

RESEARCH ARTICLE

The Conservation Value of Degraded Forests for Agile Gibbons
*Hylobates agilis*DAVID C. LEE^{1,2*}, VICTORIA J. POWELL³, AND JEREMY A. LINDSELL^{2,4}¹School of Applied Sciences, University of South Wales, Pontypridd, United Kingdom²RSPB Centre for Conservation Science, Royal Society for the Protection of Birds, Sandy, United Kingdom³Harapan Rainforest, Jambi, Sumatra, Indonesia⁴A Rocha International, Cambridge, United Kingdom

All gibbon species are globally threatened with extinction yet conservation efforts are undermined by a lack of population and ecological data. Agile gibbons (*Hylobates agilis*) occur in Sumatra, Indonesia and adjacent mainland Southeast Asia. Population densities are known from four sites (three in Sumatra) while little is known about their ability to tolerate habitat degradation. We conducted a survey of agile gibbons in Harapan Rainforest, a lowland forest site in Sumatra. The area has been severely degraded by selective logging and encroachment but is now managed for ecosystem restoration. We used two survey methods: an established point count method for gibbons with some modifications, and straight line transects using auditory detections. Surveys were conducted in the three main forest types prevalent at the site: high, medium, and low canopy cover secondary forests. Mean group density estimates were higher from point counts than from line transects, and tended to be higher in less degraded forests within the study site. We consider points more time efficient and reliable than transects since detectability of gibbons was higher from points per unit effort. We recommend the additional use of Distance sampling methods to account for imperfect detection and provide other recommendations to improve surveys of gibbons. We estimate that the site holds at least 6,070 and as many as 11,360 gibbons. Our results demonstrate that degraded forests can be extremely important for the conservation of agile gibbons and that efforts to protect and restore such sites could contribute significantly to the conservation of the species. *Am. J. Primatol.* © 2014 Wiley Periodicals, Inc.

Key words: distance sampling; forest restoration; gibbon surveys; Indonesia; point counts

INTRODUCTION

Almost all forest-dependent primate species in Southeast Asia are threatened or near-threatened with extinction [IUCN, 2012]. The situation is particularly concerning for gibbons with all 15 species red-listed, 14 of them as either Endangered or Critically Endangered [IUCN, 2012]. Although degraded forests remain important for much of the region's wildlife [Harrison, 2011; Meijaard & Sheil, 2007], their value for gibbons is unclear. Gibbons are considered to have low recovery potential [Phoonjampa et al., 2011] and limited ability to respond demographically to environmental change [O'Brien & Kinnaird, 2011]. Their ability to persist in heavily degraded forest isolated from intact forest is little studied but generally assumed to be poor. Pileated gibbons (*Hylobates pileatus*) in Thailand depend on undisturbed forests but can persist in degraded areas [Phoonjampa et al., 2011]. The density of Bornean white-bearded gibbon (*H. albibarbis*) in Kalimantan is positively associated with vegetation parameters indicative of tall, relatively undisturbed forest with

good canopy cover [Hamard et al., 2010], while yellow-cheeked crested gibbons (*Nomascus gabriellae*) in Cambodia also appear to be associated with undisturbed forest with a high canopy [Traeholt et al., 2006] but could persist in selectively logged forests [Duckworth et al., 1999]. Reproduction and survivorship in siamangs (*Symphalangus syndactylus*) is linked to

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the availability of strangler figs, as a proxy for habitat quality, which decreases after fire [O'Brien et al., 2003].

The agile gibbon (*Hylobates agilis*) is the most widespread gibbon species on the island of Sumatra, where deforestation rates are among the highest in Southeast Asia [Miettinen et al., 2011]. Despite having a relatively large global range covering the extreme south of Thailand, Peninsular Malaysia, and Sumatra, the agile gibbon is listed as Endangered [IUCN, 2012] reflecting a continued population decline inferred from ongoing habitat degradation, fragmentation and loss, and collection for the illegal pet trade [Geissmann & Nijman, 2008]. They are most at risk in the Sumatran part of their range, which because of its size probably contains most of the remaining agile gibbons, although they are thought to be declining rapidly there [Geissmann & Nijman, 2008]. However, there are relatively few current density or subpopulation estimates for the species in Sumatra, especially in lowland forest [O'Brien et al., 2004; Wilson & Wilson, 1976; Yanuar, 2001, 2007; Yanuar & Sugardjito, 1993], and little understanding of their resilience to forest disturbance.

