

**Vegetation correlates of gibbon density in the peat-swamp forest of
Sabangau national park, Central Kalimantan, Indonesia.**

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Short title: **Vegetation correlates of gibbon density**

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ABSTRACT

Understanding the complex relationship between primates and their habitats is essential for effective conservation plans. Peat-swamp forest has recently been recognized as a major habitat for the Bornean agile gibbon (*Hylobates albibarbis*), but information is scarce on the factors that link gibbon density to characteristics of this unique ecosystem. The aims of this study were firstly to estimate gibbon density in different forest subtypes in a newly protected, secondary peat-swamp forest in the Sabangau National Park, Indonesia, and secondly to identify vegetation correlates of gibbon density. Data collection was conducted for three months at 13 survey sites, using auditory sampling methods and speed plotting. Gibbon densities were found to vary from 1.39 to 3.92 groups/km² between survey sites in different forest subtypes. Canopy cover, tree height, density of large trees and food availability correlated with gibbon density, identifying the preservation of tall trees and good canopy cover as a conservation priority for the gibbon population in the Sabangau forest. This survey indicates that selective logging, which specifically targets large trees and disrupts canopy cover, is likely to have adverse effects on gibbon populations in peat-swamp forests, and calls for greater protection of these little studied ecosystems.

Keywords: Bornean agile gibbon; habitat; auditory sampling

INTRODUCTION

The ability to assess accurately the population status of threatened species is of prime importance to conservation strategies (Sutherland, 2000). Moreover, as the survival of primates is connected to and dependent upon the protection of their rainforest habitats (Lucas and Corlett, 1998; Chapman et al., 2006; Link and Di Fiore, 2006), understanding links between primate abundance and the characteristics of their habitat is essential to effectively conserve the resident primates.

Peat-swamp forests have received little conservation interest in the past, as their richness in biodiversity is generally lower than other types of lowland rainforests (Page et al 1997). However, recent research has indicated that they harbor some of the largest remaining populations of Bornean orangutans (*Pongo pygmaeus pygmaeus*) (Felton et al., 2003; Morrogh-Bernard et al. 2003) and Bornean agile gibbons (*Hylobates albibarbis*) (Buckley et al., 2006; Geissmann, 2007; Cheyne et al., 2008), two species of endangered primates endemic to Borneo.

Large extents of peat-swamp forest exist in Kalimantan, but the level of protection of these ecosystems is low. Because these forests contain commercially valuable timber at high densities, they are often commercially logged, either legally or illegally (MacKinnon et al., 1997a). In addition to the removal of large trees, logging also has severe consequences for the ecosystem's balance, as canals are created to carry fallen trunks to the river, and lead to the drainage of water from the peat, which is then very vulnerable to forest fires (Morrogh-Bernard et al., 2003). Finally, large extents of peat-swamp forests are cleared for agriculture (Rieley et al., 1997). To combat these threats, considerable research efforts were made in the peat-swamp forest of the Sabangau catchment, Central Kalimantan, to highlight its importance both as a biodiversity-rich ecosystem (Page et al., 1997; Morrogh-Bernard et al., 2003) and as an important purveyor of ecological services such as carbon and water storage,

and climate regulation (Rieley et al., 1997; MacKinnon et al., 1997b; Morrogh-Bernard et al., 2003; Cheyne, 2007). These efforts led to the creation of the Sabangau National Park, which was gazetted in 2004, and the cessation of the legal logging activities which had been taking place for thirty years. However, protection of the peat-swamp forest is not enforced in many parts of the park where anthropogenic disturbance continues. Density and population estimates yielded by previous studies in the area demonstrate its importance for gibbon conservation, as the area was shown to host at least 25,000 wild gibbons (Buckley et al., 2006; Cheyne et al., 2008).

The aims of this study were: first, to survey the population of Bornean agile gibbons around the Setia Alam research station, in the north of the Sabangau catchment. Two density estimates have been published so far for this gibbon population, with previous survey efforts concentrating mainly on a 4km² study site (Buckley et al., 2006; Cheyne et al., 2008). This study included a repeat of these survey efforts in order to monitor gibbon numbers in the area. Secondly, this study was designed to identify relationships between gibbon density and habitat quality, by extending survey efforts to several sites in the forest, which exhibit different vegetation characteristics, in order to identify important habitat requirements for gibbons in the unique peat-swamp forest ecosystem.

The hypotheses which were formulated prior to the study were:

- that gibbon density estimates within the main 4km² study area would be comparable between this study and the two previous surveys;
- that gibbon density would differ between study sites and between forest types;
- that vegetation characteristics would show some variation across sites and between forest types;
- that gibbon density could be correlated to vegetation characteristics, as shown in Table 1.

