

RESEARCH ARTICLE

Vegetation Correlates of Gibbon Density in the Peat-Swamp Forest of the Sabangau Catchment, Central Kalimantan, Indonesia

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Understanding the complex relationship between primates and their habitats is essential for effective conservation plans. Peat-swamp forest has recently been recognized as an important habitat for the Southern Bornean gibbon (*Hylobates albibarbis*), but information is scarce on the factors that link gibbon density to characteristics of this unique ecosystem. Our aims in this study were firstly to estimate gibbon density in different forest subtypes in a newly protected, secondary peat-swamp forest in the Sabangau Catchment, Indonesia, and secondly to identify which vegetation characteristics correlate with gibbon density. Data collection was conducted in a 37.1 km² area, using auditory sampling methods and vegetation “speed plotting”. Gibbon densities varied between survey sites from 1.39 to 3.92 groups/km². Canopy cover, tree height, density of large trees and food availability were significantly 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. *Am. J. Primatol.* 72:607–616, 2010. © 2010 Wiley-Liss, Inc.

Key words: auditory sampling; conservation; habitat; Southern Bornean gibbon

INTRODUCTION

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

Borneo is an excellent region in which to study relationships between habitat characteristics and primate occurrence and abundance. The island, politically divided between Indonesia, Malaysia and Brunei, is home to some 13–15 species of primates [Meijaard & Nijman, 2003; Nijman & Meijaard, 2008]. It still harbors one of the largest expanses of tropical forest in Asia despite rapid conversion of forest into agricultural or industrial land [Fredriksson et al., 2007; MacKinnon et al., 1997; Meijaard et al., 2005; Morrogh-Bernard et al., 2003]. One of the most threatened forest types in Borneo is peat-swamp forest, which covers about 60,000 km² of the lowlands of Kalimantan, the Indonesian part of Borneo, alone [Rieley et al., 1997].

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, 1999; Shepherd et al., 1997]. However, recent research has indicated that they harbor some of the largest remaining populations of Bornean orangutans (*Pongo pygmaeus*) [Felton et al., 2003; Morrogh-Bernard et al., 2003] and Bornean agile gibbons (*Hylobates albibarbis*) [Buckley et al., 2006; Cheyne et al., 2008; Geissmann, 2007], two species of endangered primates endemic to Borneo.

The level of protection of the peat-swamp forest is low: less than 10% of it is included in the protected area network [MacKinnon et al., 1997; Morrogh-Bernard et al., 2003]. Because these forests contain commercially valuable timber at high densities, they are often commercially logged, either legally or illegally [MacKinnon et al., 1997]. In addition to the removal of large trees, logging also has severe consequences for the

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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 [Morrogh-Bernard et al., 2003; Page et al., 1997, 1999; Shepherd et al., 1997] and as an important purveyor of ecological services such as carbon and water storage, and climate regulation [Cheyne, 2007; MacKinnon et al., 1997; Morrogh-Bernard et al., 2003; Rieley et al., 1997]. Through efforts by local NGO's there has been a significant decline in illegal logging activities, which started following the end of the thirty year legal logging concession. However, protection of the peat-swamp forest is not enforced in many parts of the catchment where anthropogenic disturbance continues. Population density and size 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].

Our aims in 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 4 km² 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. Second, this study was designed to identify relationships between gibbon density and habitat type, 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.

As gibbons are exclusively arboreal [Bartlett, 2007; Johns, 1986] and have been found to prefer high canopy levels [Gittins, 1983; MacKinnon & MacKinnon, 1980; Mather, 1992a,b; Whitten, 1982], it is hypothesized that tree height and canopy cover will be positively correlated with gibbon density. Similarly, food availability has been found to be correlated with gibbon density at other sites [Cheyne et al., 2006; Chivers, 2001; Mather, 1992a,b; but see Marshall, 2009], and it has been suggested that the abundance of a small number of tree species might provide an indication of gibbon density [Mather, 1992a,b]; the existence of such correlations was tested at the study site.