Gibbon population estimates often rely on point count surveys [Brockelman et al., 2009; Cheyne et al., 2008; Gray et al., 2010; Hamard et al., 2010] or line transects [Haus et al., 2009; Le Trong et al., 2009; Marshall, 2009; Nijman & Menken, 2005]. Point surveys map gibbons heard giving early morning territorial long calls, which may carry for more than 1 km [Phoonjampa et al., 2011], over a known area to estimate density [Brockelman & Ali, 1987; Brockelman & Srikosamatara, 1993]. Points are often considered preferable because gibbons are difficult to see from transects [Brockelman & Ali, 1987; Brockelman & Srikosamatara, 1993; Nijman & Menken, 2005] and singing groups are detectable over greater distances than sightings [Davies, 2002], making points more time efficient than transects [Nijman & Menken, 2005]. However, the method has been criticized over the accuracy of estimated distances to, and cumulative mapping of singing groups, the validity of using non-random survey points, the application of correction factors to temporally variable singing frequencies, and the assumption that all groups are detected within a given radius [Rawson, 2010]. Distance sampling which accounts for imperfect detection [Buckland et al., 2001] is widely used to estimate densities of forest primates [Lindsell et al., 2011; Plumptre, 2000], but with limited application to either point count surveys [Phoonjampa et al., 2011] or line transect surveys [Marshall, 2009] of gibbons.

Anecdotal evidence from Harapan Rainforest (HRF), a dry lowland forest site in Sumatra, suggested that agile gibbons are able to persist in heavily degraded forest [D.C. Lee, pers. obs., 2008].

The aim of this study was to survey the gibbon population at this site and assess the capacity of the species to survive in degraded forest. We test the application of established gibbon survey methods to produce reliable density and population estimates in this part of the species' range. We generate habitat-specific estimates related to the level of forest degradation to support effective forest management and restoration activities that benefit the conservation of gibbons at the site. We also provide recommendations for future monitoring of the species and other hylobatids throughout their range.

METHODS

Study Site

HRF is an ecosystem restoration concession in southeast Sumatra, Indonesia (103°17'49"E, -2°12'94"S) (Fig. 1). The site covers 985.5 km² of previously logged dry lowland forest with an elevation ranging from 30 to 120 m asl over mostly flat terrain. Annual rainfall of around 2,500 mm falls year round with a dry season from June to August. Monthly mean temperature ranges from 25 to 27°C.

The site is managed for ecosystem restoration under a 100-year license by an Indonesian company, which is guided by a consortium of local and international conservation non-government organizations. Other than in a few small degraded and

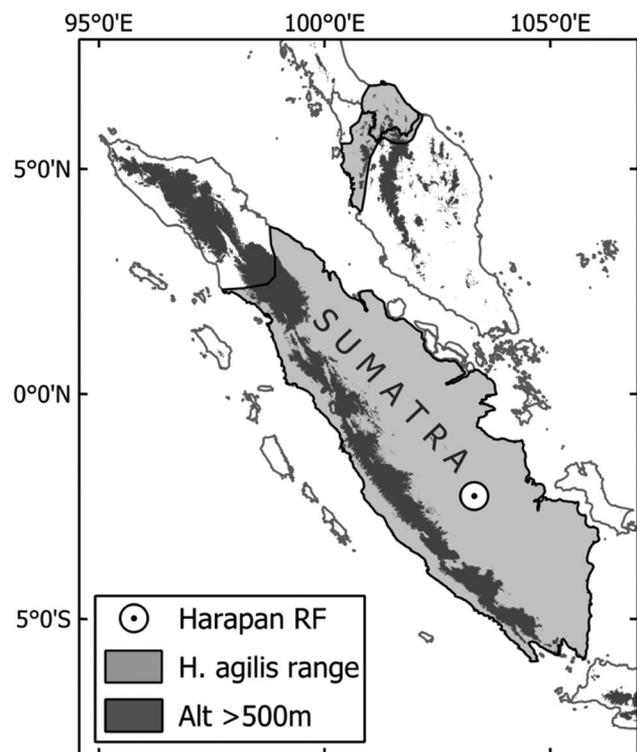


Fig. 1. Location of Harapan Rainforest, Sumatra, within the global range of Agile Gibbons.

cleared areas, active restoration of the site (e.g., enrichment planting and thinning) had not started at the time of the study. Consequently, forest restoration had no impact on the gibbon numbers we observed.