Table 1: Hypothesised relationships between vegetation variables and gibbon densities.

Variable name	Expected relationship to gibbon density	Justification	Reference
Mean canopy cover at 20m	Gibbon density higher where canopy cover is higher	Gibbon are exclusively arboreal and use continuous canopy for their locomotion	Johns, 1986; Bartlett, 2007
Median tree height	Gibbon density higher where trees are higher	Gibbon prefer to use higher canopy levels. High trees are used for singing and sleeping.	MacKinnon and MacKinnon, 1980; Whitten, 1982; Gittins, 1983; Mather, 1992
Mean DBH	Gibbon density higher where trees are larger	Large trees provide more canopy cover and represent more abundant food sources.	Cowlshaw and Dunbar, 2000
Density of large trees	Gibbon density higher where large trees are numerous		
Total cross-sectional area of all trees	Gibbon density higher where total biomass of trees is higher	Gibbons are exclusively arboreal. A high biomass of trees means a larger number of trees and/or the presence of large trees.	Bartlett, 2007
Total cross-sectional area of large trees	Gibbon density higher where biomass of large trees is higher		
Total cross-sectional area of gibbon food trees	Gibbon density higher where food availability is higher	Gibbon density has been found to be correlated to food availability at other field sites.	Mather, 1992; Chivers, 2001; Cheyne et al., 2006
Total cross-sectional area of top 20 gibbon food trees	Gibbon density higher where biomass of preferred food trees is higher	There are indications that the availability of a small number of tree species might be used as a correlate of gibbon density.	Mather, 1992

METHODS

Study site

The Sabangau National Park, designated in November 2004, covers 568 000 hectares of peat-swamp forest between the Sabangau and Katingan Rivers in Central Kalimantan. The study area is located within the Natural Laboratory for the Study of Peat-swamp Forest (Laboratorium Alam Hutan Gambut, LAHG), a 500km² area situated in the north of the national park, 20 km south-west of Palangkaraya, the provincial capital of Central Kalimantan (Fig. 1). This area is operated by the Centre for International Cooperation in Sustainable Management of Tropical Peatland (CIMTROP). Within this area, the main research station, Setia Alam Field Station, is located 2° 20' 42'' south and 114° 2' 11'' east. At the time of the field surveys the area was protected and timber extraction had stopped at the survey locations. Small-scale harvesting of non-timber forest products (bark, rattan, orchids and latex) was still taking place. The forest is secondary closed-canopy evergreen forest, which is flooded for most of the year, and is home to a high diversity of mammals (Morrogh-Bernard et al., 2003) and birds (Page et al., 1997).

Estimation of gibbon density

Gibbon density was estimated using fixed-point counts, as described by Brockelman and Ali (1987) and following the protocol described in Buckley et al. (2006) and Cheyne et al. (2008), at thirteen distinct survey sites within the research area (Figure 1). This method has been recommended for the survey of gibbons for the following reasons: first, because the gibbons' inconspicuous behavior and preference for high canopy makes the use of line transects for surveying unsuccessful (Brockelman and Ali, 1987; Brockelman and Srikosamatara, 1993; Nijman and Menken, 2005). Secondly, because the territorial behavior of gibbons allows efficient mapping of triangulated points (Sutherland, 2000). The animals'

loud calls, audible from a considerable distance, allow their detection from greater distances than by using sightings (Davies, 2002). Finally, fixed-point counts allow quick, time-efficient surveys, with more reliable results than a line transect survey conducted within the same time frame (Nijman and Menken, 2005). This method has proved efficient in several primate surveys (e.g. Brockelman and Srikosamatara, 1993; Gursky, 1998; Estrada et al., 2002; Estrada et al., 2004; Nijman, 2004) and has been used in two previous surveys at the study site (Buckley et al., 2006; Cheyne et al., 2008), allowing the comparison of their results to those yielded by the present survey.

