of mature and tall trees with a large, well-connected canopy. Our second hypothesis (H2) is that the more folivorous siamang is more adaptable to canopy structural disturbance than the lar gibbon. Therefore, we predict that siamang group densities will show fewer relationships with specific forest structural elements than those of lar gibbons. Our third hypothesis (H3) is that siamang and lar gibbon groups perform territorial calls at different times to avoid competition between these ecologically similar species. Therefore, we predict an inverse relationship between group densities of siamang and lar gibbons, and temporal separation of morning calling bouts.

Methods

Study area

The study area measures ~57 km^2 and is located within the Langkat district of North Sumatra (04°58'-04°59' N and 98°04'- 98°05' E) on the eastern edge of Gunung Leuser National Park (GLNP) measuring 7,927 km^2, in the Leuser Ecosystem (26,000 km^2; Figure 1). The study area is dominated by lowland dipterocarp forest, mixed with rich alluvial forest along rivers (Knop et al. 2004). The climate is humid with an annual rainfall of 2000-3000mm and a mean monthly temperature of 27.4 °C, ranging from 26.1 °C to 30.4 °C (Roth et al. 2020). Elevation extends 30-500 m above sea level. The forest is characterised by low levels of fruit availability, with 2.1% of trees and lianas bearing fruit on average (range 0.3-13.4 %; Roth et al. 2020). This resembles fruiting in Bornean forests (3.0-6.8 %), where only one gibbon species is present in each habitat, and is markedly lower than fruiting rates in other Sumatran forest sites (6.9-30.6 %) (Roth et al. 2020; Wich et al. 2011).

The survey area was subjected to large and small-scale logging operations commencing in the late 1960s and continuing intermittently until late into the 1990s (Knop et al. 2004; Priatna et al. 2004). Presently, even with full protection, illegal logging and complete land clearing still occurs, in addition to other illegal activities including resin extraction, bird trapping, hunting and fishing. Despite this anthropogenic disturbance and related forest structural changes, it is one of the few remaining areas of lowland dipterocarp forest able to support arboreal primates, and is contiguous with large tracts of undisturbed forest in the national park. In addition to the two species of gibbon, five other primate species inhabit the region: long tailed macaque (*Macaca fascicularis*), pig tailed macaque (*M. nemestrina*), Thomas langur (*Presbytis thomasi*), Sunda slow loris (*Nycticebus coucang*) and Sumatran orangutan (*Pongo abelii*). Although predation on gibbons is rarely observed in the wild (Clarke et al.

2012), potential predators of gibbons at the study site include Sumatran tiger (*Panthera tigris sondaica*), clouded leopard (*Neofelis nebulosa*) changeable hawk-eagle (*Nisaetus cirrhatus*) and the reticulated python (*Malayopthon reticulatus*).

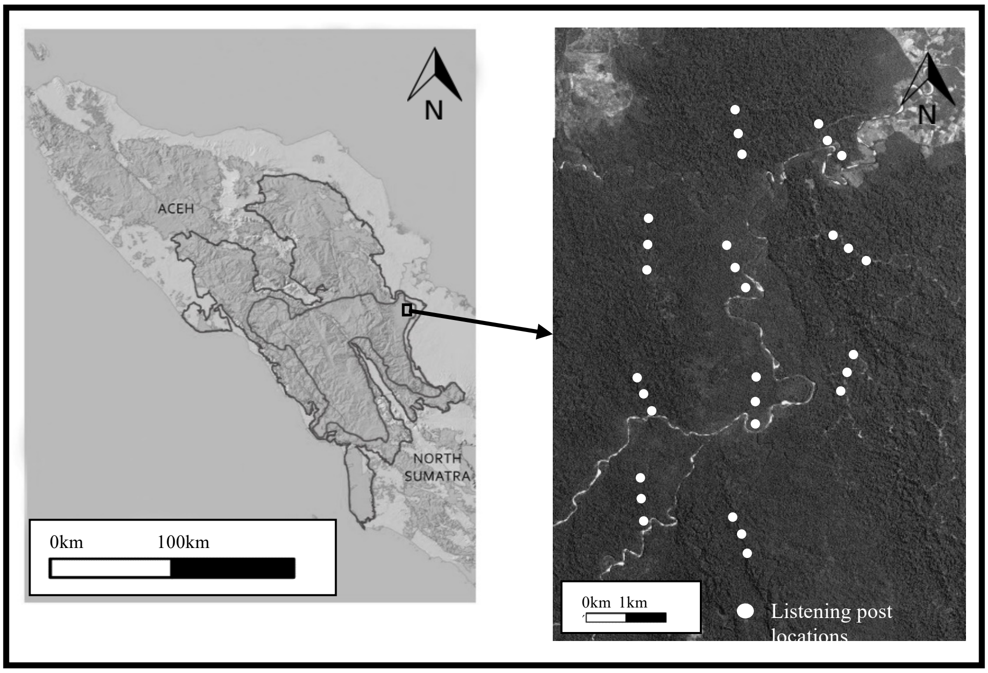

Figure 1. Location of our research area (small rectangle, left panel) in Gunung Leuser National Park (inner outline, left panel) in northern Sumatra, encompassed by the Leuser ecosystem (outer outline, left panel), and the location of 10 sets of 3 listening posts used to determine the group density of lar gibbons and siamangs (right panel), March to August 2016.

Data collection

We established 10 survey locations (arrays) across the survey area (Figure 1). We estimated the group densities of both gibbon species using auditory sampling at three fixed points (listening posts) within each of those 10 locations (Brockelman & Ali 1987; Brockelman & Srikosamatara 1993). This commonly used method allows comparisons to be made with other study sites across Indonesia and Malaysia (Gursky 1998; Estrada et al. 2002; Estrada et al. 2004; Nijman 2004; Cheyne et al. 2008; Hamard et al. 2010). The 10 locations represented the available range of habitat types: alluvial forest adjacent to rivers, higher elevated forest, and more intensively logged expanses of forest that also encompassed old logging roads. We placed the first array in the Sikundur trail system (top north-eastern corner of the research area). Outmost listening posts of adjacent arrays were positioned ≥2 km away from each other to avoid recording the same gibbon groups at more than one array. We set up three listening posts at each array in a linear order spaced 300-500 m apart (well within the listening range of groups) to allow detection of groups from more than one post (Kidney et al. 2016). We adjusted the exact locations of posts to avoid impassable vegetation and deep valleys where vocalisations may be missed or direction misinterpreted (Hamard et al. 2010). This resulted in some size variation of the sampling areas at each array, but suitable post locations are more important than ensuring uniform distance between posts (Phoonjampa et al. 2011). We chose a linear post design over the traditional triangular design as a study showed this yielded a lower variance and reduced bias when compared to non-linear designs of the same size (Kidney et al. 2016).

At each listening post, two observers recorded all gibbon group vocalisations heard between 04:30h and 10:30h for four consecutive, rain free days. We did not collect data on rainy days as rain negatively influences singing behaviour (Brockelman & Srikosamatara 1993; Cheyne 2007b; Lee et al. 2015). Prior to the start of data collection during March 1-8 2016, field teams trained together in survey methods to ensure measurements taken by team members were comparable and to determine the optimum time of singing. The same trained field teams collected data over 40 days between March 10 and August 1, 2016. We only included groups that produced at least one female great call and the male's responding call (indicative of a pair) in the analyses to avoid counting solitary individuals, which do not inhabit an exclusive home range (Cheyne et al. 2008).

For each call heard, the team recorded the compass bearing, estimated distance to the group, the time, and the species calling. To ascertain the number of groups per array, we determined group locations for each day by establishing the intersection of distances and compass bearings for calls heard from at least two listening posts with a matching time stamp (triangulation; Phoonjampa et al. 2011). We mapped groups heard from only one listening post (15% of calls) if they originated further than 800 m (lar gibbons) and 700 m (siamangs) from another group, and if the observer could distinguish them as a different group based on the time and location of the calls. For example, if an observer at one of the outer posts heard a group at the same time as they heard another group from a different location and in the opposite direction from the other listening posts, we recorded these as separate groups.

To determine whether a new call came from a different group than any calls heard earlier/later in the same day, we used a species-specific minimum separation distance between the estimated location of the calls. Gibbons defend their core home range area, which makes up approximately 75% of their entire home range (Cheyne et al. 2019). Home range sizes differ significantly depending on location and habitat (Savini et al. 2008) so we used species specific knowledge of home range and exclusive territory sizes for these gibbons in north Sumatra and the Sikundur area to calculate the separation distance (estimated diameter of the core area). For lar gibbons, we calculated a separation distance of 800 m based on a defended core area the size of 75% of the typical ~60 ha home range; and for siamang we used 700 m based on 75% of their ~50 ha home range (Harrison et al. 2020; Keller 2019, unpubl. data).

Analysis of density data

Auditory sampling methods have become common practise amongst gibbon researchers (Brockelman & Ali 1987; Cheyne et al. 2008; Hamard et al. 2010). Various methods are used in estimating densities from auditory surveys using distance sampling software (Gilhooly et al. 2015; Vu et al. 2018a) and more recently spatially explicit capture-recapture SECR protocols (Kidney et al. 2016). However, density values from the same study population vary with the method used, and the gibbonSECR model produces much lower and inaccurate densities in all studies (Cheyne, unpubl. data).