The site is surrounded by industrial oil palm, rubber, acacia plantations, and small-scale agriculture. It was heavily logged from the 1970s until 2006, with most areas logged twice during that time, although reliable off-take records are not available. This has left a mosaic of three broad forest habitats within the concession: “High secondary forest” (HSF), which covers 37.0% of the site, with a closed canopy of mixed species, especially Fagaceae and Myrtaceae but few dipterocarps, sometimes a subcanopy and often a well-developed understory; “Medium secondary forest” (MSF; 15.2%) with relatively sparse herbaceous layers and closed canopies of a mixture of pioneer and old secondary species; and “Low secondary forest” (LSF; 42.5%) characterized by an open canopy dominated by *Macaranga gigantea* and *Bellucia pentamera* but lacking large trees and with an often dense understory of herbs (typically Zingiberaceae and Marantaceae) [Briggs et al., 2012; Lee & Lindsell, 2011; Schweter, 2009]. None of the forest has very high biomass due to the removal of most large trees during logging. The remainder of the site (5.3%) consists of rubber and oil palm plantations, scrub, agriculture and open ground. We did not observe agile gibbons in these non-forest habitats, which we therefore excluded from our survey. Siamangs also occur at the site, but records of these are rare, with none recorded in or around our study locations.

Survey Methods and Data Collection

We used point counts and variable distance line transects to survey gibbons in 10 locations, which we selected randomly from a systematic grid of points that covered the entire study site (Fig. 2). We assigned observers randomly to points or transects to minimize observer bias [Jones, 1998]. We conducted a preliminary study between July 20 and August 20, 2009 to assess the optimum time of day for point count surveys (0530–0830 hours), number of survey days required to detect a singing group (four), detection distance of singing groups (1,200 m) [Brockelman & Ali, 1987; Brockelman & Srikosamatara, 1993], and to train and assess field teams. The same trained observers carried out the point and transect surveys from September 2009 to May 2010. We monitored observer consistency in direction and distance estimation throughout the survey [Jones, 1998]. We did not carry out a survey if it was raining or had rained the previous night as this negatively influences singing behavior (and detectability) of gibbons [Brockelman & Ali, 1987; Brockelman &

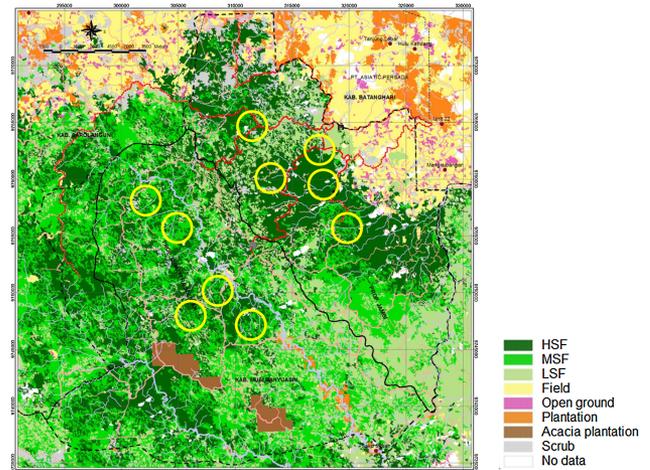


Fig. 2. Locations of the 10 survey locations in Harapan Rainforest. Each site (yellow circle) represents three points and three transects.

Srikosamatara, 1993; Cheyne, 2007; Cheyne et al., 2007].

For point counts, sets (or clusters) of three points were arranged in a triangle of ca. 500 m length sides [Brockelman & Ali, 1987; Brockelman & Srikosamatara, 1993; Phoonjampa & Brockelman, 2008]. We adjusted point positions up to 50 m to avoid deep gullies or waterlogged areas resulting in some variation in the area sampled per location (5.75–6.28 km²). Two observers per point recorded all gibbon groups heard duetting between 0530 and 0830 hours for 4 consecutive rain-free days. A single duetted song comprised one female great call and the male’s answering coda [Cheyne et al., 2007]. Observers recorded the exact start time of the duetted song, compass bearing, estimated distance to the group, and any counter-singing by neighboring groups [Phoonjampa & Brockelman, 2008]. They also noted differences in song organization (number of notes per female great call, duration of the climax note, number and duration of the post-climax notes) that might distinguish individual groups [Cheyne et al., 2007]. We used two-way radios throughout each survey to corroborate singing groups and assign them a group number. We used triangulation to map groups heard from at least two points for each survey day, and considered groups to be different if they were mapped >500 m apart [Brockelman & Ali, 1987; Brockelman & Srikosamatara, 1993; Cheyne et al., 2008; O’Brien et al., 2004]. We mapped groups heard from only one point if they were detected >500 m from any triangulated group heard calling on the same day, or if they were within 250 m of a point and could be distinguished as a different group by the observers at the nearest point. We combined group locations to estimate the total number of groups heard over the

4 days and divided this by the listening area of each location to calculate group density.