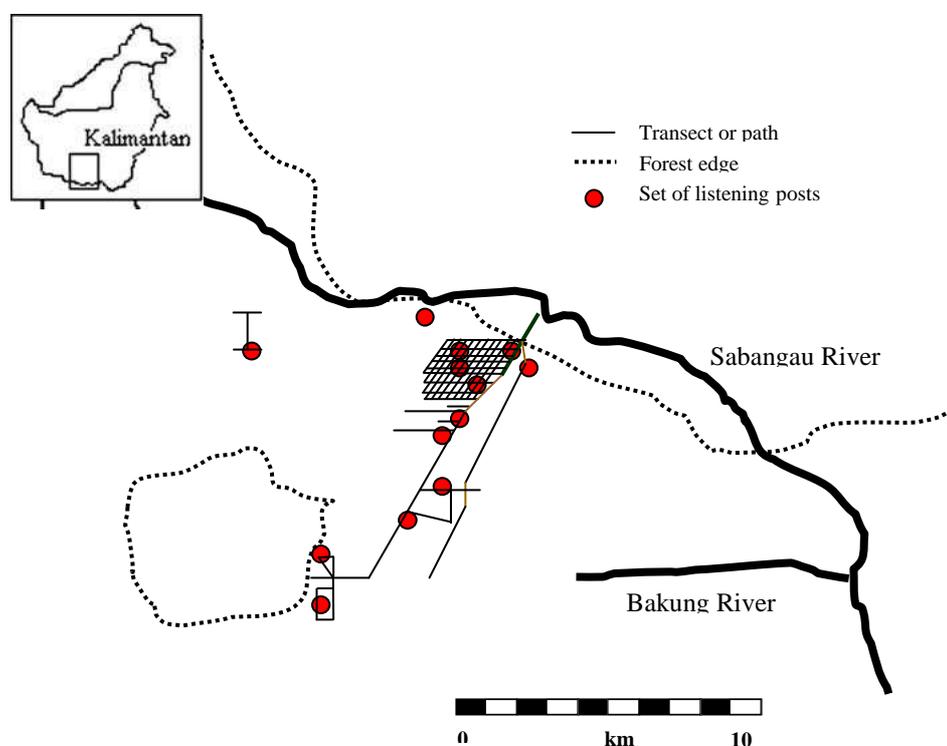


Figure 1: Detailed map of the study area, showing the thirteen sets of listening posts used for auditory sampling. Vegetation sampling was conducted at the same sites, along transects. Relevant transect names are indicated by the letter T.

Data collection took place between May 7th and July 27th, 2008 at nine sets of listening posts. Additional data were obtained from previous studies for two of the sites within the main grid system (Cheyne et al., 2008), and collected in the summer of 2007 for the two remaining survey sites.

Data collection excluded rainy mornings and mornings for which rain had stopped less than two hours before the planned start of data collection, as rain has been found to influence negatively the gibbons' singing behavior (Brockelman and Ali, 1987; Brockelman and Srikosamatara, 1993). Because of this, the survey period was reduced to three days at three of the survey sites, and two days at one survey site. However, correction factors included in the formula to estimate density ensured the data were comparable between all survey sites (Brockelman and Ali, 1987; Brockelman and Srikosamatara, 1993). Only groups for which at least one great call, indicating a family group, was heard during the survey time were included in the analysis, in order to avoid counting solitary animals (Brockelman and Ali, 1987).

The total survey effort covered 37.1 km² across the three main forest types, during 49 survey days.

Measurements of vegetation characteristics

Habitat characteristics were measured in plots of 10m x 10m situated along transects around the listening posts, in the same time frame as the auditory sampling. Previous studies investigating relationships between forest structure and primate densities have used small plots (e.g. Rendigs et al., 2003; Blakham, 2005). Ten plots per site were analyzed, with the exception of five sites within the grid system, for which six plots were analyzed because of time constraints. In each plot the following data were recorded: 1/ canopy cover at 20m, at each corner and in the middle of the plot, using visual estimation by the same observer throughout the survey; 2/ diameter at breast height (DBH) of all trees exceeding 10cm DBH; 3/ height of all trees exceeding 10cm DBH, placing each tree into classes from 0-5m to 35m+ by visual estimation by trained researchers; 4/ local name of the species of all measured trees; 5/ total number of trees in the plot. Additional data were obtained for two of the sites (Koran and Jelutong, see Figure 2) for which 100m x 5m plots were used by another team of

researchers in 2007 and only DBH and tree species were recorded. DBH was then converted into cross-sectional area using the formula $\text{cross-sectional area} = (\text{DBH}/2)^2 \times \pi$ and used as an indicator of tree biomass.

All the collected data were then summarized into nine variables for each plot: 1/ mean canopy cover, 2/ median tree height, 3/ mean DBH, 4/ density of all trees $\geq 10\text{cm}$ DBH, 5/ density of large trees ($\geq 20\text{cm}$ DBH), 6/ total cross-sectional area of all trees $\geq 10\text{cm}$ DBH, 7/ total cross-sectional area of large trees ($\geq 20\text{cm}$ DBH), 8/total cross-sectional area of known gibbon food trees, 9/ total cross-sectional area of trees belonging to the 20 species eaten most frequently by gibbons in the area. Gibbon food trees were defined as tree species whose edible parts (leaves, flowers, fruits, seeds) are known to be eaten by gibbons in the area. Information to obtain the two last variables were based on long-term behavioral research on the gibbons' feeding ecology in the area (Cheyne and Shinta, 2006; Cheyne, 2008). Tree species were identified by Hendri Setia Sabangau, a local field assistant with extensive knowledge of forestry in the area.

