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Vol. 30: 133–143, 2016
doi: 10.3354/esr00734

ENDANGERED SPECIES RESEARCH
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Published May 31

Population mapping of gibbons in Kalimantan, Indonesia: correlates of gibbon density and vegetation across the species' range

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ABSTRACT: The first comprehensive survey of gibbons (*Hylobates* spp.) across Indonesian Borneo was carried out over 3 years to (1) determine whether densities of gibbon species are correlated with vegetation characteristics, and if so, whether the same characteristics are correlated with density across all forest types; and (2) determine population densities in the survey areas and identify threats to the areas. To achieve this, a total of 8 forest blocks were surveyed, involving 53 independent survey locations and repeat surveys in 3 forest blocks. Our data show that gibbons are ubiquitous where there is forest; however, the quality of forest affects population density, forest block size affects longevity of populations, and populations are susceptible to the 'compression effect', i.e. populations occupy smaller fragments at unsustainably high densities. We show the effects of forest disturbance (logging, fire, fragmentation) on gibbon distribution and density and highlight issues for long-term conservation. We discuss the use of minimum cross-sectional area, habitat variables and presence of top foods to determine population density and to identify a threshold below which gibbons cannot persist. We discuss the conservation issues facing all Bornean gibbons, including natural hybrids (*H. muelleri* × *H. albibarbis*). The answers to these research questions will help mitigate threats to gibbons and their habitat, as well as identify key habitat for gibbon populations within and outside the protected area network.

KEY WORDS: *Hylobates* · Gibbons · Survey methods · Triangulation · Conservation · Habitat · Density

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Publisher: Inter-Research · www.int-res.com

INTRODUCTION

Studies around the world have found that primate densities are influenced by the quality of their habitat. Wildfires and logging have negatively affected the abundance of primates (Felton et al. 2003, Michalski & Peres 2005) and have resulted in lower densities of gibbons, principally because of a decrease in food availability (Johns 1985, 1987, 1988, O'Brien et al. 2003b, 2004). Furthermore, primates have been found to be less abundant near forest edges (Lehman et al. 2003). Studies have suggested that gibbons, small apes native to Southeast Asia, are able to persist in disturbed forests thanks to their dietary flexibility (Harrison et al. 2005, Cheyne 2010), but that their reproductive potential is lowered by this shift towards folivory (O'Brien et al. 2004). The density of the southern Bornean white-bearded gibbon *Hylobates albibarbis* was found to be negatively correlated with elevation in the Gunung Palung National Park, West Kalimantan, Indonesia, which coincided with fewer large trees and lower availability of gibbon food items (Marshall & Leighton 2006, Marshall 2009). Detailed data on the other gibbon species (*H. muelleri*, *H. abbotti* and *H. funereus*) are limited.

Available analyses

Three current methods for surveying gibbons and one proposed method modified from camera trap studies are available. Here we briefly discuss each of these and their applicability.

Fixed-point triangulation

For a rapid assessment of gibbon density under time and financial constraints, the triangulation method may be most appropriate (Cheyne et al. 2008, Hamard et al. 2010, Gilhooly et al. 2015). However, triangulation represents increased effort over other methods for several reasons. First, a correction factor is needed to mitigate variability-induced error issues with converting singing frequency into a density estimate. Correction factors require knowledge of group composition and singing behaviour, which is difficult to collect from unhabituated groups during short studies. Second, distance estimates are required to plot group detections (Brockelman & Srikosamatara 1993). Third, triangulation requires more than one group of researchers, allowing a larger area to be sampled in a short period. Finally, collecting detection/non-detection data from single points is straightforward and requires limited training when compared to the 3 points and subsequent training needed for triangulation. This is a labour-intensive method and requires researchers to have an understanding of the precise distance to the singing gibbons. More people are required to set up listening points at suitable distances so as to avoid re-surveying the same area.