We surveyed three parallel line transects of 2.5–2.8 km length, each spaced 1 km apart, in each location (total effort = 80 km) in the same week as the corresponding point counts. We disregarded existing trails, ridge tops, or valleys when setting transect locations to minimize bias, and cut and marked transects 1 week before the survey to minimize disturbance [Buckland et al., 2010]. We surveyed one transect per morning between 0700 and 1000 hours at a speed of ca. 1 km/hr with perpendicular distance recorded to all groups of gibbons seen or heard [Buckland et al., 2001]. We surveyed transects later in the morning than point counts so observers could safely traverse over rough terrain and effectively record sightings of animals as well as auditory-only detections. Where possible, we used a laser rangefinder to measure distances to gibbons. When we were unable to note group size, due to not having a clear view of the group detected, we used mean group sizes from ad hoc observations made in the relevant forest type. We also used these group sizes for the point surveys. A recent land cover classification [Schweter, 2009] allowed us to estimate the proportion of each forest type in each survey location. We used this classification to categorize each gibbon observation by forest type. We excluded non-forest areas when calculating habitat-specific densities. We used a GIS to measure the distance of points and transects from the site boundary.

The fieldwork was conducted under the requirements of the ecosystem restoration license issued for the site's management, approved by the Directorate General of Forest Protection and Nature Conservation in Indonesia, and in adherence to Indonesian law and the American Society of Primatologists principles for the ethical treatment of primates.

Distance Analysis

When applying distance sampling to the point count data, detections, and distances of gibbons from points within a cluster were not fully independent since observers at different points assisted one another in detecting gibbon groups. As this would violate the method's independence assumption [Buckland et al., 2001], we used the distance from the central point of each cluster of points to the triangulated position of the group; variance estimation was based on the cluster of points while it was assumed all groups were detected within 250 m of the central point [L. Thomas, pers. comm., 2013]. If a group's position could not be triangulated, that is a group had been recorded from one point, the distance that was estimated in the field was used to calculate distance from the central point. Each group heard was included in the data set once per survey day.

We carried out distance analysis of the survey data using Distance 6.0 release 2 [Thomas

et al., 2010], with detection function models selected using AIC [Akaike, 1973]. We right-truncated distances from points at 900 m and from transects at 500 m, removing the furthest 5% of estimated distances to calling groups in each data set. Although the general models in distance are pooling robust [Buckland et al., 2001], when exploring the transect data we found that the detection functions for the different cue types—visual or auditory—were too different to satisfy this property. We were unable to analyze the transect data using the Multiple Covariate Distance Sampling engine of distance with cue type as a covariate because the distribution of distances from the transect in the population is influenced by cue type [Marques et al., 2007]. Therefore, we excluded visual cues ($N = 7$) and analyzed the transect data based on 67 auditory detections (this did not affect the magnitude of the overall density estimates for the site).

We adjusted survey effort for a given point or transect according to the area of each habitat available within a given survey area to estimate density by forest type. We post-stratified survey data by forest type to account for potential detectability differences across habitats and generate habitat-specific abundance estimates. We used the post-stratified parameters as the more reliable estimate of abundance if the combined AIC for individual habitat detection functions was greater than the post-stratified AIC for all forest types [Buckland et al., 2008]. We took the mean of individual habitat densities weighted by survey effort as an estimate of the density and population of gibbons for the whole site, since points and transects proportionally represented the broad habitat types of the study area. We present abundance estimates \pm coefficient of variation (CV, which is the standard error expressed as a percentage of the estimate).

Landscape Covariates and Gibbon Food Trees

We collected tree inventory data from 362 plots of 0.25 ha (20 m \times 125 m) systematically positioned across the southern half of the study site. We recorded the diameter of all trees over 20 cm diameter at breast height (dbh) and identified species where possible. We extracted scientific names of gibbon food tree species from the literature and included species known to be eaten as well as trees found to be actively selected by gibbons [Brockelman et al., 2005; Cheyne & Sinta, 2006; Fan et al., 2009; McConkey, 2000; McConkey et al., 2002; Muzaffar et al., 2007; Palombit, 1997; Ungar, 1995]. The review covered all gibbon species and included references from insular Southeast Asia. We filtered the site dataset according to the literature search to identify per forest type the density of tree species or genera fed on by gibbons.

Data Analysis

We used parametric tests to compare encounter rates and density estimates from different survey methods (paired *t*-tests), habitat-specific density estimates from distance sampling survey methods (*Z*-tests, $\alpha=0.05$), habitat-specific group sizes, and singing frequencies (one-way ANOVA with Tukey's HSD multiple comparisons test). We used a Kruskal-Wallis test with Tukey's HSD test to check whether density estimates from variable distance point counts stabilized after 4 survey days. We compared density using 4 days of survey data with subsets from 1, 2, and 3 days. We correlated density estimates from different survey methods, and used linear regression to test for any relationship among habitat quality, gibbon density, and distance from the site boundary.