All vegetation characteristics were then averaged for each study site, except median tree height which was directly calculated for all measured trees within a study site. Measures of species diversity were then added to the analysis: species richness, defined by the number of tree species identified in each study site; Shannon-Weiner's diversity index and Simpson's diversity index, calculated as described in Ganzhorn (2003) and Douglas (2006). Both Shannon-Weiner and Simpson's indexes were calculated, as both are biased towards either dominant species (Simpson's index) or rare species (Shannon-Weiner index) (Stiling, 2002).

Statistics

Vegetation characteristics between sites were compared using Kruskal-Wallis ANOVA non-parametric test. Pair-wise comparisons of means for each of the variables were

carried out between forest types using Mann-Whitney's U test. After testing for the normality of each variable using Kolmogorov-Smirnov test, potential correlation between gibbon density and each of the variables obtained from vegetation characteristics was investigated using Pearson's correlation test. A factor analysis was performed to obtain a single component retaining most of the variation contained in the vegetation data set. Finally, a linear regression analysis was used to test the relationship between this single component and gibbon density. All tests were carried out using SPSS v.16, with a significance level of $p < 0,05$. Standard error, which is used to assess the accuracy of calculated means in the population (Fowler et al., 1998), was used to measure variability in the analysis, rather than standard deviation.

RESULTS

Calling probabilities and calculations of gibbon density

Based on the number of groups calling on each sampling day and the total number of groups heard for each site, the probability for a group to be calling on any given day $p(1)$ was calculated. The cumulative probability of hearing all gibbon groups during a sample period of m days, $p(m)$, was deducted from $p(1)$ as described in the methods section. Table 2 summarizes the parameters of calling probabilities and effective listening areas for all survey sites, as well as resulting gibbon density estimates.

Table 2: Parameters calculated for the estimation of gibbon density at each site, and resulting density estimates. Reduced sampling periods (m) were due to weather conditions. Reduced effective listening areas (E) were due to forest edges or areas of forest destroyed by wildfires. MSF: Mixed-Swamp Forest, LPF: Low Pole Forest, TIF: Tall Interior Forest.

Site name and site number	Number of groups heard	p(1)	m (days)	p(m)	E (km ²)	Gibbon density (groups/km ²)
MSF 1	5	0.67	5	1.00	1.97	2.53
MSF 2	8	0.53	4	0.95	3.12	2.69
MSF 3	8	0.59	4	0.97	2.78	2.96
MSF 4	7	0.67	5	1.00	2.85	2.81
MSF 5	7	0.64	4	0.98	2.86	2.49
MSF 6	6	0.5	4	0.94	3.00	2.41
MSF 7	7	0.5	4	0.94	2.86	2.61
Transition 1	7	0.64	4	0.98	3.10	2.30
Transition 2	5	0.55	4	0.96	3.06	1.71
LPF 1	3	0.33	3	0.70	3.08	1.39
LPF 2	4	0.50	2	0.75	3.13	1.70
TIF 1	8	0.54	3	0.90	2.26	3.92
TIF 2	8	0.54	3	0.90	3.04	2.91

The density estimates given above are in groups per square kilometer, as no determination of the average group size in the area was attempted during this survey. However, previous research in the main study area has established an average group size of 4.05 for gibbons in the MSF (Cheyne et al., 2008). Using this group size, the density estimate yielded by this study for the MSF is 10.70 ± 0.19 individuals/km².

Vegetation characteristics and determination of forest types

Three main forest types can be identified in the Sabangau peat-swamp forest: a low pole forest (LPF) with short, small trees, a very scarce canopy cover at 20m and few large trees ($\geq 20\text{cm}$ DBH); a tall interior forest (TIF) with high, large trees, high canopy cover and high gibbon food availability; and a mixed-swamp forest (MSF), situated closest to the river, with a more heterogeneous vegetation. Two survey sites, situated between MSF and LPF, were labeled transition forest. Only sites for which vegetation information was obtained from 10x10m plots are included in the calculation of species richness and diversity indicators. A total of 61 species or groups of species of trees were identified during this study, representing 33 families.

Overall, the vegetation in sites situated in the MSF exhibits high species richness (average $s = 27.4$) and contains evenly distributed, relatively rare species (average $J = 0.92$), which results in high Shannon-Weiner indexes (average $H = 3.04$) and low Simpson's indexes (average $C = 0.05$). Sites in LPF exhibit poor species richness (average $s = 21$) and low species diversity (average $H = 2.63$; average $C = 0.08$). Finally, TIF vegetation is species-rich (average $s = 26$) but unevenly distributed (average $J = 0.78$), with notably *Palaquium leiocarpum* (hankang) trees dominating in both sites and representing 29% and 43% of the trees in sites km12N and km12S, respectively. This results in a high average Simpson's index ($C = 0.15$) and a low Shannon-Weiner index ($H = 2.65$) for TIF.