Occupancy modelling

Neilson et al. (2013) modelled occupancy of *Hylobates pileatus* using fixed-point sampling of elevation, tree height, tree density, tree diversity and disturbance covariates along with detection of gibbons based on them singing (groups not habituated to humans). Modelling demonstrated that 83% of the sites were occupied by *H. pileatus* and that the detectability of the species varied positively with elevation. No clear relationship between habitat quality covariates and occupancy emerged. They also found some weak indication that the probability of occupancy may increase with tree diversity. Tree diversity has been found to be an important habitat requirement of gibbons (Caldecott 1980, Fan & Jiang 2008, Phoonjampa et al. 2010, Cheyne et al. 2012). Low tree-species diversity in the survey areas indicates that some inter-group resource competition may occur and that the probability of gibbon occupancy increases in areas of high tree diversity (Mitani 1985, Brockelman & Srikosamatara 1993, Nijman 2004, Fan et al. 2009).

Occupancy modelling allows researchers to sample a larger area in a short period. Collecting detection/non-detection data from single points is straightforward and requires limited training once fixed points have been designated for site visits. Moreover, no additional equipment is necessary to generate detection histories over several seasons, and modelling can provide information on the probability of detection of gibbons in different areas. However, this method does not yet have a provision for calculating the proportion of lone, non-singing gibbons in the population, so accurate density estimates are not possible.

Line transects and distance sampling

Höing et al. (2013) surveyed *H. klossi* and showed that both line-transect and distance-sampling methods may provide estimates with similar accuracy but that line transects can result in more precise esti-

Table 1. Evaluation of each survey method. Evaluation of line transects here only applies if combined with DISTANCE software methods. SECR: spatially explicit capture-recapture

	Fixed point triangulation	Occupancy modelling	Line transects	SECR
Type of data needed	Singing	Singing, sighting and sign	Sighting	Singing
No. of people required	High	Low	Low	High
Budget	Low	Low	Low	Low
Time (mo)	1	1	1	1
Good for population density estimates?	Yes	No	Yes	Possibly
Good for abundance?	Yes	Yes	No	No
Knowledge of gibbons needed?	Yes	No	Yes	Yes
Lone gibbon correction factor known?	Yes[a]	No	Yes	No

[a]Data from Cowlishaw (1996)

mates and allow assessment of other primate species if used in combination with DISTANCE analysis (http://distancesampling.org). Simply walking trails will not be an effective way to survey gibbons. The authors found no difference in the estimations of cluster (i.e. groups of singing gibbons) or individual densities using triangulation and line transect sampling and therefore assumed similar accuracy from both methods. The true number of gibbons present in the area, however, is unknown, as is the proportion of lone gibbons in the area, so individual density estimates gained by triangulation cannot be corrected for this potential bias (Cheyne et al. 2008). Both methods (line transects and triangulation) used may underestimate individual density slightly. We also do not know the levels of under-recording of lone gibbons and those close to observers.

Spatially explicit capture-recapture

Spatially explicit capture-recapture (SECR) makes use of observations at an array of detectors (traps) that may be summarised as spatial encounter histories. The primary aim of SECR is to estimate the population density of free-ranging animals (Efford et al. 2004, Efford & Dawson 2012). Animals are assumed to be distributed independently in space and to occupy home ranges.

As yet there are no case studies using this method for gibbons, but this method is consistently used in camera-trap studies where fixed points (cameras) are used to survey the density of independently distributed, home-range occupying large mammals. This method could potentially remove some of the issues with surveying gibbons in more mountainous terrain, but the modelling and analysis will require experts. For 3 of the above-described methods (triangulation, line transects and SECR), knowledge of average group size is needed for complete accuracy. The efficacy of each method is compared in Table 1.

Population estimates

Care must be taken not to extrapolate across a landscape without considering the habitat type/subtype (Cheyne et al. 2008, Hamard et al. 2010, Gilhooly et al. 2015). With this project, we sought to address the following research questions:

(1) Do densities of the Bornean gibbon species correlate with vegetation characteristics in different field sites and forest types?

(2) If so, are the same vegetation characteristics correlated with gibbon density across all forest types, or are different habitat parameters linked to gibbon density depending on the forest type?

(3) What are the estimated populations in the survey areas, the threats to the areas and the status of the forest?

We hope that the answers to these research questions will help inform Indonesia's management of protected areas in order to mitigate threats to gibbons and their habitat, as well as identify key habitat characteristics that are important to the survival of gibbon populations within and outside the protected area network.