The IUCN Species Survival Commission (SSC) Primate Specialist Group's Section on Small Apes recently developed an acoustic spatial capture-recapture (ASCR) package that is recommended as the most accurate way of analysing primate acoustic data (Cheyne, unpubl. data). Studies comparing methods have concluded that the standard triangulation technique remains an important and effective method (Gilhooley et al. 2015; Cheyne et al. 2016), that has proved reliable in several surveys (Brockelman & Srikosamatara 1993; Gursky 1998; Estrada et al. 2002; Estrada et al. 2004; Nijman 2004; Cheyne et al.

2008; Hamard et al. 2010). Therefore, we use this method alongside the new ASCR analysis to compare gibbon group densities. We do not attempt to determine an overall density/population estimate for the entire area, only group density estimates for each survey array.

Triangulation technique for calculating gibbon densities

We calculated gibbon group densities per array using the package for calculating gibbon population density from auditory surveys developed by Vu and Rawson (2011) in Excel (Microsoft Office Professional 2013). This package uses the following formula (Brockelman & Ali 1987):

$$\mathbf{D} = n/[p(m) \times E]$$

Where **D** = gibbon group density at an array in groups/km^2, ***n*** = number of groups heard in each sampling period at each array, ***m*** = number of sampling days at each array (typically 4); ***p(m)*** = calling probability at an array over the sampling period ***m*** (estimated proportion of groups expected to sing during the sampling period of ***m*** days, also known as the correction factor); and ***E*** = total effective listening area of the array. Both ***p(m)*** and ***E*** need to be calculated for each study. We calculated ***p(m)*** by first establishing ***p(1)***, which is the probability of a call happening on any one day at any array using the combined data for each species:

$$\mathrm{p(m)} = 1-[1-p(1)]^{m}$$

where ***p(1)*** = call probability based on data obtained across all 10 survey areas across all sampling days (n = 40) for each species (see below). We estimated ***p(1)*** based on data from all survey days and arrays (Vu and Rawson, 2011) using the equation:

$$\mathrm{p(1)} = \frac{1}{2}\left(3 - \frac{\sqrt{4.N}}{n} - 3\right)$$

where ***n*** = mean number of gibbon groups detected per day (if groups called more than once in a day this still counted as one case) and ***N*** = cumulative number of gibbon groups detected in the 40-day period.

We calculated the effective listening area for each array by first calculating the effective detection radius, or detection distance (EDR). The probability of detection decreases significantly with the distance of the group from the listening post, and an important pitfall in previous estimates of gibbons is using a fixed effective listening area (E), in which all gibbons are assumed to be detected (Cheyne et al. 2008; Chandra Ray et al. 2015; Vu et al. 2018b). However, error using this method can greatly affect the density estimate. Instead, we calculated the EDR using the software program DISTANCE (Thomas et al. 2010; Poonjampa et al. 2011; Gilhooly et al. 2015; Lee et al. 2015). We obtained the EDR by entering all calling data including estimated direction and distance from all listening posts separately for each species into the programme DISTANCE (v.7.3). We used all data across arrays to obtain one species-specific EDR to calculate the detection area (E) per array. We calculated E (in km^2) for each array by using QGIS (v.2.18.18). We set up a buffer with the calculated EDR around each listening post, omitting areas of overlap between posts, and the combined area within this buffer zone for the three posts was considered the sampling zone. The E differs per array due to variation in distance between listening posts, and because 0.19 km^2 of the survey area for array 1 was deemed uninhabitable for use by gibbons as this was farmland containing no trees, and therefore was excluded. All other arrays contained similar forested habitat presumed suitable for gibbons.

Acoustic spatial capture-recapture technique for calculating gibbon densities

We analysed gibbon group density based on the same acoustic data described above using the ASCR package (Stevenson 2019). This package models group density based on observer estimated distances and bearings from the observer to the call, which improves the precision of density estimates (Borchers et al. 2015; Stevenson et al. 2015). We inputted the group ID, occasion, post ID, bearing and distance to post into the model. We applied a half normal detection function, which assumes the probability of detection has a half normal distribution (commencing at 1, and exponentially decreasing as distance from the listening post increases) therefore fixing the g0 (probability of detection at 0 m) at 1. As researchers were at the listening post before dawn, remaining still and quiet, and each post was surveyed for four consecutive days, we assumed that we would not miss a group at 0 m. We calculated group density estimates in the ASCR model using the online interface application (Jones-Todd 2019), which works in conjunction with the ASCR package implementing software to fit spatial capture-recapture (SCR) models for acoustic data. We used density estimates produced using ASCR to further investigate any relationships with forest structure.

Measurements of vegetation structure

To ascertain forest vertical and structural complexity, we randomly placed between four and six 25 m x 25 m vegetation plots within the effective listening area of the 10 arrays. We measured vegetation structural characteristics in the same 4 day time frame as the auditory fixed-point count surveys. We recorded the following variables at each plot for all trees with a Diameter at Breast Height (DBH) ≥10cm: DBH (cm); tree height (m) and height to first major bole (m) measured using a Nikon Laser Rangefinder Forestry Pro; crown area (m^2) quantified using the following formula: $A = \pi \left(\frac{N-S\ width}{2}\right) x \ (\frac{E-W\ width}{2})$; and percentage tree canopy connectivity (%) determined by visually estimating the percentage of tree crown that intersected with or touched the neighbouring crown in 5% categories (5%, 10%, 15%, etc). The same observer undertook these measurements throughout the surveys to improve consistency.

We analysed the relationship between gibbon density and forest structure in two ways. Firstly, we used correlations to assess relationships between gibbon group densities and median values of forest structure variables per array. Secondly, we calculated the percentage of trees within each array characterised by having a low, intermediate or high value for each vegetation variable (Table 1). We decided on the relevant categories for each variable based on what is known about gibbon habitat use and the observed variance for each variable in the dataset. We considered these categories as indicative of whether areas were suitable for gibbons, as gibbons do not need to use every tree in their home range, and can survive as long as there are enough trees that are structurally suitable for their requirements. These categories were specific for this area and would not be suitable to use in surveys of other rainforest areas. We did not quantify anthropogenic disturbance in this study.

Table 1. Low, intermediate and high categorial classification of trees for each measured vegetation variable within the survey area in Gunung Leuser National Park, north Sumatra, March-August 2016.

Vegetation categories	DBH (cm)	Height (m)	Height to first bole (m)	Crown Area (m^2)	Connectivity (%)
Low	<30	<20	< 10	<50	<15
Intermediate	30 – 100	20 – 35	10 – 25	50 – 100	15 – 50
High	100 – 200	35 – 50	25 – 40	100 – 300	50 – 100

Statistical analysis

We tested all vegetation variables measured and gibbon group density estimates obtained for normality using Shapiro-Wilkinson and Kolmogorov-Smirnov tests. We evaluated structural differences in vegetation variables between arrays, and between vegetation plots within arrays, using non-parametric Kruskal-Wallis tests to look for variance within and between arrays. We used paired T tests to compare the group density estimates produced from the triangulation and ASCR methods and to evaluate differences between group densities of the two species at the same array. We used a Wilcoxon signed Rank test to examine differences between the calling times of the two species, and Spearman's rho correlations to examine relationships between the calling times of the two gibbon species, and between gibbon group densities (based on ASCR analyses) and median values of structural forest characteristics (DBH, tree height, first major bole height, crown area, and tree connectivity) (Sokal & Rohlf 1995). In addition, once we had calculated the percentage of trees that fell within the 'high', 'intermediate' and 'low' categories, we used Spearman's rho correlations to assess relationships between these percentages and group densities at arrays for both gibbon species. We obtained critical values for post hoc tests through sequential Bonferroni correction.

We carried out all tests using SPSS v.26, and set alpha to 0.05. We only analysed the relationship between vegetation structure and gibbon group densities using the density estimates obtained from the ASCR analyses. We provide density estimates in groups/km^2, not individuals per km^2, because no prior information was available to determine the average group size and composition within the study area.

Data availability

The datasets analysed in this study are available from the corresponding author on reasonable request.

Ethical note

All field research was permitted by the Ministry of Research, Technology and Higher Education of the Republic of Indonesia (RISTEKDIKTI), and Gunung Leuser National Park authorities (TNGL). This study adhered to all the legal requirements of Indonesia, with the required research visa acquired (Permit Number: 50/SIP/FRP/E5/Dit.KI/II/2016), and a SIMAKSI from the National Park authorities prior to study. This research did not involve following, handling or disturbing wildlife, and adhered to the IPS guidelines and Codes of Best Practices for Field Primatology. All authors have no conflict of interest in publishing this manuscript.

RESULTS

Triangulation and ASCR analysis

The overall calling probability (***p(1)*** = the probability of a call happening on any single day at any array based on all data collected per species) was 0.808 for lar gibbons and 0.998 for siamangs. The correction factor (***p(m)*** = estimated proportion of groups expected to sing during the sampling period of ***m*** days) was 0.747 for lar gibbons, and 0.988 for siamangs. The EDR (effective listening distance) obtained through DISTANCE (v.7.3) was 1078 m for lar gibbons and 1160 m for siamangs, producing a total surveyed area of 50.21 km^2 for lar gibbons and 57.02 km^2 for siamangs.

