

ASSESSMENT OF CENSUS TECHNIQUES FOR ESTIMATING DENSITY AND BIOMASS OF GIBBONS (PRIMATES: HYLOBATIDAE)

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ABSTRACT. – Censuses were conducted to establish densities and biomass of the Müller's gibbon *Hylobates muelleri* in two forest areas, i.e. Kayan Mentarang National Park [KMNP] and Sungai Wain Protection Forest [SWPF], East Kalimantan, Indonesia. The data were collected using three different techniques, i.e., range mapping, repeated line transects, and fixed point counts. First, range mapping within an area of 3.8 km² (KMNP) and 5.0 km² (SWPF) was executed to locate all groups and to map their ranges. Second, repeat line transects were run on permanent transects and along ridges, and data were analysed using variable distance estimates and fixed-width bands. Third, fixed point counts were executed, which make use of the frequent calling of gibbons; the locations from where gibbons were vocalising were mapped during the early morning (06.00-09.00 hrs) from listening points at summits and ridges, and densities were calculated for two sets of data based on the distance (0.7 and 1.0 km) from listening posts. Overall, density estimates in both areas were relatively similar with between 2.1 and 2.9 groups km⁻². The lowest density estimate for KMNP, obtained from the 1.0 km radius fixed-point counts (2.1±0.1 groups km⁻² or 6.9±2.2 individuals km⁻²) was some 30% lower than the highest estimate which was obtained by the line transect technique (2.9±0.2 groups km⁻² or 9.9±3.3 individuals km⁻²). The lowest density estimate for SWPF, obtained by the line transect technique (2.4±0.4 groups km⁻² or 7.9±5.8 individuals km⁻²), was up to 17% lower than the highest estimate obtained by the 0.7 km radius fixed point counts (2.7±0.1 groups km⁻² or 9.5±3.5 individuals km⁻²). The interaction between site and census technique explained a larger part of the variation in density than census technique alone. These data suggest that care must be taken when interpreting density estimates from different areas obtained by different techniques.

KEY WORDS. – Borneo, Indonesia, fixed point count, line transect, range mapping.

INTRODUCTION

Population parameters of animals such as densities and biomass, can be estimated by a large variety of techniques. Most of these techniques have been developed in temperate regions in open terrain and are often based on the estimated number of individuals divided by the sample area (e.g. Krebs, 1998). In tropical forest areas, where visibility is often severely limited and the terrain often difficult to traverse, many of the most common techniques have to be adapted as to meet these difficulties.

In tropical rain forests, the most common techniques for estimating population parameters are based on mapping the ranges of all individuals in a given area, repeat line transects, or in the case of highly vocal animals, mapping of the locations from where (certain) individuals vocalise. Here, we will compare techniques that have been used to estimate population parameters in tropical forest primates. We will illustrate this in a case-study into the densities and biomass

of Müller's gibbon in two areas in Indonesian Borneo. Müller's gibbon is endemic to the island of Borneo, and, like all gibbons, is completely arboreal and confined to closed canopy forest (Nijman, 2001b). Gibbons are territorial and live in monogamous family groups consisting typically of an adult pair and up to four offspring. Pairs regularly perform elaborate duet songs that are thought to form and maintain the pair bond and to establish and maintain the territory (Raemaekers & Raemaekers, 1985; Mitani, 1984; Leighton, 1987). The population may also contain a number of floating (sub-adult) males and females that call rarely.

Range mapping of all known primate groups in a given area is generally considered to provide the most accurate approximation of true density for rain forest primates (NRC, 1981; Skorupa, 1987). However, forest primates are difficult to map accurately. Because of the three-dimensional structure of evergreen closed canopy forests—in South-east Asia trees can reach heights of 60 m and more—arboreal primates are difficult to locate. Range mapping is, furthermore, labour

intensive, and as the ranges of many species partially overlap several groups need to be mapped in order to obtain a reliable estimate of density. It therefore is only applicable in relatively small accessible areas. The technique is furthermore not suitable for rugged or mountainous terrain, where access can only be obtained via ridges.

Although range mapping is considered more accurate, the most commonly used technique of estimating primate population density is the (repeated) line transect (NRC, 1981; Whitesides et al., 1988; Buckland et al., 1993). This technique depends on the detection of animals (or sometimes merely animal signs such as nests) on one or both sides of a survey path. Ideally, transects should be placed randomly or through a stratified random technique and should follow a straight line. In practice, however, transects often follow geographic features as crests, ridges and spurs (Blouch, 1997), or logging roads (Johns, 1985; Grieser-Johns, 1997). The technique allows accurate density estimates to be made over relative large areas and can be employed in unexplored terrain. It has been employed for survey work (Davies & Payne, 1982; Bennett & Dahaban, 1995; Nijman & van Balen, 1998; Nijman 2004a), comparative studies (Johns & Skorupa, 1987; Johnson & Overdorff, 1999), and for estimation of population parameters in areas where other methods (mark-recapture, complete counts, and home range or territory mapping) are not feasible (Green, 1978).