RESULTS

We recorded gibbons in all 10 locations and in each of the three forest types. In total, we mapped 157 different gibbon groups from 308 encounters recorded within 1.2 km of survey points, at an encounter rate of $7.7 \pm \text{CV } 23.2$ groups/day (Table I). By comparison we recorded 67 singing gibbon groups from line transects at an encounter rate of $0.84 \pm \text{CV } 16.3$ groups/km. This equated to 2.23 groups/day, assuming one transect is surveyed per day. Encounter rates (per unit time) were lower from line transects than from point counts (*T*-test: $t=16.13$, $\text{df}=9$, $P<0.001$). Group sizes ranged from three to seven individuals (mean = $4.1 \pm \text{CV } 24.4$; $N=49$) and were significantly smaller in LSF ($3.5 \pm \text{CV } 14.3$; $N=15$) than in MSF ($4.4 \pm \text{CV } 27.3$; $N=16$) and HSF ($4.4 \pm \text{CV } 22.7$; $N=18$; ANOVA: $F=3.41$, $\text{df}=2$, $P<0.05$).

Density Estimates

We modeled variable distance point count data using a hazard rate detection function with post-

TABLE I. Number and Total Encounters (*N*) of Distinct Groups Heard From Points, and Location Encounter Rates

Location	Groups	<i>N</i>	Encounter rate (per day \pm CV)
Danau Rohani	16	35	8.8 ± 7.2
Halilintar	17	37	9.3 ± 14.7
Hulu Kapas	18	31	7.8 ± 12.3
Simpang Gas	12	24	6.0 ± 3.9
Simpang Rohani	17	32	8.0 ± 6.5
SPAS	16	41	10.3 ± 9.9
Sungai Badak	15	23	5.8 ± 23.0
Sungai Kapas I	17	34	8.5 ± 3.7
Sungai Kapas II	14	22	5.5 ± 3.2
Sungai Kapas III	15	29	7.3 ± 5.8
Average	15.7 ± 8.8	30.8 ± 61.6	7.7 ± 23.2

stratification by habitat ($N=257$; $\text{AIC}_{\text{Post-stratified}}=3,474.7$, $\text{AIC}_{\text{Pooled}}=3,478.4$). Pooled and post-stratified models for transect data resulted in the same AIC and number of model parameters ($\text{AIC}=809.1$, parameters=3; $N=67$). We used the pooled estimates as they were more precise. We modeled HSF, MSF, and LSF transect data by uniform, hazard rate, and half-normal detection functions, respectively.

Both fixed radius (FRPC) and distance sampling point counts (DSPC) resulted in significantly higher group density estimates than line transects (*T*-test: $t_{\text{FRPC}}=4.53$, $\text{df}=9$, $P<0.001$; $t_{\text{DSPC}}=4.16$, $\text{df}=9$, $P=0.002$) with distance sampling points producing the highest overall group density ($3.0 \pm \text{CV } 39.2$; Table II). We recorded a positive correlation between group density estimates from FRPCs and line transects ($r=0.726$, $P=0.017$, $N=20$). Estimates from variable distance points tended to stabilize after 3 days of surveying ($H=7.20$, $P=0.027$, $\text{df}=2$; Table III), changing significantly from 2 to 3 survey days but not from 3 to 4 days (Tukey's HSD post hoc test: $q=3.31$, $\text{HSD}=5.234$, $P<0.05$). Regardless of survey method, density estimates tended to be higher in more intact forest (Table II). The different methods resulted in a range of population estimates for HRF from 6,070 (line transects) to 11,360 (DSPC).

Tree plot data from the southern half of the site showed a very low density of larger trees (>40 cm dbh) in all three habitats (Fig. 3) with similar stem densities in HSF, MSF, and LSF (respectively, 25.7, 24.1, and 21.4 stems per ha; $F_{2, 322}=2.48$, $P=0.09$). There was no significant relationship between point count group density estimates or forest quality and distance from the site boundary ($r_{\text{FRPC}}=0.176$, $P=0.627$, $N=10$; $r_{\text{DSPC}}=0.231$, $P=0.521$, $N=10$; $r_{\text{Quality}}=0.411$, $P=0.238$, $N=10$).