MATERIALS AND METHODS

Study species

Following Groves (2001) and Geissmann (2007) the Bornean agile or white-bearded gibbon has been recognized as a separate species designated *Hylobates*

Table 2. Summary of gibbon species involved in this study

Scientific name	Common name	Distribution	IUCN status
Hylobates albibarbis	Bornean agile gibbon, Bornean white-bearded gibbon	Kalimantan (West and Central)	Endangered
H. muelleri	Müller's gray gibbon, southern gray gibbon	Kalimantan (South-east)	Endangered
H. funereus	Northern gray gibbon	Kalimantan (North), Sabah, Sarawak and Brunei	Endangered
H. muelleri × *H. albibarbis*	Bornean hybrid gibbon	Kalimantan (Central)	No official status but benefit from protected status of parent species

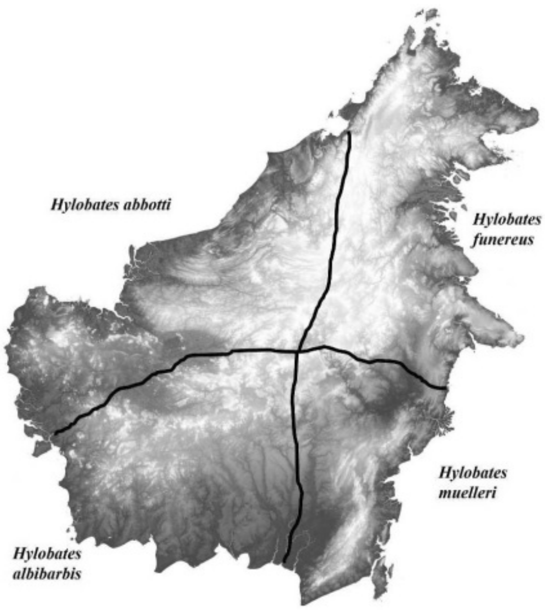

Fig. 1. Distribution of the different study species of gibbons in Kalimantan (Borneo), Indonesia. White shading indicates high elevation, dark grey shading indicates low elevation

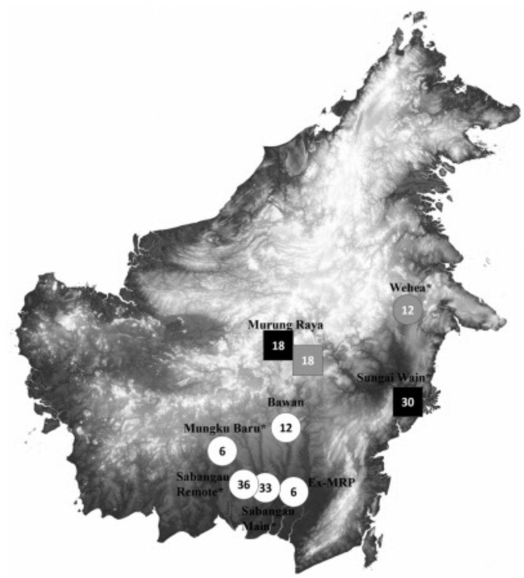

Fig. 2. Study sites in Kalimantan (Borneo), Indonesia: white circles: *Hylobates albibarbis*; black square: *H. muelleri*; grey circle: *H. funereus*; grey square: *H. muelleri* × *H. albibarbis*. Numbers within each symbol indicate the total number of listening posts established at that site, and asterisks indicate areas that have some level of protection. White shading indicates high elevation, dark grey shading indicates low elevation. Ex-MRP: Ex-Mega Rice Project

albibarbis. Also following Groves (2001) and the IUCN Species Survival Commission Primate Specialist Group Section on Small Apes, we recognize the previously described subspecies of *H. muelleri* as separate species of *H. muelleri*, *H. funereus* and *H. abbotti* as well as the unique population of viable hybrids (*H. muelleri* × *H. albibarbis*, Table 2, Fig. 1).

Study sites

The surveys were carried out at 9 sites in 8 habitats/landscapes across Central and East Kalimantan, Indonesia, and involved 171 listening posts (Fig. 2) and 57 separate locations (Table 3). Habitat sizes were obtained from GIS surveys carried out by the authors and/or from protected area maps. The study sites varied across habitat types and climate (Table 3).

Analysis of density data

Gibbon density was estimated using fixed-point counts, as described by Brockelman & Ali (1987) and following the protocol described by Buckley et al. (2006), Cheyne et al. (2008) and Hamard et al. (2010).