All vegetation variables, averaged for each forest type, are presented in Table 3.

Table 3: Average vegetation characteristics for the forest types of the Sabangau peat-swamp forest. All values are given with standard errors.

Forest type	Mean canopy cover (%)	Median tree height (m)	Mean DBH (cm)	Density large trees (trees/ha)	Cross-section area all trees (cm ²)	Cross-section area large trees (cm ²)	Cross-section area food trees (cm ²)	Cross-sectional area top20 food trees (cm ²)
MSF (n=42)	40.9 ±3.8	11-15	16.3 ±0.5	231.2 ±24.9	2546 ±190	1443 ±178	2018 ±167	1012 ±107
Transition (n=20)	20.8 ±3.9	11-15	15.5 ±0.7	220.0 ±49.5	3332 ±569	1852 ±545	2469 ±404	1113 ±200
LPF (n=20)	10.0 ±1.6	11-15	16.0 ±0.7	150.0 ±28.0	2094 ±254	1067 ±218	1712 ±251	572 ±93
TIF (n=20)	61.8 ±3.4	16-20	19.4 ±0.9	385.0 ±41.8	4198 ±419	3104 ±442	3455 ±357	1037 ±210
Kruskal-Wallis	$\chi^2 = 49.0$ p=0.001	$\chi^2 = 22.5$ p=0.001	$\chi^2 = 14.0$ P=0.003	$\chi^2 = 18.2$ p=0.001	$\chi^2 = 17.4$ p=0.001	$\chi^2 = 16.4$ p=0.001	$\chi^2 = 16.9$ p=0.001	$\chi^2 = 8.1$ p=0.04

Significant differences were found between forest types for all variables. Pair-wise analysis revealed that MSF and transition forest had similar floristic characteristics except for canopy cover, which was significantly higher in MSF (U=173.5, p=0.004). MSF also had significantly higher canopy cover (U=72, p=0.01) and median tree height (U=189, p=0.01) than LPF and contains more of the top 20 gibbon food trees (U=231, p=0.004). Canopy cover (U=126, p=0), median tree height (U=181.5, p=0.007), density of large trees (U=187, p=0), total biomass of trees (U=197, p=0.001) and large trees (U=189.5, p=0.001) were all significantly higher in TIF than in MSF, as was total biomass of gibbon food trees (U=174,

p=0.01). The biomass of the top 20 gibbon food trees did however not differ between TIF and MSF.

Relationship between vegetation characteristics and gibbon density

Average gibbon densities were calculated for each forest type identified previously. The lowest gibbon density was found in the LPF (1.54 groups/km²), followed by the transition forest (2.00 groups/km²). The average gibbon density in MSF was 2.64±0.07 groups/km². The TIF had the highest gibbon density with 3.42 groups/km². The values obtained for transition forest, LPF and TIF are indicative values only, as the sample size is too small to be able to calculate a standard error.

All vegetation variables had a normal distribution, as did gibbon density ($Z = 0.6$, $p = 0.864$ for gibbon density). Gibbon density was found to be correlated to all the measured vegetation variables, except the density of all trees and the biomass of the top 20 gibbon food trees (Table 4).

Table 4: Correlation between gibbon density and habitat characteristics across study sites composed of nine vegetation characteristics and retaining 77% of the variation in the data set.

		Mean canopy cover (%)	Median tree height	mean DBH	Density of trees >10cm DBH	density of trees >20cm DBH	total x-sectional area of trees >10cm DBH	total x-sectional area of trees >20cm DBH	total x-sectional area of gibbon food trees	total x-sectional area of top20 gibbon food trees
Gibbon density (gp/km²)	Pearson Correlation	.802**	.768**	.591*	.255	.664*	.633*	.657*	.573**	.463
	Sig. (2-tailed)	.003	.006	.034	.401	.013	.020	.015	.041	.111
	N	11	11	13	13	13	13	13	13	13

** correlation is significant with $p < 0.01$ *correlation is significant with $p < 0.05$

Factor analysis on all vegetation variables identified one component, called PCA1. Two sites in the MSF (MSF 6 and MSF 7) were excluded from the PCA analysis because data on canopy cover and tree height were missing at those sites. PCA1 allowed easy discrimination between forest types (Figure 2).