Singing Frequency and Detectability

On average, gibbon groups gave $8.1 \pm \text{SE } 0.32$ duetted songs/morning. The number of songs emitted on any given morning did not vary by site (ANOVA: $F=1.48$, $\text{df}=9$, $P=0.151$) or season, wet, or dry (ANOVA: $F=1.23$, $\text{df}=1$, $P=0.268$). However, time of morning had a significant effect on singing frequency (ANOVA: $F=65.89$, $\text{df}=5$, $P<0.001$). The likelihood of singing was highest between 0630 and 0700 hours ($0.53 \pm \text{SE } 0.03$; 26.3% of singing), and significantly higher during earlier 30-min periods (0600–0730 hours, but not before 0600 hours) than later 30 min periods 0730–0830 hours (Tukey's HSD post hoc test: $q=4.75$, $\text{SE}=0.021$, $\text{MSD}=0.099$, $P<0.01$). Consequently, time of day had a significant impact on the density estimates from points: densities were significantly higher from points surveyed up to 0700 hours ("early") than from points surveyed after 0700 hours ("late"; *Z*-test: $Z_{\text{Individual}}=2.049$, $P<0.05$; $Z_{\text{Population}}=2.053$, $P<0.05$; Table III). Densities estimated from "late" point counts were no

TABLE II. Density (per km² ± CV) and Population Estimates (95% CI) Derived From the Different Survey Methods and Analytical Approaches

Survey method	Group density				Individual density			Population estimate
	Overall	LSF	MSF	HSF	LSF	MSF	HSF	
FRPC	2.6 ± 27.1	1.7 ± 63.9	2.7 ± 57.2	3.4 ± 28.5	6.0 ± 63.9	11.7 ± 57.2	15.1 ± 28.5	10,400 (8,070–12,740)
DSPC	3.0 ± 39.2	2.1 ± 42.8	3.0 ± 48.9	3.9 ± 42.5	7.4 ± 42.8	13.0 ± 48.9	17.3 ± 42.5	11,360 (5,390–23,950)
DSLTL	1.7 ± 40.5	1.3 ± 37.7	1.9 ± 93.1	2.0 ± 55.0	4.6 ± 37.7	7.1 ± 93.1	7.9 ± 55.0	6,070 (3,470–11,530)

Note. FRPC, fixed radius point counts; DSPC, distance sampling point counts; DSLTL, distance sampling line transects; LSF, low secondary forest; MSF, medium secondary forest; HSF, high secondary forest.

different to those from line transects surveyed at the same time of day (Z -test: $Z_{\text{Individual}} = 1.450$; $Z_{\text{Group}} = 1.465$, $P > 0.05$).

Gibbon Food Trees

Of the 3,341 trees in the plot data identified to at least genus level 1,742 (52.1%) were in genera known to be eaten by gibbons, six of which were preferentially so. Six species identified to species level as fed on by gibbons were identified *Eusideroxylon zwageri*, *Garcinia parvifolia*, *Koompassia malaccensis*, *Nephelium lappaceum*, *Polyalthia glauca*, and *Xerospermum noronhianum* though only *N. lappaceum* and *P. glauca* have been reported as being consistently over-selected by gibbons [McConkey et al., 2002]. The proportion of gibbon food trees was similar in all three forest types, although for the smallest trees (up to 30 cm dbh); there was a marginally higher proportion of such trees in LSF and MSF compared to HSF (Wilcoxon test: $W = 7,587$, $P < 0.05$).

DISCUSSION

Our study shows that HRF, as one of the last and largest remaining tracts of dry lowland forest in Sumatra, is an extremely important site for agile gibbons, supporting a population of at least 5,390 and perhaps as many as 23,950 individuals (95% confi-

dence intervals for the DSPC estimate of 11,360 individuals). This is despite the highly degraded nature of the site with few large trees remaining. Gibbons occurred at relatively high densities in all forest types including the most degraded areas, providing there was still tree cover. While tempered by some assumptions of the approaches taken, this result is significant for the following reasons.

The average densities of between 6.5 and 12.2 individuals/km², from line transects and DSPC, respectively, were high for lowland Sumatra: island estimates range from 1.4 to 8.6 individuals/km² [O'Brien et al., 2004; Wilson & Wilson, 1976; Yanuar, 2001; Yanuar & Sugardjito, 1993]. Our point count estimates are among the highest recorded for any lowland population of agile gibbons: estimates range from 6.1 to 18.9 individuals/km² in Malaysia [Chivers, 1974; Gittins & Raemaekers, 1980]. Group sizes, even in the most degraded forest, were at the upper end of the reported range for both the agile and Bornean white-bearded gibbons: 2.6–4.1 individuals [Buckley et al., 2006; Cheyne et al., 2008; O'Brien et al., 2004]. We would expect that densities and group sizes in HRF are higher than those from southern Sumatra [O'Brien et al., 2004] since both tend to increase from south to north [O'Brien et al., 2004], although our estimates are still higher than those in the most northern latitudes of the species' range [Chivers, 1974; Gittins & Raemaekers,

TABLE III. Density (per km² ± CV) and Population Estimates (95% CI) Derived From Distance Sampling Point Counts With Varying Survey Effort*

Effort	<i>N</i>	Group density	Individual density	Population estimate
Days/point				
1	88	2.3 ± 14.9	9.2 ± 15.1	8,580 (6,360–11,590)
2	159	6.1 ± 77.0	24.9 ± 77.0	23,270 (6,040–89,620)
3	214	3.0 ± 36.9	12.2 ± 37.0	11,390 (5,620–23,100)
4	257	3.0 ± 39.2	12.2 ± 39.3	11,360 (5,390–23,950)
Time				
“Early”	213	1.9 ± 17.2**	8.0 ± 17.6**	7,450 (5,250–10,570)**
“Late”	44	0.6 ± 50.5**	2.5 ± 47.4**	2,310 (930–5,760)**

Note. *N* is the cumulative number of groups heard singing across survey days.