Table 3. Description of gibbon (*Hylobates* spp.) density survey sites (9 in 8 habitats/landscapes) including characteristics of the sites, species of gibbon surveyed, habitat type and protected status. PSF: peat swamp forest, MSF: mixed swamp forest, LIF: low interior forest, TIF: tall interior forest, NA: not available

Site	Habitat	Size (km²)	Forest status	No. of independent survey locations	GPS coordinates	Species	Elevation range (m a.s.l)	Average rainfall (mm yr⁻¹)	Temperature range (°C)	Logging status/last logged (yr)	Fire history
Bawan	Lowland dipterocarp/PSF/mosaic. Logged secondary and pristine	546	Not protected	4	1° 36' S 113° 59' E	*H. albibarbis*	10–50	2500	12–35	Current	Burnt
Mega Rice Project	PSF (ombrogenous), fragmented and degraded	1000	Not protected	2	2° 20' S 114° 1' E	*H. albibarbis*	2–20	3000	12–35	>20	Burnt
Mungku Baru	PSF (ombrogenous). Pristine and close canopy	160	Community forest	2	1° 35' S 113° 45' E	*H. albibarbis*	10–50	2500	12–35	>20	Burnt
Murung Raya	Lowland montane. Pristine and remote	500	Not protected	12	0° 17' N 114° 26' E	*H. muelleri* and *H. muelleri* × *H albibarbis*	200–1600	4000	24–35	NA	Unburnt
Sabangau main	MSF/LIF/TIF	5700	National park/conservation area	11	2° 18' S 113° 54' E	*H. albibarbis*	3–30	3000	12–35	>10	Burnt
Sabangau remote	PSF (ombrogenous). Logged	990	National park/conservation area	12	2° 30' S 113° 11' E	*H. albibarbis*	3–30	3000	12–35	>10	Burnt
Sungai Wain	PSF/lowland dipterocarp. Logged and burnt	100	Nature reserve	10	1° 05' S 116° 49' E	*H. muelleri*	50–200	3000	12–35	>20	Burnt
Wehea	Lowland montane. Pristine and remote	380	Protection forest	4	1° 35' N 116° 44' E	*H. funereus*	250–1750	3000	24–35	NA	Unburnt

These 4 studies have recommended this method for surveying gibbons for the following reasons: (1) The gibbons' inconspicuous behaviour and preference for high canopy makes the use of line transects for surveying unsuccessful (Brockelman & Ali 1987, Brockelman & Srikosamatara 1993, Nijman & Menken 2005). (2) The territorial behaviour 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). (3) 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 (Brockelman & Srikosamatara 1993, Gursky 1998, Estrada et al. 2002, 2004, Nijman 2004, Cheyne et al. 2008, Hamard et al. 2010), allowing the comparison of their results across sites. Occupancy is not the best technique for obtaining detailed population density estimates, which was the aim of these surveys, hence the use of triangulation. We recognize that the data on *H. muelleri* and *H. funereus* are limited compared to the data for *H. albibarbis* and *H. muelleri* × *H. albibarbis* and therefore, the analysis of these data may be somewhat weaker.

Data collection took place between 04:30 and 08:00 h each morning for 4 consecutive days at each survey site excluding rainy mornings and mornings on which rain had stopped less than 2 h before the planned start of data collection, as rain has been found to negatively influence the singing behaviour of gibbons (Brockelman & Ali 1987, Brockelman & Srikosamatara 1993). Groups were clustered based on singing location and time of singing to ensure that any given group singing twice in the same day was not recorded as a new group. Maps were created daily to plot all groups. This mapping allows groups to be correctly identified over several days and to determine the number of groups heard from each listening post and for each set of listening posts over the survey days. The compass bearings and estimated distances of gibbon calls were recorded from 3 listening posts situated in a triangular formation, with a distance of 300 to 600 m between posts (Fig. 3).

Due to rain, the survey period was reduced to 3 d at 3 of the survey sites, and 2 d at 1 survey site. Correction factors included in the formula to estimate density ensured that the data were comparable between all survey sites (Brockelman & Ali 1987, Brockelman & Srikosamatara 1993). Only groups for which at least 1 female great call and 1 male coda, indicating a duetting family group (Haimoff 1984), were 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 and input into a density formula yielding density estimates (D), developed by Brockelman & Ali (1987):

$$D = n / [p(m) \times E] \quad (1)$$

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

$$p(m) = 1 - [1 - p(1)]^m \quad (2)$$

where $p(1)$ is the singing probability for any given day, and m is 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 2 of the research teams could hear gibbons singing. Areas that 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.