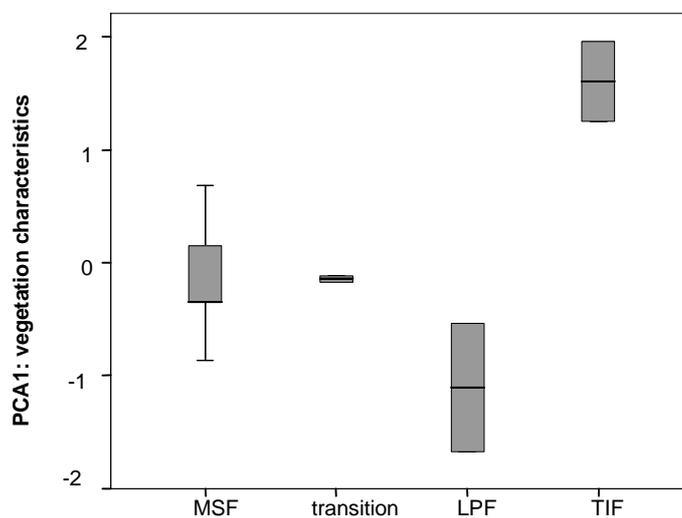


Figure 2: Vegetation characteristics, as summarised by the principal component PCA1, between forest types

The distribution of PCA1 was found to be normal ($Z = 0.577$, $p = 0.893$) and there was a strong relationship between PCA1 and gibbon density ($R^2 = 0.579$, $p = 0.007$) (Figure 3).

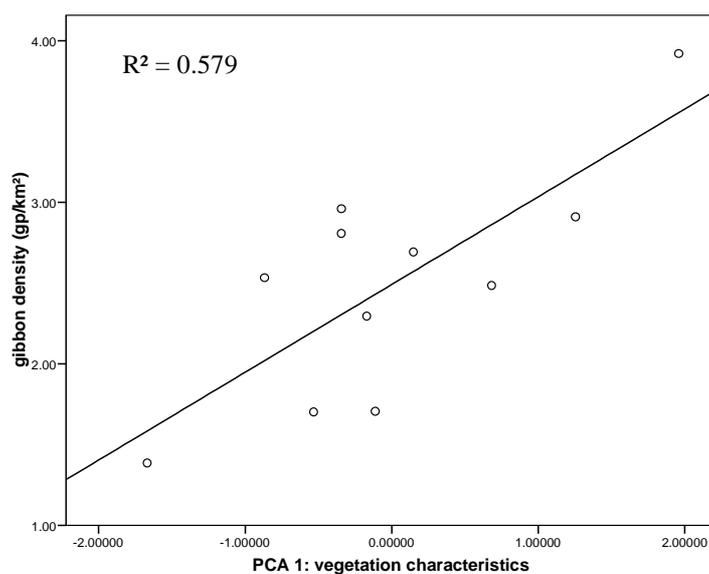


Figure 3: Relationship between vegetation characteristics, as summarized by the principal component PCA1, and gibbon density across survey sites (n=11).

Calling probability

Correlation was tested between calling probability ($p(1)$, see Table 2) and gibbon density in this study (Figure 5), and there was no significant effect of gibbon density on calling probability (Pearson's correlation coefficient = 0.276, $p = 0.44$). Relationship between calling probability $p(1)$ and vegetation characteristics, and particularly the density of large trees (≥ 20 cm DBH) was tested. No significant correlation was found between calling probability and either density of large trees (Pearson's correlation coefficient = 0.322, $p = 0.363$) or all vegetation characteristics as summarized by PCA1 (Pearson's correlation coefficient = 0.221, $p = 0.539$).

DISCUSSION

Gibbon density estimates

The gibbon densities found in the MSF during this study were similar to the two previous estimates published for the same area, showing that the auditory sampling method is replicable. Gibbon density was highest in the TIF, which also harbors the greatest diversity of animal species in the Sabangau (Page et al., 1997) and the highest density of orangutans (Morrogh-Bernard et al., 2003). Overall, gibbon density estimates found during this study are within the mid-range of published estimates for other field sites and compare to estimates at sites with similar forest types (Table 5).

Table 5: Comparison between Bornean agile gibbon density estimates in Kalimantan. Numbers between brackets are calculated from given estimates and published mean group sizes.*calculated with a mean group size of 3.4 (Buckley et al., 2006).**calculated with a mean group size of 4.1 (Mitani, 1990, Cheyne et al., 2008).*** calculated with a mean group size of 2.3 (Cheyne, personal observation).