Lar gibbon and siamang group densities

We recorded 36 different lar gibbon groups in 156 individual vocal encounters across the 10 arrays. Group densities obtained ranged from 0.53 to 3.10 groups/km^2 using ASCR analysis, and 0.57-2.88 groups/km^2 using triangulation (Table 2). We found siamangs in 9 of the 10 arrays, with 23 different siamang groups identified in 68 vocal encounters. We found siamangs at much lower densities than lar gibbons, with 0.00-1.00 groups/km^2 using the ASCR method, and 0.00-1.96 groups/km^2 using triangulation (Table 2). Group density estimates generated by the two methods were not significantly different for lar gibbons (paired T-test: t=1.05, df=9, P=0.322), but there was a significant difference in siamang group densities (t =2.60, df=9, P=0.031), with a difference of 0.28 groups/km^2 ± SD 0.47.

Lar gibbon group density was significantly higher than siamang group density across all arrays (t=4.158, df=9, P=0.002; ± SD 0.88, mean difference 1.03 groups/km^2 ± SD 0.79), and species group densities in each array were not significantly correlated (Pearson's correlation r=0.452, P=0.189; Figure 2 a). There was a significant difference between the calling times of the two gibbon species (Wilcoxon signed rank test: Z=-4.752, P<0.0001, N = 363). Lar gibbons called between 07:10 h and 08:18 h (median 07:36 h) and siamangs between 08:00h and 09:30h (median 08:37 h; Figure 2 b). The number of calls recorded for each individual group in each array was positively and significantly correlated to the number of groups of that species present in that array for both lar gibbons (Spearman's rank: r_s =0.942, P<0.001, N = 10) and siamangs (r_s =0.939, P<0.001, N = 10). However, group densities of lar gibbons did not affect the calling frequency of siamang groups (r_s =0.441, P=0.202, N = 10) nor did group densities of siamangs affect the calling frequency of lar gibbon groups (r_s=0.432, P=0.213, N = 10, Figure 2 c and d) in each array.

Table 2. Gibbon group density based on the standard triangulation and acoustic spatial capture-recapture methods in Sikundur, north Sumatra, March-August 2016.

Array number	**Groups heard (N)**	**Effective Listening Area (E) (km²)**	**Estimated density triangulation (groups/km²) (lower and upper 95% CI)**	**Estimated density ASCR (groups/km²) (2.5%CI and 97.5% CI)**	**Akaike Information Coefficient of the ASCR model**
Lar gibbon					
1	3	4.60	**1.53** (1.28 – 1.78)	**1.90** (0.004 – 0.034)	310.01
2	3	5.09	**1.57** (1.12 – 2.02)	**1.50** (0.003 – 0.026)	371.01
3	5	4.87	**2.47** (2.07 – 2.86)	**3.10** (0.009 – 0.053)	688.18
4	5	4.87	**2.88** (2.33 – 3.41)	**3.00** (0.010 – 0.051)	496.30
5	3	5.34	**0.57** (0.56 – 0.92)	**0.53** (-0.002 – 0.013)	88.79
6	3	5.34	**0.56** (0.56 – 0.80)	**0.64** (-0.002 – 0.014)	140.40
7	4	5.34	**1.50** (0.99 – 2.00)	**1.30** (0.002 – 0.023)	229.26
8	3	4.95	**1.42** (1.11 – 1.72)	**1.30** (0.002 – 0.024)	320.71
9	4	5.02	**1.80** (1.64 – 1.96)	**2.20** (0.006 – 0.037)	424.04
10	3	4.79	**1.25** (1.09 – 1.42)	**1.30** (-0.004 – 0.030)	311.65
Siamang					
1	2	5.26	**0.58** (0.57 – 0.85)	**0.69** (-0.002 – 0.007)	143.78
2	2	5.77	**0.70** (0.42 - 0.98)	**0.76** (-0.001 – 0.017)	109.84
3	3	5.54	**1.27** (0.95 – 1.59)	**0.86** (0.000 – 0.018)	240.32
4	3	5.54	**1.27** (0.90 - 1.64)	**0.75** (0.000 – 0.054)	211.42
5	0	6.04	**0.00** (0.00 – 0.00)	**0.00** (0.000 – 0.000)	00.00
6	2	6.04	**0.50** (0.37 - 0.96)	**0.57** (-0.002 – 0.013)	92.11
7	3	6.04	**1.33** (0.84 - 1.82)	**0.96** (0.001 – 0.018)	271.46
8	4	5.63	**1.96** (1.30 – 2.63)	**1.00** (0.000 – 0.020)	254.29
9	2	5.70	**1.06** (0.87 – 1.25)	**0.59** (-0.002 – 0.014)	187.8
10	2	5.46	**0.55** (0.55 – 0.56)	**0.23** (0.002 – 0.007)	86.44

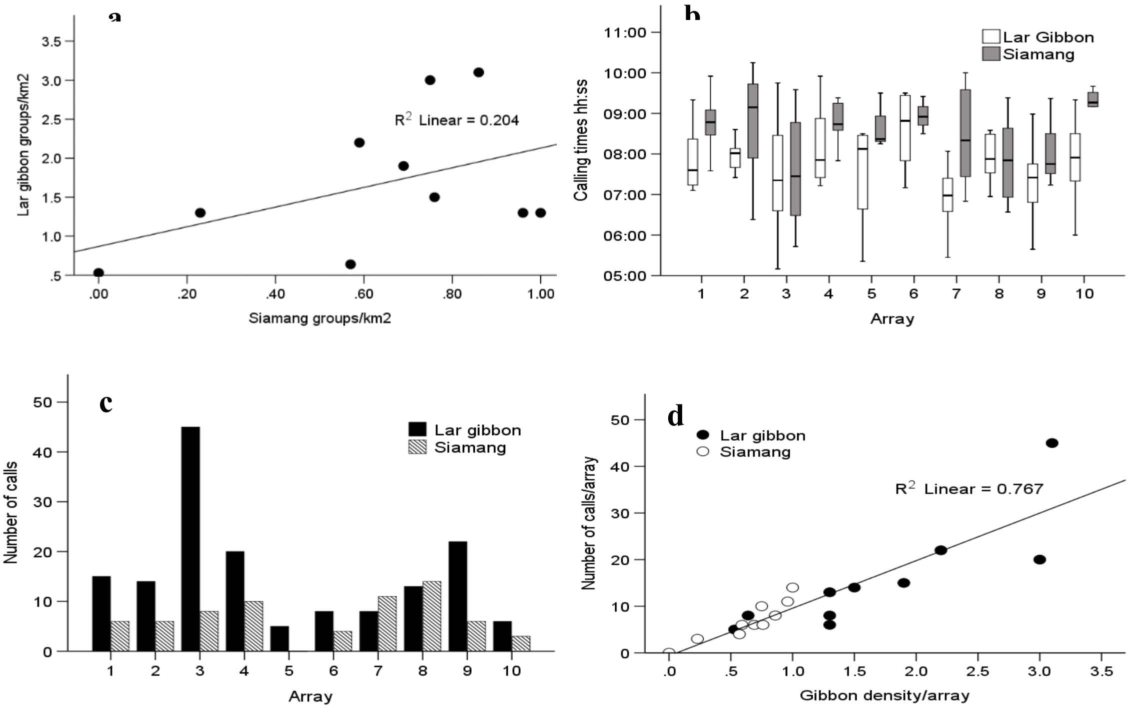

Figure 2. Results of surveys of lar gibbons and siamangs in Gunung Leuser National Park, north Sumatra, March-August 2016. (a) Relationship between lar gibbon and siamang group density by array. (b) Comparison of median calling times for both gibbon species at each array (vertical line = median; box = Q1-Q3; whiskers = minimum and maximum). (c) Total number of calls recorded by both gibbon species at each array. (d) Relationship between lar gibbon and siamang group densities (calculated using ASCR) and the total number of calls recorded at each array.

Vegetation Structure

All vegetation variables had a non-normal distribution (Shapiro-Wilk test: DBH W=0.970, P<0.001, height W=0.916, P<0.001, height first bole W=0.936, P<0.001, crown area W=0.691, P<0.001, connectivity W=0.929, P<0.001) and differed significantly among arrays (Table 3). Additionally, vegetation variables differed between plots within each array (Table S1: values in bold show significant differences).

Table 3. Median values and inter-quartile ranges (Q1-Q3) of forest structural variables for 10 arrays, and results of Kruskal-Wallis tests for differences between arrays in Gunung Leuser National Park, north Sumatra, March-August 2016.