Analysis of habitat data

Habitat characteristics were measured in plots of 10 × 10 m situated along transects around the listening posts, in the same time frame as the auditory sampling. These plots covered a total of 1000 m^2 at each set of 3 listening posts within the effective listening areas of ~3.5 km^2 representing a sample of the

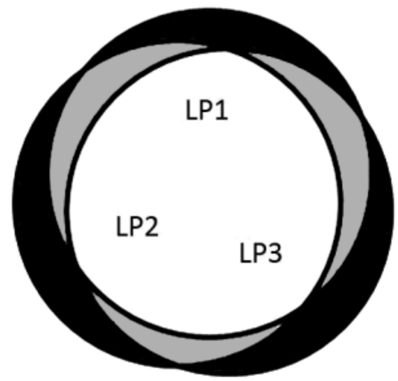

Fig. 3. Effective listening area (ELA) for all 3 listening posts (LPs). Grey areas are only audible at 2 LPs and black areas are only audible at 1 LP

available habitat. Previous studies investigating relationships between forest structure and primate densities used plots of 10 × 10 m (Rendigs et al. 2003, Blackham 2005, Hamard 2008, Gilhooly et al. 2015). Ten plots per habitat were analysed, with the exception of 5 habitats, for which 6 plots per site were analysed 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 using visual estimation by trained researchers; (4) local name of the species of all measured trees; (5) total number of trees in the plot. DBH was then converted into cross-sectional area using the formula $(DBH/2)^2 \times \pi$ and used as an indicator of tree biomass.

RESULTS

Population density

Bawan Forest has an estimated density of 7.04 groups km^{-2}, but a low population size (based on available forest for each area; Fig. 4); this density is more than double that of the next closest value (2.8 groups km^{-2} in Sungai Wain). Fig. 5 shows the average population density of each species including data from all available sites. A full list of sites used is given in Table S1 in the Supplement at www.int-res.com/articles/suppl/n030p133_supp.pdf. Only 1 site was available for *Hylobates funereus* which may

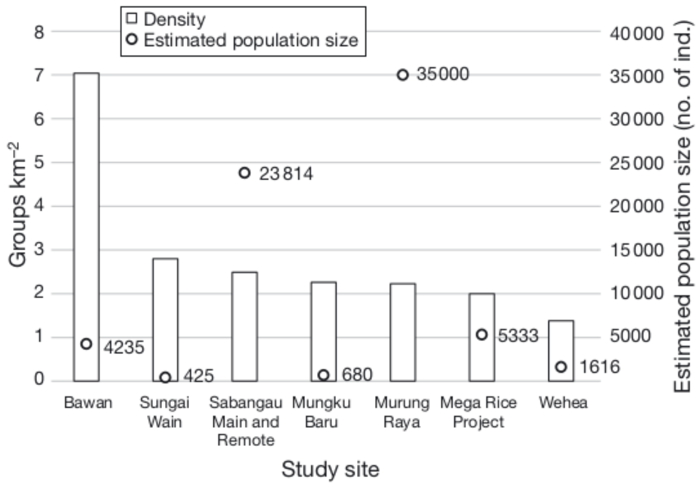

Fig. 4. Density (number of groups km^{-2}) and population size of gibbons *Hylobates* spp. at each survey site. Sites that are part of the same contiguous land scape were combined

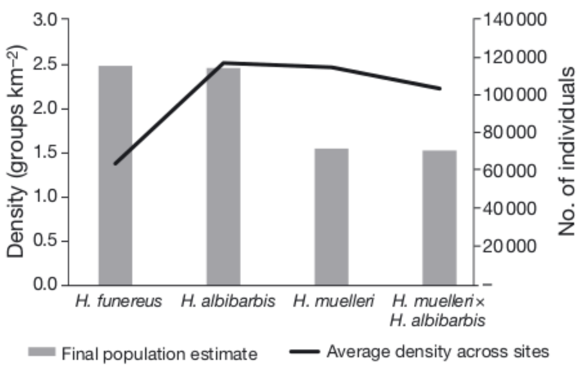

Fig. 5. Density of each gibbon species (*Hylobates* spp.) averaged across sites (see Table S1 for a full list) and population estimates for all 3 species and hybrid gibbons (*Hylobates* spp.)

contribute to the lower average density. Based on available forest (protected and non-protected) the largest populations of gibbons are represented by *H. albibarbis* and *H. m. funereus* (Fig. 5).