METHODS

Study Site

The Sabangau catchment covers 5,680 km² of peat-swamp forest between the Sabangau and

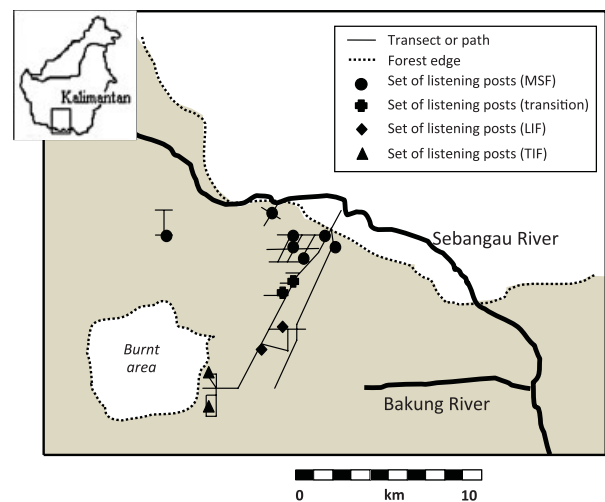


Fig. 1. Map of the study area, showing the 13 sets of listening posts used for auditory sampling. Vegetation sampling was conducted at the same sites, along transects.

Katingan Rivers in Central Kalimantan. The study area [2°20'42"S, 114°2'11"E] is located within the Natural Laboratory for the Study of Peat-swamp Forest, a 500 km² area situated in the north of the catchment, 20 km south–west of Palangkaraya, the provincial capital of Central Kalimantan (Fig. 1). At the time of the field surveys the area was protected and timber extraction had stopped at the survey locations. Small-scale harvesting of nontimber 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]. The research is carried out in collaboration with the University of Palangkaraya and the Centre for International Cooperation in Sustainable Management of Tropical Peatland (CIMTROP), under sponsorship of the Indonesian Ministry of Science and Technology. The research-protocols followed the Animal Behavior Society's Guidelines for the Treatment of Animals in Behavioural Research and Teaching, and were approved by the respective institutions.

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 13 distinct survey sites within the research area (Fig. 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 & Ali, 1987; Brockelman & Srikosamatara, 1993; Nijman & Menken, 2005].

Second, 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 & Menken, 2005]. This method has proved efficient in several primate surveys [e.g. Brockelman & Srikosamatara, 1993; Estrada et al., 2002, 2004; Gursky, 1998; 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.

Data collection took place between 7 May and 27 July 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.

The compass bearings and estimated distances of gibbon calls were recorded from three listening posts situated in a triangle formation, with a distance of 300 to 600 m between them, for four consecutive days at each survey site. Data collection took place between 04:30 hr and 08:00 hr each morning excluding 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 & Ali, 1987; Brockelman & 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 & Ali, 1987; Brockelman & 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 & Ali, 1987]. After plotting all recorded singing bouts on a map using Microsoft Excel, the number of groups within each surveyed location could be determined by triangulation or quadrangulation and input into the density formula.

The density estimates (D) were obtained with the following formula, developed by Brockelman and Ali [1987]: $D = n/[p(m) \times E]$, where n is the number of groups heard in an area as determined by the mapping, $p(m)$ is the estimated proportion of groups expected to sing during a sample period of m days, and E is the effective listening area. The correction factor $p(m)$ was determined at each site with the formula $p(m) = 1 - [1 - p(1)]^m$, with $p(1)$ being the singing probability for any given day, and m being the number of survey days. The effective listening

area was calculated for each site using a fixed radius of 1 km around each listening post, and was defined by the area in which at least two of the listening posts could hear gibbons singing. Areas which were not covered in forest (outside the forest edges and in burnt areas) were deducted from the effective listening area using satellite images and GPS maps. 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 10 m × 10 m 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. Blackham, 2005; Rendigs et al., 2003]. Ten plots per site were analyzed, with the exception of five sites within the grid system, for which six plots per site were analyzed because of time constraints. In each plot the following data were recorded: 1, canopy cover at 20 m, 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 10 cm DBH; 3, height of all trees exceeding 10 cm DBH, placing each tree into classes from 0–5 m to 35 m+ 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 & Jelutong, see Fig. 2] for which 100 m × 5 m 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 cross-sectional area = (DBH/2)² × π and used as an indicator of tree biomass.