*Point count data were right truncated at 900 m. “Early” point counts were surveyed between 0530 and 0700 hours; “Late” point counts were surveyed between 0700 and 0830 hours. Significant pair-wise comparisons are indicated by ** $Z \geq 2.576$, $P < 0.01$.

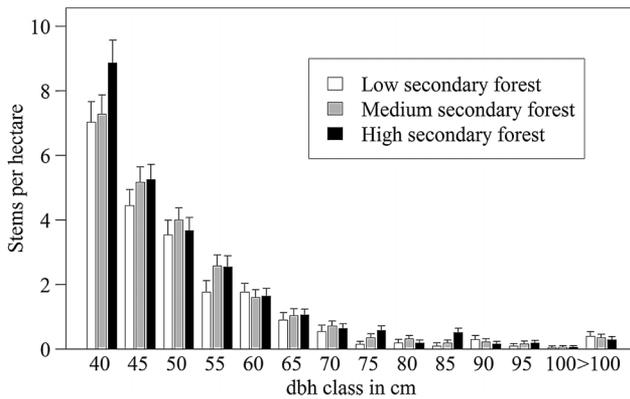


Fig. 3. Density of trees in different size classes in the three main forest types at Harapan Rainforest.

1980]. The average number of duetted songs per morning (around eight per group; and where multiple duetted songs could comprise a song “bout”) was high compared to other studies [e.g., Bornean white-bearded gibbon; Cheyne et al., 2008], which probably reflects the relatively high density of gibbon groups in the survey area. We observed no reduction in gibbon singing frequency in poorer habitat, as might be expected when the density of gibbons is low [Brockelman & Srikosamatara, 1993; Chivers, 1974; Geissmann & Nijman, 2008; Nijman, 2004].

A lack of dispersal opportunities arising from isolation of the site may account for the larger group sizes we recorded. This would imply that HRF has acted historically as a source for surrounding areas but we have no evidence to confirm this possibility. The conversion of the surrounding landscape to plantations and agriculture may have forced gibbons into HRF, but they are considered poor dispersers in fragmented landscapes [Yanuar, 2007]. Furthermore, gibbons are highly territorial and, while some overlap of home ranges is possible [Cheyne et al., 2008], it is unlikely they are able to tolerate substantial increases in density.

The high densities may arise from greater availability of fruit resources. As past logging activities targeted dipterocarp species, the fruits of which are rarely eaten by gibbons [McConkey et al., 2002], it is possible that more favorable food tree species have benefited from competitive release, resulting in greater availability of food resources. Detailed information on the diet of agile gibbons in the site and the availability of their preferred food trees is lacking. Nonetheless, the observation that over half of all the larger trees are in genera known to be eaten by gibbons elsewhere suggests there is an abundant food supply. The role of the invasive non-native *Bellucia pentamera* in the diet of gibbons needs investigating since this has a heavy crop of fruit and is found throughout the site.

It is possible that the presence of this pioneer species has offset the impact of habitat degradation on the gibbons.

Gibbon density and group size increased with forest quality in the site (but see also our comments on home range sizes below), which has been observed elsewhere [Hamard et al., 2010; Traeholt et al., 2006]. Less disturbed forests in HRF are characterized by taller trees, more closed canopy and higher tree biomass [Lee & Lindsell, 2011], enabling gibbons to move more freely within the higher vegetation layers [Brockelman & Ali, 1987; Johns, 1985; Nijman, 2001]. The movements of gibbons are presumably restricted by the reduced canopy cover in the poorer forest [Brockelman et al., 2009]. The more intact forest may also have richer food resources [Cheyne et al., 2008; Chivers, 2001; Marshall, 2009]. However, no areas of the site resembled anything like undisturbed forest; even the areas of high canopy cover lacked numbers of large trees (over 60 cm dbh; Lee & Lindsell, 2011). Our results further emphasize the value of protecting degraded forest sites [Harrison, 2011; Sheil & Meijaard, 2010] especially where few intact forests remain.