Array number	**N**	**DBH (cm)**	**Tree height (m)**	**Height first bole (m)**	**Crown area (m^2)**	**Connectivity (%)**
1	234	21(15.9.0-31.2)	16.8 (13.2-21.2)	9.95 (7.8-14.5)	27.5 (15.9-46.1)	20 (10-40)
2	167	19.7 (14.6-29.9)	17.8 (14.0-24.0)	11.8 (9.2-16.2)	25.8 (13.9-42.6)	20 (10-40)
3	103	25.2 (16.6-42.7)	19 (14.0-3.0)	14 (8.0-20.0)	86.4 (22.0-212.0)	50 (25-50)
4	180	21.35 (14.3-32.3)	18.2 (14.5-24.1)	12.1 (9.0-17.0)	53.4 (12.0-134.3)	25 (20-50)
5	122	19.1 (14.0-28.7)	15 (10.9-19.4)	8.1 (5.9-11.6)	31.3 (12.1-60.2)	25 (10-30)
6	115	17.8 (14.0-25.5)	12.4 (10.4-17.7)	9 (6.0-11.0)	29.4 (15.7-56.5)	20 (10-30)
7	144	15.9 (12.7-23.7)	14.8 (11.3-20.8)	10.2 (8.0-13.5)	28.2 (14.1-46.6)	30 (10-50)
8	132	20.7 (14.3-30.3)	18.2 (14.2-24.3)	11.9 (8.9-16.0)	28.3 (15.9-50.2)	30 (10-50)
9	102	19.1 (14.2-32.1)	14 (11.0-20.3)	9 (6.0-12.0)	26.55 (17.3-48.8)	30 (10-50)
10	93	17.8 (14.3-25.7)	16.8 (13.8-21.6)	9.8 (7.3-14.1)	22.3 (13.2-35.9)	20 (10-40)
X^2		**31.13**	**109.63**	**119.71**	**73.06**	**87.91**
p		**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**

Gibbon densities and vegetation structure

Lar gibbon group density was significantly and positively correlated with median tree DBH, while group densities of both species were significantly and positively correlated with median height to first bole (Table 4). Group densities showed no significant positive correlations with any other median structural variable.

Table 4. Results of Spearman's correlations between vegetation variables and gibbon densities (N=10) in Gunung Leuser National Park, north Sumatra, March-August 2016.

	Density (groups/km^2)			
	Lar gibbon		**Siamang**	
Vegetation variables	*rho*	*P*	*rho*	*P*
Median DBH (cm)	0.716*	0.020	0.035	0.343
Median height to first bole (m)	0.658*	0.038	0.802*	0.005
Tree top height (m)	0.549	0.100	0.524	0.120
Crown area (m^2)	0.153	0.672	0.164	0.651
Tree connectivity (%)	0.360	0.306	0.540	0.107

*Correlation is significant at the 0.05 level.

In general, a large percentage of trees present within the arrays were characterised by low DBH (<30 cm), low heights (<20 m), low first boles (<10 cm) and small crown areas (<50 m^2), with only a small percentage of trees characterised as large, tall, and with large crown areas (Table 5). The exception was tree connectivity, which varied less across categories (Table 4).

Table 5. Percentage of trees characterised as low, intermediate and high based on their values for structural variables at 10 survey sites in Gunung Leuser National Park, north Sumatra, March-August 2016.

Array number		**DBH (cm)**			**Tree height (m)**			**Height first bole (m)**			**Crown area (m^2)**			**Connectivity (%)**		
	N	**Low (<30)**	**Intermediate (30-100)**	**High (100-200)**	**Low (<20)**	**Intermediate (20-35)**	**High (35-50)**	**Low (<10)**	**Intermediate (10-25)**	**High (25-40)**	**Low (<50)**	**Intermediate (50-100)**	**High (100-300)**	**Low (<15)**	**Intermediate (15-50)**	**High (50-100)**
1	234	73	26	1	71	27	3	50	47	3	80	14	6	36	46	18
2	167	75	20	4	58	37	6	29	64	7	79	17	4	37	40	2
3	103	62	38	0	52	43	6	29	54	17	34	18	48	8	42	51
4	180	71	29	0	57	38	5	31	64	6	49	17	34	22	41	38
5	122	78	22	0	77	21	2	63	37	0	67	23	10	40	41	19
6	115	82	17	1	83	16	2	64	36	1	72	17	10	46	38	16
7	144	82	18	0	74	22	4	41	56	3	76	19	5	27	39	34
8	132	74	24	2	58	34	8	33	63	5	72	24	5	30	44	26
9	102	72	25	4	70	26	5	59	37	4	77	17	7	30	39	30
10	93	84	14	2	68	27	5	51	44	5	82	9	10	34	51	15

Lar gibbon group densities were significantly and positively correlated with the percentage of trees with intermediate DBH (30-100 cm), height (20-35 m), and canopy connectivity (15-50 %), and percentage of trees with a high first bole height (25-40 m) and a large crown area (100-300 m^2). Group densities were significantly and negatively correlated with the percentage of trees with a small DBH (<30 cm), and a low (<15 %) canopy connectivity (Table 6).

Siamang group densities were significantly and positively correlated with the percentage of trees with a highly connected canopy of 50-100 %. Group densities were not significantly correlated with any other vegetation category. (Table 6).

Table 6. Results of Spearman's correlations between structural vegetation categories and gibbon densities (N=10) in Gunung Leuser National Park, north Sumatra, March-August 2016.

	Lar gibbon		**Siamang**	
Vegetation variables	*rho*	*P*	*rho*	*P*
Tree DBH				
Low (<30cm)	-0.816*	0.004	-0.388	0.267
Intermediate (30cm-100cm)	0.794*	0.006	0.374	0.287
High (100-200cm)	-0.062	0.865	-0.031	0.971
Height				
Low (<20m)	-0.652	0.041	-0.519	0.124
Intermediate (20m-35m)	0.680*	0.003	0.438	0.206
High (35m-50m)	0.411	0.238	0.681	0.030
Height to first bole				
Low (<10m)	-0.541	0.107	-0.664	0.036
Intermediate (10-25m)	0.402	0.249	0.667	0.035
High (25m-40m)	0.748*	0.013	0.370	0.293
Connectivity				
Low (<15%)	-0.849*	0.002	-0.507	0.135
Intermediate (15%-50%)	0.787*	0.007	0.072	0.843
High (50%-100%)	0.483	0.157	0.795*	0.006
Tree crown area				
Low (<50m^2)	-0.683	0.030	-0.204	0.572
Intermediate (<50m^2-100m^2)	0.507	0.135	0.049	0.893
High (<100m^2-300m^2)	0.814*	0.004	0.236	0.511

*Correlation is significant at the 0.016 level following sequential Bonferroni correction (Armstrong 2014) for 3 tests per analysis.

Discussion

In this study we found that this historically degraded lowland rainforest in north Sumatra is still an important habitat for these gibbon species, and that the effect of variation in forest structure on gibbon group densities is species-specific. Although varying in density, lar gibbon groups were present at all arrays, and siamang groups in all but one. This indicates that both species possess a degree of behavioural flexibility to somewhat adjust to forest structural changes, allowing them to persist in these structurally altered habitats. We also confirmed that group density estimates vary with the method used to calculate them.

Forest structure is a fundamental element of habitat quality and has long been identified as a key determinant of biological diversity (MacArthur & MacArthur 1961). Structural variation influenced the presence of both gibbon species. We hypothesised that gibbons and siamangs fare best in mature, highly connected forest with sufficient emergent trees. In support of our hypothesis, lar gibbons showed a positive relationship with high and intermediate values of all measured structural vegetation variables. However, siamangs only showed a positive relationship with a high level of canopy connectivity and a median height to first bole. Consequently, siamang group densities were less clearly linked to the other forest structural variables supporting our second hypothesis, that the siamang is more adaptable to changes in the structure of the canopy than lar gibbons. Siamang group densities were significantly lower than lar gibbons at all arrays, although no inverse relationship between the species was identified, suggesting a level of co-existence between the species. However, territorial calls by each species were performed at different times, suggesting a competition avoidance approach, supporting our third hypothesis.

Comparison of methods for calculating gibbon densities

We used two techniques to calculate population density. Spatially explicit capture-recapture (SECR) methods are a promising tool in acoustic analysis and have been used successfully in studies of other species (Borchers et al. 2015). The acoustic spatial capture-recapture package takes into account both distance and bearing error, and there is no constraint on the value of the detection function at zero (Borchers et al. 2015). The traditional triangulation method suffers from commonly known errors, such as the difficulty in determining the probability that gibbons call each day during the sampling period (Rawson 2010; Vu et al. 2018b). This can be especially problematic because calling probability is affected by the group density, and calling can be stimulated by the calling of other, conspecific groups (Nijman 2004). We confirmed such a positive relationship between the number of calls heard and the group density for both species at Sikundur. Rain and wind can also negatively affect calling probability (Brockelman & Ali 1987; Brockelman & Srikosamatara 1993; O'Brien et al. 2004), but we did not collect data on days with rain or heavy wind. The population densities obtained using the two methods did not differ significantly for lar gibbons, but the ASCR method estimated significantly lower densities for siamangs than the triangulation method. The low group density obtained for siamangs was based on calling groups, which was low, therefore the probability of calling (correction factor) used to compensate for this in the triangulation analysis may have caused an overestimate to the group density (Rawson 2010). Even using the program DISTANCE to calculate the effective listening area more accurately, densities may still have been slightly overestimated with the triangulation method as it is difficult to estimate distance to the calling group over varying terrains (Rawson & Tuong Bach 2011). As no other density study has been conducted in this area, it is difficult to draw conclusions about the accuracy of ASCR, but our analysis shows promising results and we recommend that ASCR is trialled in areas with known gibbon densities.