Site name	Species studied	Group density per km ²	Individual density per km ²	Forest type(s) surveyed	Reference
		2.2	7.5*		Buckley et al. (2006)
Sabangau National Park, Central Kalimantan	<i>H. albibarbis</i>	2.6	10.7**	Peat-swamp forest (MSF)	Cheyne et al. (2008)
		2.6	[10.7]**		This study
		3.1	[12.8]**	Peat-swamp forest (TIF)	Cheyne et al. (2008)
		3.4	[13.9]**		This study
		1.5	[3.5]***	Peat-swamp forest (LPF)	This study
Gunung Palung National Park	<i>H. albibarbis</i>	3.6	14.9	Montane forest, mangrove forest, peat-swamp forest, lowland rainforest	Mitani (1990)
Tanjung Puting National Park	<i>H. albibarbis</i>	[2.1]**	8.7	Lowland rainforest, mangrove forest, peat-swamp forest	Mather (1992b)
	<i>H. albibarbis</i>	[3.0]**	12		Mather (1992b)
Barito Ulu	<i>H. albibarbis</i>	[2.6]**	10.5	Lowland dipterocarp forest	(1992b)
	<i>H. albibarbis</i> x	[4.4]**	18		
	<i>H. muelleri</i>	[2.0]**	8.2		McConkey (2002)

Moreover, the density estimate yielded by this study for the MSF gives a number of gibbon groups of 11 in a 4km² area, which is exactly the number of groups present in the 4km² main study area, where behavioral research is conducted (Cheyne, pers. comm.).

Fixed point counts using auditory sampling do have a number of biases associated with the method. Firstly, the method excludes lone animals from the estimate, as only duets are taken into account into the analysis. A study of the proportion of lone animals, mostly sub-adult individuals, in a population of *H. albibarbis* in West Kalimantan (Cowlshaw, 1992) found that unpaired individuals represented approximately 5.5% of the paired population.

This problem only affects estimates of individual density however; estimates of density of groups per square kilometer, which are included in this study, remain unchanged. Secondly, auditory sampling is dependent on weather conditions during data collection, which can affect singing frequency (Raemaekers et al., 1984; Brockelman and Ali, 1987; Leighton, 1987; Brockelman and Srikosamatara, 1993). Rain has been shown to affect the time when the gibbons started singing in the study area but not the singing frequency (Buckley et al., 2006), although other studies (e.g. O'Brien et al., 2004) did not find any effect of rain on singing start times or frequency. Although no detailed weather data were collected during this study, efforts were made to avoid data collection on rainy mornings and on mornings directly following heavy rain during the night, which restricted data collection to three or even two days at some survey sites. The duration of data collection was also extended well beyond the last singing bout heard, to avoid missing groups that could have sung later because of weather conditions. Despite cloud cover having been found correlated with singing frequency in pileated gibbons (Brockelman and Srikosamatara, 1993) and to a lesser extent, in a population of agile gibbons (O'Brien et al., 2004), it was found to have no effect on singing in the study area (Buckley et al., 2006, Cheyne, 2007). Consequently, cloud cover was not recorded during this survey. Finally, wind has been shown to affect singing in pileated gibbons (Brockelman and Srikosamatara, 1993) and siamangs (O'Brien et al., 2004), but not agile gibbons (O'Brien et al., 2004; Cheyne, 2007). Wind conditions were calm on every survey morning, and thus are unlikely to have had any effect on singing, even though no wind measurements were recorded.

It has been proposed that low densities (less than two groups per square kilometre) may affect singing probability, as singing can be stimulated by other duets from neighbouring groups (Mitani, 1987; Brockelman and Srikosamatara, 1993). Brockelman and Ali (1987)

found however that singing was not stimulated by other groups in agile gibbons. In this study, no correlation was found between singing probability ($p(1)$, see table 2) and gibbon density. Gibbons sing preferentially from large, high trees (Mather, 1992a) and calling probability has been found to have decreased after selective logging which specifically targets those large trees (Johns, 1985). No significant correlation was found between calling probability and either density of large trees or all vegetation characteristics as summarized by PCA1.

Finally, as this study's aim was to compare densities between survey sites sharing the same methodology and surveyed in the same period of time, rather than to obtain exact density estimates, any bias associated with the method that could have affected the calculation of gibbon density did not affect the subsequent comparative analysis.

Habitat characteristics and vegetation correlates of gibbon density

The use of a large number of small plots for habitat measurements proved efficient in this study and allowed the detection of fine-scale differences in vegetation characteristics. This is a time-efficient method that can easily be associated with auditory sampling, as a small number of plots can be measured each day after the collection of the singing data, making vegetation sampling less fastidious and labor-intensive than larger plots.