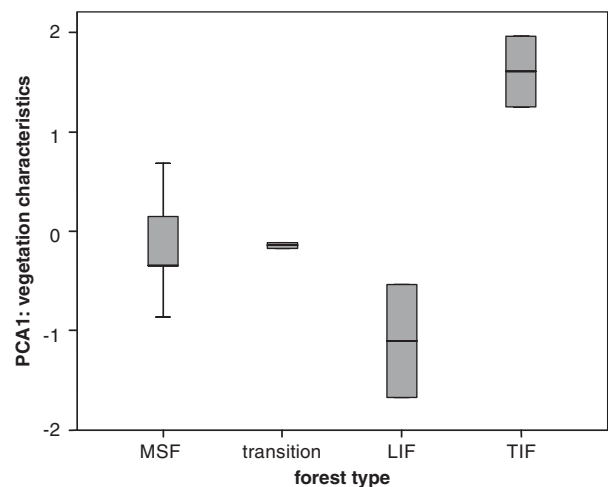


Fig. 2. Vegetation characteristics, as summarized by the principal component PCA1, between forest types.

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 ≥ 10 cm DBH; 5, density of large trees (≥ 20 cm DBH); 6, total cross-sectional area of all trees ≥ 10 cm DBH; 7, total cross-sectional area of large trees (≥ 20 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 [Cheyne, 2008a,b; Cheyne & Shinta, 2006]. 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 nonparametric test. Pair-wise comparisons of means for each of the variables were carried out between forest types using Mann–Whitney *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 $P < 0.05$. The 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 I summarizes the parameters of calling probabilities and effective listening areas for all survey sites, as well as resulting gibbon density estimates.

The density estimates in Table I are provided 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.

TABLE I. Parameters Calculated for the Estimation of Gibbon Density at Each Site, and Resulting Density Estimates

Site name and site number	Groups heard (<i>N</i>)	<i>p</i> (1)	<i>m</i> (days)	<i>p</i> (<i>m</i>)	<i>E</i> (km ²)	Estimated 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	0.50	4	0.94	3.00	2.41
MSF 7	7	0.50	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
LIF 1	3	0.33	3	0.70	3.08	1.39
LIF 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

Reduced effective listening areas (*E*) were due to forest edges or areas of forest destroyed by wildfires. MSF: mixed-swamp forest, LIF: low interior forest, TIF: tall interior forest. Reduced sampling periods (*m*) were due to adverse weather conditions.

Vegetation Characteristics and Determination of Forest Types

Three main forest types can be identified in the Sabangau peat-swamp forest: a low interior forest (LIF) with short, small trees, a very scarce canopy cover at 20 m and few large trees (≥ 20 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 LIF, were labeled transition forest. Only sites for which vegetation information was obtained from 10×10 m 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 LIF 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* (hang-kang) trees dominating in both sites and representing 29 and 43% of the trees in sites TIF1 and TIF2, 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 II.

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 LIF 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 LIF (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, LIF 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 III).

Factor analysis on all vegetation variables identified one component, called PCA1, composed of the nine vegetation characteristics and retaining 77% of the variation in the data set. 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 (Fig. 2).

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 ($R^2 = 0.579$, $P = 0.007$) (Fig. 3).

TABLE II. Average Vegetation Characteristics (\pm SE) for the Forest Types of the Sebangau Peat-Swamp Forest

	Forest types				Kruskal–Wallis χ^2 and P
	MSF ($n = 42$)	Transition ($n = 20$)	LIF ($n = 20$)	TIF ($n = 20$)	
Mean canopy cover at 20 m (%)	40.9 \pm 3.8	20.8 \pm 3.9	10.0 \pm 1.6	61.8 \pm 3.4	$\chi^2 = 49.0$; $P = 0.001$
Median tree height (m)	11–15	11–15	11–15	16–20	$\chi^2 = 22.5$; $P = 0.001$
Mean DBH (cm)	16.3 \pm 0.5	15.5 \pm 0.7	16.0 \pm 0.7	19.4 \pm 0.9	$\chi^2 = 14.0$; $P = 0.003$
Density large trees (trees/ha)	231.2 \pm 24.9	220.0 \pm 49.5	150.0 \pm 28.0	385.0 \pm 41.8	$\chi^2 = 18.2$; $P = 0.001$
CSA all trees (cm ²)	2,546 \pm 190	3,332 \pm 569	2,094 \pm 254	4,198 \pm 419	$\chi^2 = 17.4$; $P = 0.001$
CSA large trees (cm ²)	1,443 \pm 178	1,852 \pm 545	1,067 \pm 218	3,104 \pm 442	$\chi^2 = 16.4$; $P = 0.001$
CSA food trees (cm ²)	2,018 \pm 167	2,469 \pm 404	1,712 \pm 251	3,455 \pm 357	$\chi^2 = 16.9$; $P = 0.001$
CSA top20 food trees (cm ²)	1,012 \pm 107	1,113 \pm 200	572 \pm 93	1,037 \pm 210	$\chi^2 = 8.1$; $P = 0.04$

CSA = cross sectional area. MSF = mixed swamp forest; LIF = low interior forest; TIF = tall interior forest.