Gibbon densities and vegetation structure

Forest structure in Sikundur is highly heterogeneous both between and within arrays, due to historical selective and intensive logging. This heterogeneity in vegetation structure produces a large range associated with median values. This may explain the small number of significant relationships found between median tree structural values and gibbon group densities. Additionally, the median values of vegetation variables are low in comparison to primary lowland forest in Sumatra, which has average tree heights of 30-40 m and DBH of >50cm (Lamonier 1997). Although there is evidence of regeneration in the area (Priatna et al. 2004), only a small percentage of trees possess a structure that reflects that of an undisturbed, primary rainforest. While these gibbon species occupy a home range in a generally suitable habitat, they assess appropriate structural elements in patches or microhabitats that possess trees with specific features and/or structures required (Orians & Wittenberger 1991). Therefore, by characterising the trees into categories according to high, intermediate and low structural values, we ascertained a more representative relationship between structural elements and the presence of gibbons.

Canopy connectivity is an important structural variable for gibbons (Hamard et al. 2010; Phoonjampa et al. 2011; Lee et al. 2015) and other arboreal primates, including tufted capuchin monkeys (*Sapajus apella)* (Di Bitetti et al. 2000), orangutans (Felton et al. 2003; Knop et al. 2004), and bald faced saki monkeys *(Pithecia irrorata)* (Palminteri et al. 2012). The group density of both gibbon species was significantly positively correlated with canopy connectivity: siamangs were positively correlated with the percentage of trees with a highly connected canopy (50-100 %) whereas lar gibbon density was significantly positively correlated with the percentage of trees with intermediate connectivity (15-50 %). This is likely associated with species differences in gap-crossing abilities and size. When crossing canopy gaps, the larger, heavier siamangs perform more regular brachiation, bridging and torso-orthograde clambering, which necessitates stronger supports (present in more connected forest patches) to travel through their range, whereas the smaller, lighter lar gibbon uses leaping and ricochetal brachiation (Feagle 1976; 1980). The lar gibbon's ability to use ricochetal brachiation and leaping is thought to be an adaptation to cross canopy gaps in order to obtain scattered and highly patchy fruit resources characteristic of dipterocarp forests (Cannon & Leighton 1996), and allows lar gibbons to travel through forest areas with lower canopy connectivity than the siamang is able to do so. However, lar gibbon group density was also significantly negatively correlated with the percentage of trees with low connectivity (<15%). The lar gibbons locomotor adaptations for gap crossing are likely to have a higher energy expenditure than locomotor behaviours used to travel through more connected canopy, and therefore these routes would be less desirable.

Siamang group densities were also positively correlated to median height to first bole, whereas lar gibbon group densities were positively correlated to categories of all measured vegetation variables which represented bigger and taller trees with large crown areas. Gibbon species tend to choose the tallest trees to perform territorial calls and to sleep (Phoonjampa et al. 2010; O'Brien & Kinnaird. 2011; Cheyne et al. 2012), although they are relatively adaptable to variable tree heights (Nijman 2000), providing trees have sufficient connectivity. There are very few trees in Sikundur above 35m in height, and heights classified within our intermediate category are more representative of emergent trees in Sikundur. Agile gibbons have been recorded to sleep in mid-canopy height trees when tall emergent trees are unavailable, concealing themselves in the vegetation for safety (O'Brien and Kinnaird 2011). Lar gibbons reuse sleeping trees infrequently as an anti-predator strategy (Reichard 1998; Cheyne et al. 2012), and individuals of the same group often sleep in separate adjacent trees (Reichard 1998). In comparison, siamangs choose the highest trees in their home range with small crown areas (Reichard 1998), and have been found to reuse the same sleeping tree frequently in Sikundur (Harrison et al. 2020) commonly sleeping together in the same tree. Therefore, lar gibbons require a high number of suitable sleeping trees in their home range, whereas less are required by siamangs. However, the larger size and group sleeping of the siamang mean that a high first major bole height that is strong enough to support the weight of several individuals may be an important variable in their habitat choice. This study found a positive relationship between lar gibbon densities and percentages of trees with a larger DBH. Tree stability is also a known preference in gibbon sleeping tree choice (Cheyne et al. 2012), as larger trees are more stable in high winds and rain and would thus be a safer choice for a sleeping tree.

Lar gibbon and siamang densities

Lar gibbon group densities obtained in this study fall within the intermediate range of published group densities on peninsular Malaysia (1.8 groups/km^2, Mackinnon & Mackinnon 1980), agile gibbons in south Sumatra (0.9-3.8 groups/km^2, Yanuar & Sugardjito 1993; Yanuar 2009), and lar gibbons in north Sumatra (1.4-2.4 groups/km^2, Palombit 1992; Keller 2019, unpubl. data). Conversely, siamang group densities are low in comparison to published density estimates, which range from 0.7 to 5.4 groups/km^2 in Malaysia and southern Sumatra (Mackinnon & Mackinnon 1980; Yanuar & Sugardjito 1993; O'Brien et al. 2004; Yanuar 2009). The low siamang densities support the range-wide pattern, with the highest densities recorded in the southern extent of their range, declining northwards (O'Brien et al. 2004). Sumatran lar gibbons are only found in northern Sumatra, but agile gibbons, which are ecologically comparable, show the reverse trend in population densities, increasing from south to north in relation to specific habitat requirements (Yanuar 2001).

Lar and agile gibbon and siamang groups are inversely related in other study locations across their range where they occur together, due to competition over food resources from home range and dietary overlap (O'Brien et al. 2004; Yanuar 2009). Studies have reported siamangs displacing lar gibbons from high quality feeding sites such as fig trees, and lar gibbons actively avoiding siamangs (O'Brien and Kinnaird. 2011). However, we found no such inverse relationship in this study. Furthermore, calling times differed between the species in Sikundur: siamang groups produced territorial calls ~60 minutes later than lar gibbons. This supports results of studies in Malaysia, suggesting competition avoidance between the species (Yanuar & Chivers 2010).

Siamang group densities obtained in our study were lower than expected based on density data from other field sites (Mackinnon & Mackinnon 1980; Yanuar & Sugardjito 1993; O'Brien et al. 2004; Yanuar 2009). Siamangs in Sikundur consume less fruit in comparison to other Sumatran sites, have larger home ranges which significantly overlap with other siamang and lar gibbon groups in the area, and travel further daily than recorded in other areas (Chivers 1984; Harrison et al. 2020). Generally, home ranges are larger and overlap in areas where required resources are found in lower densities (Börger et al. 2008), such as in Sikundur where fruit resources are low in comparison to other Sumatran sites, including the availability of fig patches. Although siamangs are known as flexible foragers, and are able to survive on a largely folivorous diet when there is less high energy food resources (such as figs) available, this is not without its costs (O'Brien et a. 2003). Juveniles cannot digest leaves as efficiently, and require a higher foraging time than adults, resulting in nutritional stress and as such an increase in juvenile mortality. The lowland forest of Sikundur is characterised by dipterocarp trees known for their dispersed and scattered fruits. This is optimal habitat for lar gibbons (O'Brien et al. 2004) and their smaller body size and more efficient travel allows them to exploit these resources, thus potentially explaining why they attain higher densities than the siamang. The optimal habitat for siamangs is montane forest and lowland forest is sub-optimal, where they are forced to co-exist with both the lar gibbon and other primates such as the Sumatran orangutan and macaque species, which may have a competitive edge when it comes to obtaining high quality food resources (Marshall & Leighton 2006). Therefore, siamang densities may be higher in the elevated areas to which they are better-suited, deeper inside the national Park. As gibbon species in Sikundur are not targeted specifically by hunting, we do not consider this a reason for low siamang group densities.

Conclusion

This study identified the habitat and home range structural preferences of two sympatric gibbon species in a lowland rainforest. Variables describing forest structure differed in their contribution to habitat use by these gibbon species, however, densities of both species were lower than expected from previous density estimates across their range. This historically degraded forest, containing many areas with high percentages of short, small trees, with low connectivity and low fruiting has potentially impeded the natural group densities that would be present in an undisturbed primary lowland Sumatran rainforest. We found that sympatric gibbon species choose different structural variables when selecting a home range, as found in other studies (Singh et al. 2018) and in other sympatric species such as great apes (Morgan et al. 2018), macaques (Zhou et al. 2014), lemurs (Fensoa et al. 2018) and south American primates (Gouveia et al. 2014) to allow co-existence. Investigating forest structural variables in relation to habitat preference in arboreal primates can provide essential data to allow effective conservation plans to be created for these increasingly rare and endemic species. Nevertheless, the alarming rate of species declines and extinctions around the world and the increasing threat of climate change points to the fact the most important factor is to stop the clearance and destruction, and protect these important rainforest ecosystems.

References

Akers, A. A., Islam, M.A., & Nijman, V. (2013). Habitat characterization of western hoolock gibbons *Hoolock hoolock* by examining home range microhabitat use. *Primates*, 54, 341–348.