Habitat variables and density

All vegetation variables had a normal distribution, as did gibbon density ($Z = 0.69$, $p = 0.774$). All vegetation variables, averaged for each forest type, are presented in Table 4. Significant differences were found between forest types for all variables. Pairwise analysis revealed that Borah and Tujang had the highest canopy cover, median tree height and mean DBH. However, the vegetation in both of these areas is unevenly distributed. The most degraded forest (ex-Mega Rice Project, MRP) showed low species richness and low species diversity with a relatively even distribution.

A MANOVA with general contrasts was performed on gibbon density and habitat type with survey effort as a covariate (based on the number of independent survey locations). There were no significant differences between gibbon densities across habitat types. When data were analysed by habitat type and specific density, gibbon density was also correlated to all measured vegetation variables, except the cross-sectional area of all tree classes (Table 5).

DISCUSSION

Populations and density

Of 4 species found on Borneo, density data exist for all except *Hylobates abbotti*. Of 22 populations, the majority (17) can be considered to exist in moderate densities, being below the figure defined as high density (5–6 groups km^{-2}), but with only 5 being below the threshold (2 groups km^{-2}) used to indicate low density (Brockelman & Srikosamatara 1993). Overall, densities of gibbons in tropical peat-swamp forest (TPSF) ranged from 1 to 4 groups km^{-2}, well within the values of 0.06 to 9 groups km^{-2} reported for all gibbon species (S.M. Cheyne unpubl. data based on a survey of 67 published studies of which only 29 reported density information). Thus, TPSF would appear to be potentially important habitat for all of the region's gibbons, but particularly for *H. albibarbis*. Due to the large size of Murung Raya forest, it is likely to hold the largest population of gibbons of all sites surveyed. These figures for gibbon population size and density are only based on data from this study and should be considered in the wider context of all gibbon populations across Kalimantan. We suspect the very high density recorded in Bawan is due to a compression effect in Bawan where the gibbons are being compressed into a small area of suitable forest thereby creating an unusually high density. The forest has been affected by both logging and fire, and some of the unaffected forest is unsuitable for supporting gibbons. The long-term sustainability of this density is unknown.

Table 4. Mean ± SE vegetation characteristics for the different habitat types. Data on tree species are not available for all areas due to a lack of qualified botanists. Data from Sabangau are from Hamard et al. (2010), data from Bawan and Mungku Baru are from Harrison et al. (2010, 2012). Data from Tujang and Borah are from Cheyne et al. (2012), and data from Sungai Wain are from Gilhooly et al. (2015). DBH: diameter at breast height, CSA: cross-sectional area, MSF: mixed swamp forest; LIF: low interior forest; TIF: tall interior forest; Ex-MRP: ex-Mega Rice Project; NA: not available

Variable	Locations and forest types									
	Sabangau (MSF)	Sabangau (LIF)	Sabangau (TIF)	Sungai Wain (disturbed primary lowland)	Tujang (disturbed lowland montane)	Borah (primary lowland montane)	Ex-MRP (degraded MSF)	Bawan (mosaic)	Mungku Baru (primary mosaic)	Wehea (lowland montane)
Mean canopy cover at 20 m (%)	40.9 ± 3.8	10.0 ± 1.6	61.8 ± 3.4	73.66 ± 4.28	81.8 ± 5.7	88.8 ± 6.1	18.0 ± 1.99	59.57 ± 5.97	19.8 ± 3.9	5.72 ± 7.8
Median tree height (m)	11–15	11–15	16–20	16–20	21–25	21–25	6–11	16–20	11–15	11–15
Mean DBH (cm)	16.3 ± 0.5	16.0 ± 0.07	19.4 ± 0.9	61.84 ± 4.23	66.53 ± 5.68	86.53 ± 3.25	14.0 ± 0.11	21.7 ± 15.0	19.5 ± 0.7	22.71 ± 0.78
CSA – all trees (cm^2)	1443 ± 190	2094 ± 254	4198 ± 419	3982 ± 447	4998 ± 354	5455 ± 411	994 ± 154	779.8 ± 222	3542 ± 338	4485 ± 399
Species richness (*S*)	27.4	21	26	43	28	32	18	NA	NA	NA
Shannon-Wiener index (*H*)	3.04	2.63	2.65	3.28	2.86	3.88	1.63	NA	NA	NA
Evenness (*J*)	0.92	0.51	0.78	0.51	0.81	0.77	0.66	NA	NA	NA
Simpson's index (*C*)	0.05	0.08	0.15	0.94	0.64	0.86	0.07	NA	NA	NA