Calling Probability

Correlation was tested between calling probability ($p(1)$, see Table I) and gibbon density in this study, 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

TABLE III. Correlation Between Gibbon Density and Habitat Characteristics Across Study Sites

	Gibbon density (groups/km ²)		
	Pearson correlation	Sig.	N
Mean canopy cover (%)	0.802	0.003	11
Median tree height	0.768	0.006	11
Mean DBH	0.591	0.034	13
Density of trees > 10 cm DBH	0.255	0.401	13
Density of trees > 20 cm DBH	0.664	0.013	13
CSA of trees > 10 cm DBH	0.633	0.020	13
CSA of trees > 20 cm DBH	0.657	0.015	13
CSA of gibbon food trees	0.573	0.041	13
CSA of top20 gibbon food trees	0.463	0.111	13

CSA: cross-sectional area.

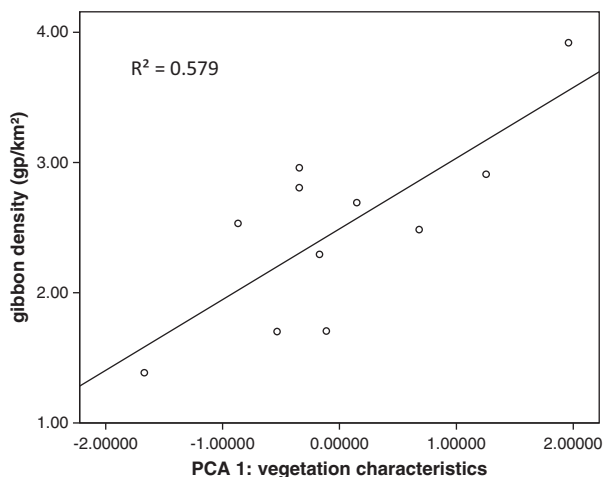


Fig. 3. Relationship between vegetation characteristics, as summarized by the principal component PCA1, and gibbon density across survey sites ($n = 11$, $R^2 = 0.579$).

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 IV).

Moreover, the density estimate yielded by this study for the MSF gives a number of gibbon groups of 11 in a 4 km² area, which is exactly the number of groups present in the 4 km² main study area, where behavioral research is conducted [Cheyne, 2010].

Fixed point counts using auditory sampling do have a number of biases associated with the method. First, the method excludes lone animals from the estimate, as only duets are taken into account into the analysis. The proportion of lone animals, mostly sub-adult individuals, in a population of *H. albibarbis* in West Kalimantan has been estimated at 5.5% of the paired population [Cowlshaw, 1992]. 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. Second, auditory sampling is dependent on weather conditions during data collection, which can affect singing frequency [Brockelman & Ali, 1987; Brockelman & Srikosamatara, 1993; Leighton, 1987; Raemaekers et al., 1984]. 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 to be correlated with singing frequency in pileated gibbons [Brockelman & 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]. Finally, wind has been shown to affect singing in pileated gibbons [Brockelman & Srikosamatara, 1993] and siamangs [O'Brien et al., 2004], but not agile gibbons [Cheyne, 2007; O'Brien et al., 2004]. Wind conditions were calm on every survey morning, and thus are unlikely to have had any effect on singing.

It has been proposed that low densities (< 2 groups/km²) may affect singing probability, as

TABLE IV. Comparison between Bornean Agile Gibbon *H. albibarbis* Density Estimates in Lowland and Hill Forest (Below 750 m above Sea Level)