Armstrong, R. A. (2014). When to use the Bonferroni correction. *Ophthalmic and Physiological Optics*, 34(5), 502-508.

Anderson, J., Rowcliffe, J.M., Cowlishaw, G. (2007). Does the matrix matter? A forest primate in a complex agricultural landscape. *Biological Conservation*, 135, 212-222.

Bartlett, T. Q. (2007). The Hylobatidae, Small Apes of Asia. In: Campbell, C., Fuentes, A., MacKinnon, K. S., Panger, M., and Bearder, S. (Eds.), *Primates in perspective* (pp. 274-289). Oxford University Press: New York.

Bicca-Marques, J.C. (2003). How do howler monkeys cope with habitat fragmentation? In: Marsh, L.K. (Ed.), *Primates in Fragments: Ecology and Conservation* (pp. 283–303). Kluwer Academic/Plenum Publishers: New York.

Borchers, D. L., Stevenson, B. C., Kidney, D., Thomas, L., and Marques, T. A. (2015). A unifying model for capture-recapture and distance sampling surveys of wildlife populations. *Journal of the American Statistical Association,* 110 (509), 195–204.

Börger L, Dalziel, B. D., & Fryxell, J. M. 2008. Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecology letters*, 11(6), pp.637-650.

Boyle, S.A. and Smith, A.T. (2010). Can landscape and species characteristics predict primate presence in forest fragments in the Brazilian Amazon? *Biological Conservation*, *143*(5), 1134-1143.

Brockelman, W. Y., & Ali, R. (1987). Methods of surveying and sampling forest primate populations. In: Mittermeier, R. A., & Walsh, C. W. (Eds.), *Primate Conservation in the tropical rainforest* (pp. 23-63). New York.

Brockelman, W. Y., & Srikosamatara, S. (1993). Estimation of density of gibbon groups by use of loud songs. *American Journal of Physical Anthropology*, 29, 93–108.

Brockelman, W & Geissmann, T. 2020. *Hylobates lar*. *The IUCN Red List of Threatened Species* 2020: e.T10548A17967253.

Brockelman, W., & Geissmann, T. (2008). Hylobates lar. *IUCN Red List of Threatened Species*.
Brockelman, W. Y. (2009). Ecology and the Social System of Gibbons. In: Whittaker, D., & Lappan, S. (Eds.), *The Gibbons, Developments in Primatology: Progress and Prospects* (pp. 211-239). Bloomington USA.

Cannon, C. H., & Leighton, M. (1996). Comparative locomotor ecology of gibbons and macaques: selection of canopy elements for crossing gaps. American journal of physical anthropology, 93(4), 505-524.

Carpenter, C.R. (1940). A field study in Siam of the behaviour and social relations of the gibbon (*Hylobates lar*). *Comparative Psychology Monographs,* 84, 1-212.

Chandra Ray, P., Kumar, A., Devi, A., Krishna, M.C., Khan, M.L. & Brockelman, W.Y. (2015). Habitat characteristics and their effects on the density of groups of western hoolock gibbon (*Hoolock hoolock*). *International Journal of Primatology*, 36, 445-459.

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual review of Ecology and Systematics*, *31*(1), 343-366.

Cheyne SM (2007a). Indonesian gibbons – *Hylobates albibarbis*. In: Rowe N. (Ed.), *All the World's Primates*. Charlestown, RI: Pogonias Press Inc.

Cheyne, S. M. (2007b). Gibbon song: effects of climate, location and human disturbance on the singing apes. *American Journal of Primatology*, 70, 386-392.

Cheyne, S. M., Thompson, C. J. H., Phillips, A. C., Hill, R. M. C., & Limin, S.H. (2008). Density and population estimate of gibbons (*Hylobates albibarbis*) in the Sabangau catchment, Central Kalimantan, Indonesia. *Primates*, 49, 50–56.

Cheyne, S. M., Höing, A., Rinear, J., & Sheeran, L. K. (2012). Sleeping site selection by agile gibbons: The influence of tree stability, fruit availability, and predation risk. *Folia Primatologica,* 83, 299–311.

Cheyne, S. M., Thompson, C. J. H., & Chivers, D. J. (2013). Travel adaptations of Bornean agile gibbons Hylobates albibarbis (Primates: Hylobatidae) in a degraded secondary forest, Indonesia. *Journal of Threatened Taxa*, 5, 3963–3968.

Cheyne, S.M., Gilhooly, L.J., Hamard, M.C., Hoing, A., Houlihan, P.R., Kursani, Loken, B., Philips, A., Rayadin, Y., Capilla, B.R., Rowland, D., Sastramidjaja, W.J., Spehar, S., Thompson, C.J.H., & Zrust, M. (2016). Population mapping of gibbons in Kalimantan, Indonesia: correlates of gibbon density and vegetation across the species' range. *Endangered Species Research,* 30, 133-143.

Cheyne, S. M., Capilla, B. R., Cahyaningrum, E., & Smith, D. E. (2019). Home range variation and site fidelity of Bornean southern gibbons (*Hylobates albibarbis*) from 2010-2018. *PloS one*, 14(7), e0217784.

Chivers, D. J. (1974). The siamang in Malaya: a field study of a primate in tropical rain forest. *Contributions to Primatology* 4, 1–335.

Chivers, D. J. (1984). Feeding and Ranging in Gibbons: A Summary. In Preuschroft, H., Chivers, D., Brockelman, W., & Creel, N. (Eds.), *The Lesser Apes* (pp. 267–281). Edinburgh: Edinburgh University Press.

Clarke, E., Reichard, U. H., & Zuberbühler, K. (2012). The anti-predator behaviour of wild white-handed gibbons (Hylobates lar). *Behavioral Ecology and Sociobiology*, 66, 85-96.

Dew, J.L. (2005). Foraging, food choice, and food processing by sympatric ripe-fruit specialists: *Lagothrix lagotricha poeppigii* and *Ateles belzebuth belzebuth*. *International Journal of Primatology, 26,* 1107-1135.

Di Bitetti, M.S., Vidal, E.M.L., Baldovino, M.C., & Benesovsky, V. (2000). Sleeping site preferences in tufted capuchin monkeys (*Cebus apella nigritus*). *American Journal of Primatology,* 50, 257-274.

Duckworth, J.W., Salter, R.E., & Khounboline, K. (1999). *Wildlife in Lao PDR: 1999 status report*. Vientiane, Laos: IUCN/ Wildlife Conservation Union.

Engstrom, L. (2000). Effects of selective hand-logging on orangutan habitat quality and population density in Gunung Palung National Park, Borneo, Indonesia; with focus on forest structure and nest resources. *Uppsala University, Sweden*.

Eppley, T.M., Verjans, E., and Donati, G. (2011). Coping with low-quality diets: a first account of the feeding ecology of the southern gentle lemur, *Hapalemur meridionalis,* in the Mandena littoral forest, southeast Madagascar. *Primates,* 52, 7-13.

Estrada, A., Garber, P.A., Rylands, A.B., Roos, C., Fernandez-Duque, E., Di Fiore, A., Nekaris, K.A.-I., Nijman, V., Heymann, E.W., Lambert, J.E., Rovero, F., Barelli, C., Setchell, J.M., Gillespie, T.R., Mittermeier, R.A., Arregoitia, L.V., de Guinea, M., Gouveia, S., Dobrovolski, R., Shanee, S., Shanee, N., Boyle, S.A., Fuentes, A., MacKinnon, K.C., Amato, K.R., Meyer, A.L.S., Wich, S., Sussman, R.W., Pan, R., Kone, I., & Li, B. (2017). Impending extinction crisis of the world's primates: Why primates matter. *Science Advances*, 3, e1600946.

Estrada, A., Castellanos, L., Garcia, Y., Franco, B., Muñoz, D., Ibarra, A., Ibarra, A., Rivera, A., Fuentes, E., & Jimenez, C. (2002). Survey of the black howler monkey, *Alouatta pigra*, population at the Mayan site of Palenque, Chiapas, Mexico. *Primates*, 43, 51−58.

Estrada, A., Luecke, L., Van Belle, S., Barrueta, E., & Meda, M.R. (2004). Survey of black howler (*Alouatta pigra*) and spider (*Ateles geoffroyi*) monkeys in the Mayan sites of Calakmul and Yaxchilan, Mexico and Tikal, Guatemala. *Primates,* 45, 33−39.

Fan, P.F., Jiang, X., & Chang-Cheng, T. (2009). The critically endangered black crested gibbon *Nomascus concolor* on Wuliang Mountain, Yunnan, China: the role of forest types in the species conservation. *Oryx*, 43, 203−208.

Felton, A.M., Engstrom, L.M., Felton, A., & Knott, C.D. (2003). Orangutan population density, forest structure and fruit availability in hand-logged and unlogged peat swamp forests in West Kalimantan, Indonesia. *Biological Conservation*, 114, 91−101.

Fenosoa, Z.S.E., Sawyer, R.M., Andrianarimisa, A., Razafindraibe, H., Rakotomanana, H. and Donati, G. (2018). Height and support use of three sympatric nocturnal lemurs in different habitats varying in disturbance on the Masoala Peninsula. *Lemur News*, 21, 39-43.