Table 5. Analysis of habitat variables. DBH: diameter at breast height; CSA: cross-sectional area, NS: not significant

Variable	Pearson correlation	Significance (2-tailed)
Mean canopy cover at 20 m (%)	0.802	0.003
Median tree height (m)	0.648	0.002
Mean DBH (cm)	0.584	0.002
CSA, all trees (cm^2)	0.248	NS

Previous studies have found that primate densities are influenced by the quality of their habitat (e.g. Hamard et al. 2010, Marshall 2010). Wildfires and logging were found to negatively affect the abundance of orangutans (Felton et al. 2003) and to result in lower densities of gibbons, principally due to a decrease in food availability (Johns 1987, 1988, Johns & Skorupa 1987, O'Brien et al. 2003a, 2004). However, gibbons were able to persist in disturbed forests due to their dietary flexibility (Harrison et al. 2005, Cheyne 2010), but their reproductive potential was lowered by the shift towards folivory (O'Brien et al. 2004). Furthermore, the density of *H. albibarbis* was negatively correlated with elevation in Gunung Palung National Park, West Kalimantan, corresponding to fewer large trees and a lower availability of gibbon food items at higher altitude (Marshall & Leighton 2006, Marshall 2009).

The Murung Raya in the central highlands of Borneo has the largest population of both hybrid gibbons and *H. muelleri* due to the vast intact forests still present in this area. However, this area is being opened up for exploration for coal and logging so its long-term future is uncertain. We believe that the very high density found in the mosaic forest (Bawan) is not natural and is a result of the gibbons being compressed into a band of forest between a burnt area and a very low productivity forest habitat (see below). While the primary forest does contain the highest densities, it is also experiencing the fewest (current) threats. These areas of primary forest need monitoring for changes in land use or threats but are currently supporting viable populations of gibbons.

The mosaic and fragmented forests are of the highest immediate priority for conservation actions, although all non-protected areas are in need of conservation. Unless the gibbons can be given access to other suitable forest, there will be a population crash. Similarly, the gibbons in fragments are isolated from other groups, so dispersal is compromised, leading to possible long-term issues with sustaining these populations. One of the keys to conserving these forests and protecting the gibbons is to provide corridors to link suitable areas of forest. There are currently no conservation actions for the natural hybrid gibbons, and they have no protection against the pet trade or habitat destruction. Recognition of these apes as a viable population (and perhaps as an important population in the understanding of species evolution), in a unique situation of natural hybridization over a restricted range in some of the most biodiverse mountain areas in Borneo, would be of great benefit to highlighting the high rates of habitat conversion in this area. The gibbons are the only ape in this area (there are no naturally occurring orangutans) and could act as a flagship species for the protection and conservation of the Kalimantan Highlands.

Habitat

Stem density was not significantly associated with gibbon density for any species or in any of the study habitats, suggesting that perhaps it is not resource availability that defines habitat quality for those species. Previous work has highlighted that the availability of most consumed gibbon foods was not a predictor of gibbon density (Hamard et al. 2010). Gibbon density was found to be highly correlated to vegetation parameters, in particular canopy cover and tree height. We do not have tree species identified at all sites nor feeding ecology data from gibbons in these habitats. Data from Sabangau suggest that in peat swamp forests, figs are not a fallback food (Cheyne 2008, 2010) as has been suggested in dryer forests (Mather 1992, Marshall & Leighton 2006). Given these differences and the lack of detailed information on gibbon diet in many forests, more work is needed on the effects of vegetation species richness, evenness and diversity on gibbon density.

Thresholds for sustaining gibbons

From this work, we have a tentative estimate of lower and upper densities which are sustainable. We recognize that without further population modelling these values are estimates only.