Line transects have been widely used for censusing all sorts of primates, including gibbons (Marsh & Wilson, 1981; Davies & Payne, 1982; Johns, 1985; Haimoff et al., 1986; Bennett & Dahaban, 1995; Blouch, 1997). However, Brockelman & Srikosamatara (1993) considered the technique not particularly suitable for this taxon. Gibbons live in small family groups which makes them difficult to detect and they can behave unpredictably when detecting humans (e.g., flee, hide, approach). Brockelman & Ali (1987) and Brockelman & Srikosamatara (1993) discussed the possibilities of estimating gibbon densities by fixed point counts making use of gibbon's great calls. Fixed point counts have the advantage of allowing density estimation over relative large areas in a short time span (O'Brien et al. 2004). Calling, however, may be greatly affected by disturbance (logging, hunting) in an unpredictable manner (Johns, 1985; Nijman, 2001 ab), and is density dependent (Brockelman & Srikosamatara, 1993; Nijman, 2004b).

METHODS

Study areas. – Data were collected in the Sungai Wain protection forest (Hutan Lindung Sungai Wain [SWPF]) in Dec. 1999-Feb. 2000 and the Kayan Mentarang National Park (Taman Nasional Kayan Mentarang [KMNP]), both situated in the province of East Kalimantan, Indonesia) in Oct.-Dec. 1996. Both field studies lasted 10 weeks. Fig. 1 depicts the location of the study areas.

Part of the Sungai Wain reserve was gazetted as a closed forest (hutan tutupan) in 1934 by the Sultan of Kutai. Since

1947, the forest received protection as a water catchment area for the oil industry in the Balikpapan region, and in 1983 it was gazetted as a protection forest (hutan lindung). In SWPF, the study site proper was in the Bugis river valley, in the surroundings of the Camp Djamaludin field station. The area consists of undulating terrain with the study conducted between c. 50 and 127 m a.s.l. SWPF covers a variety of forest types, including fresh water swamp, riverine forest, moist lowland dipterocarp forest, and dry hill dipterocarp forest. The study was conducted in the moist lowland dipterocarp forest and dry hill dipterocarp forest, with small parts in riverine forest. At present SWPF is the last remaining area covered with mature undisturbed primary rain forest in the south-eastern coastal region of East Kalimantan. In 1998, forest fires affected some half of the 100 km² large reserve, but the central core remained untouched (Fredriksson & de Kam, 1999; Fredriksson & Nijman, 2004). Some 20 introduced orang-utans are present in Sungai Wain (G.M. Fredriksson, pers. comm.); most range in the southern sections and only one individual was occasionally seen in the study area. No primatological studies have been conducted at the study site and no animals were habituated.

Located in Borneo's far interior, Kayan Mentarang was gazetted as a strict nature reserve (cagar alam) in 1980 and totals some 13,000 km². The study site proper was the Nggeng Bio river valley, in the surroundings of the Lalut Birai field station. The study site consists of rather steep hills intersected by many small streams, with the study conducted between c. 350 and 750 m a.s.l. The natural vegetation type in the area is lowland dipterocarp rain forest. The Nggeng Bio river valley has been a restricted forest (tana ulen) of the nearby village of Long Alango for at least the last 75 years. Cultivation and collection of forest products is mostly prohibited and the valley is still covered with mature, tall primary forest. Illegal hunting does occur in the park, but in the study area this is largely restricted to pigs and various

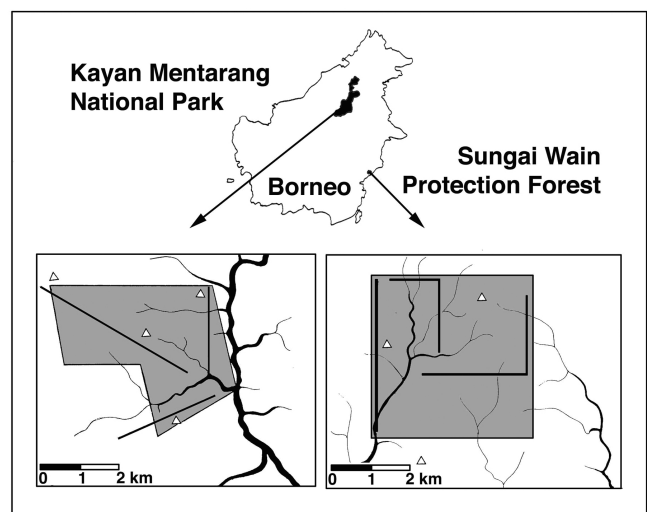


Fig. 1. The island of Borneo showing the location of the two study areas. Grey shading indicates the area in which range mapping of all gibbon groups was executed, the straight lines indicate the transects, and the triangles indicate the listening positions from which the fixed point counts were made.

species of deer. At the time of the study no zoological research had been conducted in KMNP other than a few short reconnaissance surveys (Yeager, 1991; van Balen, 1997) and no animals were habituated.