Fleagle JG. (1976). Locomotion and posture of the Malayan siamang and implications for hominid evolution. Folia Primatol. 26: 245-269.

Fleagle JG. (1980). Locomotion and posture. In: Chivers DJ, ed. *Malayan forest primates: ten years' study in tropical rain forest*. New York: Plenum Press. p 191-207.

Fleagle, J.G. (2013). *Primate adaptation and evolution*. New York: Academic Press.

Fleagle JG, Lieberman DE. (2015). Major transformations in the evolution of primate locomotion. In: Dial KP, Shubin N, Brainerd EL (eds.) Great transformations in vertebrate evolution. Chicago: Chicago University Press. p 257-278.

Garber PA. (2011). Primate locomotor behavior and ecology. In: Campbell CJ, Fuentes A, MacKinnon K, Bearder SK, Stumpf R, eds. *Primates in perspective, 2nd ed*. Oxford: University of Oxford Press. p 543–560.

Gardner, T.A., Barlow, J., Chazdon, R., Ewers, R.M., Harvey, C.A., Peres, C.A., Sodhi, N.S. (2009). Prospects for tropical forest biodiversity in a human-modified world. *Ecology Letters*, 12(6), 561–582.

Gaveau, D. L. A., Wich, S.E., Epting, E., Juhn, D., Kanninen, M., and Leader-Williams, N. (2009). The future of forests and orangutans (*Pongo abelii*) in Sumatra: predicting impacts of oil palm plantations, road construction, and mechanisms for reducing carbon emissions from deforestation. *Environmental Research Letters,* 4(3), 034013.

Geissmann, T. (2007). Status reassessment of the gibbon: Results of the Asian Primate Red List Workshop 2006. *Gibbon Journal,* 3, 5–15.

Gilhooly, L, J., Rayadin, Y., Cheyne, S, M. (2015). A Comparison of Hylobatid Survey Methods Using Triangulation on Müller's Gibbon (Hylobates muelleri) in Sungai Wain Protection Forest, East Kalimantan, Indonesia. *International Journal of Primatology,* 36, 567-582.

Gittins, S. P., & Raemaekers, J.J. (1980). Siamang, lar, and agile gibbons. In: Chivers, D.J. (Ed.), *Malayan forest primates: ten years study in tropical rain forest* (pp. 63-105). New York: Plenum Press.

Gouveia, S. F., Villalobos, F., Dobrovolski, R., Beltrão-Mendes, R., and Ferrari, S. F. (2014). Forest structure drives global diversity of primates. *Journal of Animal Ecology*, 83, 1523-1530.

Gross, M. (2017). Primates in peril. *Current Biology*, 27, 573-576.

Gursky, S. (1998). Conservation status of the spectral tarsier *Tarsius spectrum*: population density and home range size. *Folia Primatologica,* 69, 191−203.

Hamard, M. C. L., Cheyne, S. M. & Nijman, V. (2010). Vegetation correlates of gibbon density in the peat-swamp forest of the Sabangau catchment, Central Kalimantan, Indonesia. *American Journal of Primatology,* 72, 607–616.

Harrison, N.J., Hill, R.A., Alexander, C., Marsh, C.D., Nowak, M.G., Abdullah, A., Slater, H.D & Korstjen, A.H. (2020). Sleeping trees and sleep-related behaviours of the siamang (*Symphalangus*) in a tropical lowland rainforest, Sumatra, Indonesia. *Primates,* https://doi.org/10.1007/s10329-020-00849-8.

IUCN. (2020). *Red list category summary for all animal classes and orders*. The IUCN Red List of Threatened Species.

Jepson, P., Jarvie, J. K., MacKinnon, K., & Monk, K. A. (2001). Decentralization and illegal logging spell the end for Indonesia's lowland forests. *Science,* 292, 859–861.

Jones-Todd, C. M. 2019. ASCR User Interface Package. Available at:
https://cmjt.shinyapps.io/ascr_shiny/

Keller, C. (2019). *Acoustic location systems (ALS) as a tool for group density, territory and behavioural analysis of wild white-handed gibbons (Hylobates lar) in a Sumatran lowland rainforest* (Doctoral dissertation, Department of Anthropology, University of Zurich).

Kidney, D., Rawson, B.M., Borchers, D.L., Stevenson, B.C., Marques, T.A., & Thomas, L. (2016). An efficient acoustic density estimation method with human detectors applied to gibbons in Cambodia. *PLoS One,* 5, 11(5), a0155066.

Kinnaird, M. F., Sanderson, E. W., O'Brien, T. G., Wibisono, H. T., & Woolmer, G. (2003). Deforestation trends in a tropical landscape and implications for endangered mammals. *Conservation Biology,* 17, 245–257.

Knop, E., Ward, P.I. & Wich, S.A. (2004). A comparison of orang-utan density in a logged and unlogged forest on Sumatra. *Biological Conservation*, *120*, 183-188.

Kronfeld-Schor, N. and Dayan, T. (2003). Partitioning of time as an ecological resource. *Annual review of Ecology, Evolution, and Systematics*, *34*, 153-181.

Laumonier, Y. 1997. The Vegetation and Physiography of Sumatra, Kluwer Academic Publishers, Dordrecht.

Lee, D. C., Powell, V. J., & Lindsell, J. A. (2015). The conservation value of degraded forests for agile gibbons *Hylobates agilis*. *American Journal of Primatology,* 77, 76–85.

MacArthur R.H., & MacArthur J. (1961). On bird species diversity. *Ecology*, 42, 594-598.

MacKinnon, J., & MacKinnon, K. S. (1980). Niche differentiation in a primate community. In: Chivers, D. J. (Ed), *Malayan Forest Primates* (pp. 167-190). New York: Springe, Boston, MA.

Margono B., Potapov P., Turubanova S., Stolle F., and Hansen M.C. (2014). Primary forest cover loss in Indonesia over 2000–2012. *Nature Climate Change* 4, 730–5.

Marsh, C., Link, A., King-Bailey, G. and Donati, G. (2016). Effects of fragment and vegetation structure on the population abundance of *Ateles hybridus*, *Alouatta seniculus* and *Cebus albifrons* in Magdalena Valley, Colombia. *Folia Primatologica*, *87*, 17-30.

Marshall, A. J. and Leighton, M., 2006. How does food availability limit the population density of white-bearded gibbons? In: Hohmann, G., Robbins, M., and Boesch, C (Eds.), *Feeding ecology in apes and other primates: Ecological, physical and behavioural aspects* (pp311–333). Cambridge: Cambridge University Press.

Miettinen, J., Shi, C., & Liew, S. C. (2012). Two decades of destruction in Southeast Asia's peat swamp forests. *Frontiers in Ecology and the Environment*, 10, 124-128.

Mitani, J. C. (1990). Demography of agile gibbons (*Hylobates agilis*). *International Journal of Primatology,* 11, 409–422.

Morgan, D., Mundry, R., Sanz, C., Ayina, C.E., Strindberg, S., Lonsdorf, E. and Kühl, H.S. (2018). African apes coexisting with logging: comparing chimpanzee (*Pan troglodytes troglodytes*) and gorilla (*Gorilla gorilla gorilla*) resource needs and responses to forestry activities. *Biological Conservation*, *218*, 277-286.

Morrogh-Bernard, H.C., Husson, S.J., Harsanto, F.A. and Chivers, D.J. (2014). Fine-scale habitat use by orang-utans in a disturbed peat swamp forest, Central Kalimantan, and implications for conservation management. *Folia primatologica*, *85*(3), 135-153.

Nijman, V. (2000). Effects of behavioural changes due to habitat disturbance on density estimation of rainforest vertebrates as illustrated by gibbons (Hylobatidae). Pp 217-225 in Hillegers P. and de Iongh H.H. (eds) The balance between biodiversity conservation and sustainable use of tropical rainforests. Wageningen: Tropenbos Foundation.

Nijman, V. (2004). Conservation of the Javan gibbon *Hylobates moloch*: population estimates, local extinctions and conservation priorities. *Raffles Bulletin of Zoology,* 52, 271−280.

Nijman, V., Geissmann, T., Traeholt, C., Roos, C. & Nowak, M.G. 2020. *Symphalangus syndactylus*. *The IUCN Red List of Threatened Species* 2020: e.T39779A17967873.

O'Brien, T. G., Kinnaird, M. F., Nurcahyo, A., Iqbal, M., & Rusmanto, M. (2004). Abundance and distribution of sympatric gibbons in a threatened Sumatran rain forest. *International Journal of Primatology*, 25, 267–284.

O'Brien, T. G., Kinnaird, M. F., Nurcahyo, A., Prasetyaningrum, M., & Iqbal, M. (2003). Fire, demography and the persistence of siamang (*Symphalangus syndactylus:* Hylobatidae) in a Sumatran rainforest. *Animal Conservation,* 6, 115–121.

O'Brien, T.G. and Kinnaird, M.F. (2011). Demography of agile gibbons (Hylobates agilis) in a lowland tropical rain forest of southern Sumatra, Indonesia: problems in paradise. *International Journal of Primatology*, 32, 1203-1217.

Orians G, Wittenberger J. (1991). Spatial and temporal scales in habitat selection. *The American Naturalist* 137, S29–S49.