We agree with Brockelman & Srikosamatara (1993) and propose that habitats with a density <2 groups km^{-2} require further research and increased monitoring. Similarly, the Bawan population density of 7.04 groups km^{-2} is above the estimate for high density (5–6 groups km^{-2}) and also warrants further study, particularly for creating corridors to allow the gibbons to disperse into other forests. Thus, the ideal range for these species is 2 to 5 groups km^{-2}, but we recognize that a low density in a degraded but recovering habitat could mean a healthy population, as it could increase over the long term with an increase in habitat quality.

Conservation

This study represents the first ever survey of gibbon population densities across Kalimantan that has included all species present in the area. We estimate that 115 000 individuals of *H. albibarbis* are living in Kalimantan. Based on our recent data, this suggests that the populations of *H. muelleri* and *H. funereus* is about 190 000; thus, in order to equal Meijaard and Nijman's data, there would need to be about 100 000 individuals of *H. abbotti*. However, no recent density estimates are available for this species and no current fieldwork is being undertaken. There is a severe lack of data on gibbons in non-protected areas or small forest areas that may also contain viable populations. Current data suggest the population of *H. albibarbis* to be between 75 000 and 130 000 individuals throughout its range, of which at least 50% are found in TPSF. Populations of *H. muelleri*, *H. abbotti* and *H. funereus* combined are estimated at between 270 000 and 330 000 individuals with less than 25% found in TPSF (S. M. Cheyne unpubl. data, Table S2 in the Supplement at www.int-res.com/articles/suppl/n030p133_supp.pdf), although there are limited estimates for TPSF locations for these species. In the absence of a full population and habitat viability analysis, all survey data are vitally important to obtain accurate population estimates of all 4 species. Gibbons are able to maintain a good density across habitat types and time even in unprotected areas. Our population estimates are based on known forest sizes, predominantly forest with some level of legal protection. The numbers of gibbons living in non-protected forest is a cause for concern, as it is almost impossible to extrapolate current population numbers to these areas. It is crucial to remember that while these numbers indicate that gibbon populations are thriving, the habitat loss, wildlife trade and presence of so many populations in non-protected areas means that all gibbons in Kalimantan are still Endangered.

Gibbons occur in many forests where orangutans are absent, meaning they are the largest frugivores present for dispersing seeds and maintaining forest dynamics. The ability of wildlife to recover and adapt following human disturbance is crucial to their long-term survival, so these study sites are especially important.

Future actions

Accurate and recent population estimates for *H. abbotti* are urgently needed, as is population modelling for all of these species, especially in light of increased habitat loss due to fire. Unprotected areas of forest which may be home to large populations of gibbons need to be identified, and the protected status of currently designated protected areas needs to be maintained and strengthened.

Acknowledgements. This project would not have been possible without the collaboration of many individuals, organizations and universities. In Sabangau forest, Central Kalimantan, the study was carried out by the Orangutan Tropical Peatland (OuTrop) multi-disciplinary research project. We thank Badan Lingkungan Hidup in Purak Cahu, Murung Raya; Pak Purwanto, Pak Agusdin, Stan Lhota and Gabriella Fredriksson in Sungai Wain Protection Forest; University Mulawarman Samarinda; Dr. Suwido H. Limin at the Centre for the International Cooperation in Management of Tropical Peatlands (CIMTROP), University of Palangka Raya; the Indonesian Ministry of Science and Technology (RISTEK) and Director General of Nature Conservation (PHKA). We gratefully acknowledge the invaluable contribution of all of the researchers, staff, interns and volunteers. Funding for different stages of this work was kindly provided by the People's Trust for Endangered Species, the Rufford Small Grants for Nature Conservation, American Zoo Association Ape TAG Conservation Initiative, Le Valley des Singes, FFI (Indonesia) and Lewin Education, Singapore. This paper greatly benefitted from the comments and suggestions of the anonymous reviewers and the members of the Oxford Brookes University Primate Forum.

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Editorial responsibility: Anna Nekaris, Oxford, UK

Submitted: December 14, 2015; Accepted: March 29, 2016
Proofs received from author(s): May 17, 2016

Population mapping of gibbons in Kalimantan, Indonesia: correlates of gibbon density and vegetation across the species' range

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