Range mapping. – In SWPF a network of transects is present, running North - South and East - West, and spaced some 500 m apart. In KMNP a number of non-overlapping permanent transects are present; these were originally laid out to monitor the phenology of the forest. In both areas, apart from the permanent transects a number of small trails allows access to the entire area. Over the 10-week study period all records of primates were geo-referenced on a map and were considered accurate to the nearest 25 m. At both study sites, apart from the senior author, a number of researchers or field assistants were present, collecting additional data. In this way we collected data on the precise locations and group sizes of gibbons within an area of 5.0 km² (SWPF) and 3.8 km² (KMNP; excluding the field station itself and its direct surroundings), disregarding additional area due to slopes (Fig. 1). Groups that were occasionally seen, but had more than an estimated three-fourths of their range outside the sample area, were omitted. Density estimates were obtained by dividing the total number of groups or the total number of individuals found by the census areas.

Repeat line transects with variable distances. – At both study sites, three transects were selected, which were between 2 and 3 km in length. Transects were mostly laid out in a straight line, but two had a 90° angle approximately halfway (Fig. 1). These transects were walked by the senior author; in KMNP occasionally a second observer was involved but all data included in the analysis are those collected by the senior author only. Data were collected in both directions, but always after a stop of at least 45 min, and always during periods of good weather. Since gibbons become less active in the afternoon (Leighton, 1987; V. Nijman, pers. observ.) only censuses that were completed prior to noon were included for analysis. An average walking speed of c. 1.5 km h⁻¹ was maintained. A total of 172.8 km during 52 days (SWPF) and 142.5 km during 40 days (KMNP) were thus covered before noon. Densities of gibbons were estimated using the effective distance method of Whitesides et al. (1988). The density of groups km⁻² is given by:

$$D = \frac{n}{A} = \frac{n}{L \times ((2 \times Ed) + S / 2)} \quad (\text{equation 1})$$

where D = density (groups km⁻²), n = number of groups seen, A = census area (in km²), L = length censused (km), Ed = Effective distance (km, estimated in m), and S = mean group spread (km, estimated in m).

The effective distance is defined as the distance on each side of the transect at which the number of sightings at greater perpendicular distances equals the number 'missed' at nearer distances (Whitesides et al., 1988). It is determined by using a histogram of estimated perpendicular distances and calculated as

$$Ed = \frac{N_t}{N_f} \times F_d \quad (\text{equation 2})$$

where N_t = total number of sightings, N_f = the number of sightings below the fall-off distance, and F_d = fall-off distance, defined as the maximum reliable distance beyond which the number of sightings is reduced by 50% or more (Brugiere & Fleury 2000). The group spread is the diameter of the circle of equivalent area to that occupied, on average, by a group of primates. Group spread proved difficult to estimate and in order not to violate the underlying assumptions of the line transect method (such as deviating from the transect line, remaining at one position for a longer period of time, and walking backwards to obtain a better view: Buckland et al., 1993; Krebs, 1998), it was considered best to obtain group spread estimates from the range mapping technique. The variance among the means of the three transects was used as a measure of error in order to estimate confidence limits.

When the density is known in groups km⁻², the density of individuals is then calculated using the mean group size, as observed along the transect lines. For estimation of mean group size, only 'complete counts' (counts that were made when there was confidence that all members of the group had been actually observed) were included. Standard errors of the mean (SE) for individual densities were calculated following Whitney & Smith, (1998):

$$SE(ID) = GD^2 \times SE(GS) + GS^2 \times SE(GD) + SE(GS) \times SE(GD) \quad (\text{equation 3})$$

Where ID = individual density (individuals km⁻²), GD = group density (groups km⁻²), and GS = mean group size.