Gibbon density was found to be highly correlated to vegetation parameters, in particular canopy cover and tree height. As gibbons preferentially use high canopy layers throughout their activity budget (Johns, 1986; Brockelman and Ali, 1987; O'Brien et al., 2004; Nijman, 2001), this result is not surprising, although gibbons have proved to be relatively adaptable to disturbances of canopy cover following logging by shifting their use of canopy layers to the lower canopy (Johns, 1985; Johns, 1986; Nijman, 2001). Canopy cover and tree height have been found to influence the density of other arboreal primates (Tana red colobus and crested mangabey: Medley, 1993; orangutans: Felton et al., 2003), as gaps in

canopy impair their travelling. Other variables that were found to be correlated with gibbon density in this study were the density of large trees and the availability of food trees. Felton et al. (2003) reported a similar correlation between orangutan density and density of large trees in a peat-swamp forest in West Kalimantan. Similar results were reported for greater dwarf lemurs (Lehman et al., 2006) and primate species along the Tana river (Wieczowski, 2004). All the authors proposed that this relationship was due to greater availability of food where more large trees were present, which is in conformity with results linking food abundance to primate densities (e.g. Wieczowski, 2004; Mather, 1992a; Mather, 1992b). Although the correlation between cross-sectional area of food trees was weak in this study, primarily due to large variations between plots, it is supported by the results of other studies on gibbons (Mather, 1992a) which found that gibbon density was strongly influenced by the availability of their preferred food trees. No correlation was found however between the availability of the Sabangau gibbon's top 20 food trees. This could be due to the fact that the list of preferred food items was compiled based on data from the MSF only, and may thus not be applicable to other forest types. Alternatively, this could be due to the gibbons' extensive range of food trees in the study area. Their diet includes at least 65 species of trees, of which relative importance varies seasonally (Cheyne and Sinta, 2006; Cheyne, 2008), in which case a list of 20 preferred food species should be adapted according to the months during which the survey was conducted in order to account for the animals' dietary flexibility.

Implications for conservation

The influence of logging on gibbon populations has been the focus of several studies (e.g. Wilson and Wilson, 1975; Johns, 1986; Meijaard et al., 2005), as it constitutes a major threat to gibbons. Selective logging, which targets large, commercially valuable trees, has been shown to reduce canopy cover and continuity, as well as to restrict the availability of

food for the gibbons (Meijaard et al., 2005; Johns, 1988). The damage on forest trees also exceeds the sole trees that are felled, as it was found that selective removal of 3.3% of trees resulted in the destruction of over 50% of surrounding trees (Johns, 1988). Because of their dietary flexibility, gibbons may be relatively resilient to logging: Meijaard et al. (2005) listed five studies having found gibbon densities equal or higher after selective logging. Six studies cited in the same review found decreased gibbon densities after logging. Since gibbon density was highly correlated to canopy cover and tree height, the results of the present study seem to indicate that gibbons in the Sabangau may have been negatively affected by logging, even though the population survived thirty years of timber extraction in the area. Moreover, logging activities in the Sabangau catchment have resulted in disruptions in the ecosystem's hydrology, as water is drained from the peat by logging canals (Morrogh-Bernard et al., 2003). As a result the region is prone to recurrent wildfires, which have been found to drastically increase tree mortality, decrease fruit availability (Kinnaird and O'Brien, 1998; O'Brien et al., 2003; Barlow and Peres, 2006; Fredriksson et al., 2007) and to affect negatively the density of large vertebrates, such as siamangs, which are particularly vulnerable because of their territorial nature (O'Brien et al., 2003).

Conclusions and recommendations

The main results yielded by this study are:

- Gibbon densities in the research area ranged from 1.39 to 3.92 groups/km², with the highest density observed in the tall interior forest, and the lowest density observed in the low pole forest.
- Vegetation characteristics correlated strongly with gibbon density, in particular canopy cover at twenty meters and tree height. Food availability was also found to be a correlate of gibbon density.

The following recommendations can be drawn from this study:

- Because gibbon density can vary over two-fold across survey sites less than five kilometers apart, as shown by this study, surveying several locations within the same forest, for example a national park, is essential for effective conservation management. Extrapolations based on one or a few survey sites could prove largely inaccurate if vegetation characteristics vary within the forest.
- Assessing microhabitat variations within forested ecosystems can be conducted quickly and efficiently using speed plotting, in order to design conservation strategies adapted to forest subtypes with differential importance to gibbon populations.
- In order to protect the extensive gibbon population of the Sabangau forest, conservation actions should focus on the prevention of logging and of wildfires, and the enforcement of existing protection measures in the whole of the Sabangau national park, in order to allow complete regeneration of the forest after its exploitation for timber.
- Finally, as peat-swamp forest are able to support healthy populations of Bornean agile gibbons and Bornean orangutans, protection should be extended to other Indonesian peat-swamp forests to reduce the threat to these species' habitat.

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