Siamangs appear to be particularly important competitors with agile gibbons [Elder, 2009] and their densities are negatively correlated locally in a few sites [O’Brien et al., 2004]. Siamangs occur at very low densities and in restricted areas in HRF and were not recorded during this study. This may be a key factor allowing agile gibbons to achieve high densities at the site. Future surveys of agile gibbons should include areas known to be occupied by siamangs.

HRF is under active restoration management and will be for the foreseeable future. Consequently, it makes a significant contribution to the conservation of the species. Ecosystem restoration license holders are required to abide by national wildlife law under which gibbons are a protected species. Although this is no guarantee of actual protection it provides a framework under which law enforcement can take place that may be a viable alternative to traditional protected area management. Indeed, ensuring strong requirements of license holders to maintain effective protection of biodiversity within their concessions should marshal new resources for conservation. In HRF, the level of hunting is relatively low and restricted to a few species. We are not aware of any significant number of primates being taken from the site for meat, animal parts, or the pet trade [D.C. Lee, pers. obs., 2009].

The site is large enough to support a self-sustaining population and even act as a source for surrounding areas should suitable habitat and connectivity become available in the future. Agile gibbons occur in a number of protected areas on Sumatra but the actual level of protection these sites provide is uncertain, and many include montane

forests where the species occurs at lower densities [Geissmann & Nijman, 2008; O'Brien et al., 2004].

We note that some key assumptions of the survey methods were not always met [Brockelman & Srikosamatara, 1993; O'Brien et al., 2004]. We very occasionally saw gibbon groups singing within 150 m of each other as well as changing locations while singing, which would lead to under and over-estimation of densities, respectively. However, we found that point count density estimates tended to stabilize after 1.5–2 hr of a 3-hr count period suggesting that densities are not unduly inflated by double-counting or undetected movement into the survey area, at least later in the count period. Future surveys should record the movement of gibbons during the sample period, distances and rates of travel, and the frequency of calling from different trees.

We applied a 500 m buffer around gibbon detections to identify separate groups. This standard has been used in more uniform forest landscapes [e.g., O'Brien et al., 2004], whereas we have used it in a mosaic of degraded forest habitats. We acknowledge that home range size may differ across the three forest habitats in the site so further work is required to quantify home range size in the different forest habitats. Preliminary focal studies on three gibbon groups in the site suggested home range may be as small as 20 ha in some forest areas, but long-term observation of habituated groups are needed to generate robust home range data.

Our comparisons of densities from different survey methods underline the extent to which gibbon density is underestimated when using transects. This was because time of day (and the associated singing rate) has a great influence on the density estimate (estimates from line transects and “late” point counts were not different) and transects cannot be effectively surveyed as early as points during pre-dawn darkness.

We recommend that point count surveys of gibbons incorporate distance sampling where possible, which is also encouraged for primates in general [Buckland et al., 2010; Plumptre, 2000; Plumptre & Cox, 2006]. It is preferable to use distance sampling for defining the effective surveyed area rather than a fixed radius as it was clear that detectability declined significantly with distance from points. We obtained stable density estimates from points surveyed for only 3 days by incorporating uncertainty about animal detection into the method [Buckland et al., 2001]. This is possible for areas with similar calling rates, although calibrating surveys to local calling rates is required to ensure accurate density estimation. This reduction in survey effort required for established methods of surveying gibbons from points [Brockelman & Ali, 1987; Brockelman & Srikosamatara, 1993] means that site coverage can potentially be increased by 33% in the same amount

of survey time. In addition, the use of spatially explicit capture–recapture (SECR) methods may also be appropriate for surveying gibbons [L. Thomas, pers. comm., 2013]. These methods model animal capture–recapture histories of identified individuals collected from different “detectors,” for example, survey points [Borchers, 2012]. There is no constraint on the value of the detection function at zero meters, an assumption that does not always hold in conventional distance sampling [Borchers, 2012]. SECR methods make more efficient use of the data collected because not all animals are heard from all points and during each survey, or with complete distance and direction data. An assumption of distance sampling is that distances of animals from points are measured without error, and includes consistent over- or under-estimation of distances [Buckland et al., 2001]. This level of measurement accuracy is not always fulfilled: SECR models take account of distance measuring error [Borchers, 2012], which is a concern raised about the traditional approach to surveying gibbons [Rawson, 2010].

Overall, this survey demonstrates the resilience of the species to severe forest degradation and the ability of such a degraded site to support a substantial population. Given the ubiquity and high density of gibbons we recorded, there seems little doubt that degraded forest sites can make a significant contribution to the conservation of agile gibbons. Whether this is the case more generally for degraded sites in Sumatra and elsewhere in the region is unclear; generalizations in these situations are often hard to make [McConkey et al., 2012]. We assume that low hunting pressure would be a prerequisite for such densities to be possible and therefore ensuring effective implementation of wildlife protection in restoration concessions should be considered a priority.

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