Area	Forest type(s)	Density per km ²		Reference
		Groups	Individuals	
Gunung Palung	Peat-swamp, Lowland, Hill	3.6	14.9	Mitani [1990]
	Peat-swamp	2.3	7.3	Marshall [2009]
	Lowland sandstone	3.4	10.3	Marshall [2009]
	Lowland granite	2.6	6.2	Marshall [2009]
	Upland granite	1.4	4.2	Marshall [2009]
Tanjung Puting Sebangau	Peat-swamp, lowland	[2.1] ^a	8.7	Mather [1992b]
	Peat-swamp (Mixed Swamp Forest)	2.2	7.5 ^b	Buckley et al. [2006]
		2.6	10.7 ^a	Cheyne et al. [2008]
		2.6	[10.7] ^a	This study
	Peat-swamp (Tall Interior Forest)	3.1	[12.8] ^a	Cheyne et al. [2008]
Barito Ulu		3.4	[13.9] ^a	This study
	Peat-swamp (Low Interior Forest)	1.5	[3.5] ^c	This study
	Lowland	[3.0] ^a	12	Mather [1992b]
		[2.6] ^a	10.5	Mather [1992b]
		[4.4] ^a	18	Mather [1992b]
		[2.0] ^a	8.2	McConkey [2002]

Estimates from Barito Ulu in italics refer to naturally occurring hybrids between *H. albibarbis* and *H. muelleri*. Estimates between brackets are derived from the adjacent estimate using mean group sizes.

^a4.1 individuals: Mitani [1990] Cheyne et al. [2008].

^b3.4 individuals: Buckley et al. [2006].

^c2.3 individuals: SM Cheyne [unpublished data].

singing can be stimulated by other duets from neighboring groups [Brockelman & Srikosamatara, 1993; Geissmann & Nijman, 2006; Mitani, 1987; Nijman, 2004]. In this study, no correlation was found between singing probability ($p(1)$, see Table I) 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 [Brockelman & Ali, 1987; Johns, 1986; Nijman, 2001; O'Brien et al., 2004], 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 River red colobus *Ptilocolobus rufomitratu*s and crested mangabey *Cercocebus galeritus*: Medley, 1993; orangutans *Pongo pygmaeus*: 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. Marshall [2009] found that gibbon density was negatively correlated with terrain elevation at Gunung Palung (West Kalimantan); the density of gibbons was highest in lowland forest which contained larger trees than montane forest. Similarly, food availability for gibbons was reduced in montane forest where very few gibbons were found [Marshall, 2009]. 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 [Wieczkowski, 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. Mather, 1992a,b; Wieczowski, 2004]. Although the correlation between cross-sectional area of food trees and gibbon density was weak in this study, primarily due to large variations between plots, it is supported by the results of other studies on gibbons [Marshall, 2004; Marshall & Leighton, 2006; Marshall, 2009; Mather, 1992a], which found that gibbon density was strongly influenced by the availability of their preferred food trees. However, no correlation was found between the availability of the Sabangau gibbon's top 20 food trees and gibbon density. 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 & Sinta, 2006; Cheyne, 2008a,b], 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. Gibbon density has also been linked with the availability of figs, which are important fallback foods in many forest types [Marshall, 2004]. The correlation between the availability of figs and gibbon density was not evaluated in the present study, as phenology and feeding ecology data indicate that fig availability and consumption by gibbons remain roughly constant throughout the year in the Sabangau peat-swamp forest [Cheyne, 2008a,b]. This contrasts to other field sites with masting forest types, where figs are important food items for gibbons in times of low preferred fruit availability (i.e. ripe fleshy fruit) [Marshall, 2004, 2009].

Implications for Conservation

The influence of logging on gibbon populations has been the focus of several studies [e.g. Johns, 1986; Meijaard et al., 2005; Wilson & Wilson, 1975], 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 [Johns, 1988; Meijaard et al., 2005]. 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 this study seem to indicate that gibbons in the Sabangau may have been negatively affected by logging, although the population survived 30 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 in other tropical sites to drastically increase tree mortality, decrease fruit availability [Barlow & Peres, 2006; Fredriksson et al., 2007; Kinnaird & O'Brien, 1998; O'Brien et al., 2003] and to affect negatively the density of large vertebrates, including siamangs, another Hylobatid primate, which are particularly vulnerable because of their territorial nature [O'Brien et al., 2003].

This study was also designed to be used as a repeat survey to monitor the gibbon population in the Sabangau catchment over time. The population seems to have remained stable since the start of the study period in 2004 [Buckley et al., 2006; Cheyne et al., 2008]; however, with slow-reproducing primate species such as gibbons, population trends require longer monitoring periods to be detected, and we hope the present survey will be followed by others at this study site to detect such population trends.

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