Palminteri, S., Powell, G.V.N., Asner, G.P., & Peres, C.A. (2012). LiDAR measurements of canopy structure predicts spatial distribution of a tropical mature forest primate. *Remote Sensing of Environment*, 127, 98–105.

Palombit, R.A. 1992. Pair bonds and monogamy in wild siamang (Hylobates syndactylus) and white-handed gibbon (Hylobates lar) in northern Sumatra. Ph.D. thesis, University of California, Davis.

Palombit, R. A. (1997). Inter- and intraspecific variation in the diets of sympatric siamang (*Hylobates syndactylus*) and lar gibbons (*Hylobates lar*). *Folia Primatologica*, 68, 321–337.

Phoonjampa, R., Koenig, A., Brockelman, W. Y., Borries, C., Gale, G. A., Carroll, J. P., & Savini, T. (2011). Pileated gibbon density in relation to habitat characteristics and post logging forest Recovery. *Biotropica*, 43, 619–627.

Phoonjampa, R., Koenig, A., Borries, C., Gale, G. A., & Savini, T. (2010). Selection of sleeping trees in pileated gibbons *(Hylobates pileatus)*. *American Journal of Primatology,* 72, 617–625.

Pozo-Montuy, G., Serio-Silva, J. C., & Bonilla-Sánchez, Y. M. (2011). Influence of the landscape matrix on the abundance of arboreal primates in fragmented landscapes. *Primates*, *52*(2), 139-147.

Priatna, D., Kartawinata, K., Abdulhadi, R. (2004). Recovery of a lowland dipterocarp forest twenty-two years after selective logging at Sekundur, Gunung Leuser National Park, North Sumatra, Indonesia. *Reinwardtia,* 12, 237-255.

Raemaekers, J. (1984) Large versus small gibbons: Relative roles of bioenergetics and competition in their ecological segregation in sympatry. In Preuschoft, H., Chivers, D.J., Brockelman, W.Y., and Creel, N. (eds): The Lesser Apes: Evolutionary and Behavioural Biology. Edinburgh: Edinburgh Univ. Press, pp. 209-218.

Rawson, B. M., & Tuong Bach, L. (2011). Population assessment of the northern white-cheeked crested gibbon (*Nomascus leucogenys)* in Pu Mat National Park, Nghe An province. *Hanoi: Flora and Fauna International.*

Rawson, B. M. (2010). The use and abuse of gibbon survey techniques: shortcomings of auditory survey techniques. In: Nadler, T and Rawson, B. M (Eds.), *Conservation of Primates in Indo-china* (pp. 253-258). New York: Springer.

Reichard, U. (1998). Sleeping sites, sleeping places, and presleep behavior of gibbons (Hylobates lar). *American Journal of Primatology*, 46, 35-62.

Reichard, U. H., & Barelli, C. (2008). Life history and reproductive strategies of Khao Yai *Hylobates lar*: Implications for social evolution in apes. *International Journal of Primatology*, 29, 823–844.

Reichard, U., & Sommer, V. (1997) Group encounters in wild gibbons (*Hylobates lar*): agonism, affiliation and the concept of infanticide. *Behaviour*, 134, 1135–1174.

Roth, T. S., Rianti, P., Fredriksson, G. M., Wich, S. A., & Nowak, M. G. (2020). Grouping behavior of Sumatran orangutans (Pongo abelii) and Tapanuli orangutans (Pongo tapanuliensis) living in forest with low fruit abundance. *American journal of primatology*, *82*(5), e23123.

Savini, T., Boesch, C., & Reichard, U. H. (2008). Home-range characteristics and the influence of seasonality on female reproduction in white-handed gibbons (*Hylobates lar*) at Khao Yai National Park, Thailand. *American Journal of Physical Anthropology*, 135, 1-12.

Schwitzer, C., Glatt, L., Nekaris, K.A.I. and Ganzhorn, J.U. (2011). Responses of animals to habitat alteration: an overview focussing on primates. *Endangered Species Research*, 14, 31-38.

Smith, R.J. and Jungers, W.L., (1997). Body mass in comparative primatology. *Journal of Human evolution*, *32*(6), pp.523-559.

Snodderly, D.M., Ellis, K.M., Lieberman, S.R., Link, A., Fernandez-Duque, E. and Di Fiore, A. (2019). Initiation of feeding by four sympatric Neotropical primates (*Ateles belzebuth, Lagothrix lagotricha poeppigii, Plecturocebus (Callicebus) discolor,* and *Pithecia aequatorialis*) in Amazonian Ecuador: Relationships to photic and ecological factors. *PloS one*, *14*(1).

Ben C. Stevenson, Paul Dam-Bates, Callum K. Y. Young, John Measey, Chris Sutherland, (2021) A spatial capture–recapture model to estimate call rate and population density from passive acoustic surveys. Methods in Ecology and Evolution 12 (3):432-442.

Stevenson, B. C., Borchers, D. L., Altwegg, R., Swift, R. J., Gillespie, D. M., and Measey, G. J. (2015). A general framework for animal density estimation from acoustic detections across a fixed microphone array. *Methods in Ecology and Evolution*, 6, 38–48.

Singh, M., Cheyne, S.M. and Smith, D.A.E. (2018). How conspecific primates use their habitats: Surviving in an anthropogenically-disturbed forest in Central Kalimantan, Indonesia. *Ecological Indicators*, *87*, 167-177.

Sokal, R. R., & Rohlf. F, J. (1995). *Biometry*. New York: WH Freeman.

Supriatna, J., Dwiyahreni, A. A., Winarni, N., Mariati, S., & Margules, C. (2017). Deforestation of primate habitat on Sumatra and adjacent islands, Indonesia. *Primate Conservation*, 31, 71-82.

Tabarelli, M., & Gascon, C. (2005). Lessons from fragmentation research: improving management and policy guidelines for biodiversity conservation. *Conservation Biology*, *19*(3), 734-739.

Traeholt, C., Bunthoen, R., Rawson, B. M., Samuth, M., Virak, C., & Vuthin, S. (2006). Status review of pileated gibbon, *Hylobates pileatus*, and yellow-cheeked crested gibbon, *Nomascus gabriellae*, in Cambodia. Phnom Penh: *Fauna & Flora International-Indochina Programme.*

Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., ... & Burnham, K. P. (2010). Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology*, *47*(1), 5-14.

Turubanova, S., Potapov, P. V., Tyukavina, A., & Hansen, M. C. (2018). Ongoing primary forest loss in Brazil, Democratic Republic of the Congo, and Indonesia. *Environmental Research Letters*, *13*(7), 074028.

Vu Tien Thinh, and B. M. Rawson. 2011. Package for calculating gibbon population density from auditory surveys. Hanoi: Conservation International and Fauna & Flora International.

Vu, T. T., Tran, L. M., Nguyen, M. D., Van Tran, D., Doherty Jr, P. F., Giang, T. T., & Dong, H. T. (2018a). A distance sampling approach to estimate density and abundance of gibbon groups. *American Journal of Primatology*, 80(9), e22903.

Vu, T. T., Tran, L. M., Nguyen, M. D., Van Tran, D., & Ta, N. T. (2018b). Improving the estimation of calling probability and correction factors in gibbon monitoring using the auditory point count method. *International Journal of Primatology*, 39, 222-236.

Wich, S.A., Vogel, E.R., Larsen, M.D., Fredriksson, G., Leighton, M., Yeager, C.P., Brearley, F.Q., van Schaik, C.P., & Marshall, A.J. (2011). Forest fruit production is higher on Sumatra than on Borneo. *PLoS One*, 6(6).

Wilcove, D. S., Giam, X., Edwards, D. P., Fisher, B., & Koh, L. P. (2013). Navjot's nightmare revisited: logging, agriculture, and biodiversity in Southeast Asia. *Trends in Ecology & Evolution*, 28, 531-540.

Yanuar, A., & Chivers, D.J. (2010). Impact of Forest Fragmentation on Ranging and Home Range of Siamang (*Symphalangus syndactylus)* and Agile Gibbon *(Hylobates agilis).* In: Supriatna, J., & Gursky, S. L (Eds.), *Indonesian Primates* (pp. 121-156). New York: Springer.

Yanuar, A. (2009). The population 2021 distribution and abundance of siamangs (*Symphalangus syndactylus*) and agile gibbons (*Hylobates agilis*) in west central Sumatra, Indonesia. In: Lappan, S. and Whittaker, D. J (Eds.), *The Gibbons*. (pp. 453-465). New York: Springer Science & Business Media.

Yanuar, A. (2001). The population distribution and abundance of primates in Kerinci-Seblat National Park, Sumatra. *Unpublished MSc Thesis, University of Cambridge, Cambridge, UK*.

Yanuar, A., and Sugardjito, J. (1993). Population survey of primates in Way Kambas National Park, Sumatra, Indonesia. *Tigerpaper (FAO).*

Zhou, Q., Wei, H., Tang, H., Huang, Z., Krzton, A. and Huang, C. (2014). Niche separation of sympatric macaques, *Macaca assamensis* and M. mulatta, in limestone habitats of Nonggang, China. *Primates, 55,* 125-137.