Fixed-width transects. – Especially in inaccessible terrain, many surveys are conducted along geographical features, such as rivers or mountain ridges, or along existing trails. If the locations of transects are chosen subjectively or for the observers' convenience, the sample obtained might be only strictly representative of the area surveyed and thus cannot be extrapolated to other areas. With reference to line transect studies, Brugiere & Fleury (2000) expressed the need to explore the influence of topography on bias in density estimation. Therefore, in order to test for possible biases of censusing along ridges, spurs, and crests only, data from each transect line was converted into an encounter rate (average number of groups encountered within a fixed width of 50 m per km surveyed between 06.00 and 12.00 hrs), and compared with encounter rate for one (SWPF) and two (KMNP) trails following main ridges, also with a fixed-width of 50 m. The trails were walked over 6 and 8 days for SWPF and KMNP, respectively. Following Blouch (1997), perpendicular distances on ridges were estimated by assuming that the gibbons were on a plane with the observer's eye. Counts of group sizes were taken from the study area at large. As the additional area due to slopes was disregarded, the surface area on ridges thus effectively covers a larger area than the line transects, and therefore in the analysis a comparison is made using encounter rates and not densities.

Fixed point counts. – The density of gibbons was calculated by mapping localities from where gibbons were vocalising from three (SWPF) and four (KMNP) listening posts mostly

positioned at summits or ridges. These listening posts had a predetermined hearing angle of at least 240°. The bearing and distance of gibbons singing between 06.00 and 09.00 hrs were plotted on a map (scale 1: 17,000 [SWPF] and 1: 25,000 [KMNP]). This time window coincided with the time of greatest singing activity in Müller's gibbon in Kutai National Park as reported by Mitani (1984). In January sunrise in SWPF is at 05.20 hrs local time, and in November in KMNP at 05.00 hrs. In SWPF, but not in KMNP gibbons were observed to vocalise prior to dawn. Survey effort was 11 days in SWPF and 17 days in KMNP.

Mated female Müller's gibbons usually confine their singing behavior to duet song bouts only (Geissmann, 1995), although occasionally female solo songs do occur in Sungai Wain (V. Nijman, pers. observ.; Geissmann, 2002). The most prominent song contributions of female gibbons consist of a loud stereotyped phrase, the 'great call'. This great call includes an acceleration type climax with fast bubbling notes. Great calls may be audible over 2 km (V. Nijman, pers. observ.). Adult males do not produce great calls, but often produce solo song bouts. During duetting the male and the female combine their song contributions to produce complex but relatively stereotyped vocal interactions (Geissmann, 1995). For surveying, only songs that included a great call were used and it is assumed that this indicates a family group (cf. Leighton, 1987).

During calling, gibbons move only limited distances. Songs that map more than c. 500 m apart are considered to originate from separate groups (cf. Brockelman & Ali, 1987). Different groups calling simultaneously are distinguishable if one has knowledge of song organisation; those singing at different times can be distinguished with a combination of directional, distance information and occasionally by individual characteristics (but see Dallmann & Geissmann, 2001).

Since weather has been found to affect singing frequency in most if not all species of gibbon studied (e.g., Brockelman & Ali, 1987; Brockelman & Srikosamatara, 1993; this study), and since estimating distances is more difficult when it is raining or windy (V. Nijman, pers. observ.), censuses were only conducted during periods of suitable, i.e., still and dry, weather.

In a given population of gibbons on a given day there are also non-calling groups. The proportion of groups calling on an individual day (p) varies between gibbon species and between populations within gibbon species (Brockelman & Ali, 1987). For four (SWPF) and three (KMNP) groups, situated nearest to the field stations, the proportion of them calling between 06.00 and 09.00 hrs (p_{6-9}) was estimated by remaining within hearing distance of a focal group for a period between 5 and 14 days. Only song bouts that included great calls produced by the female were included.

The fixed point count technique requires knowledge of song organisation and is probably suitable for experienced observers only (cf. Brockelman & Srikosamatara, 1993). Therefore, in KMNP, prior to the fixed point counts, a three

week training period allowed improvement of distance estimation. In both study sites, during the line transect surveys and during non-census walks, vocal bouts were noted and their distance and bearing were estimated at different times. Using triangulation from different locations along the transect and with the aid of topographic maps it was possible to check the distance estimates and subsequently to test and improve skills.

The census area was obtained by plotting the locations of vocal bouts on a map. From this it was concluded that, taking into account the topography of the area, gibbon song bouts could accurately be recorded within a radius (r) of both 0.7 and 1.0 km. A radius of 1.0 km covers an area twice that of 0.7 km.

The density of gibbons was calculated by

$$D = \frac{n}{P_{6-9} \times A} = \frac{n}{P_{6-9} \times (\phi \times \pi \times r^2)} \quad (\text{equation 4})$$

where D = density (mated pairs km^{-2}), n = the average number of groups heard calling from the listening posts on a given day, p_{6-9} = proportion of groups calling between 06.00 and 09.00 hrs, A = the census area, ϕ = the proportion of a circle from where gibbons could be heard (between 240° and 360°), and r = radius from where gibbons could be mapped (either 0.7 or 1.0 km). The variance among the means from the listening stations allowed an estimate of confidence limits. Fixed point counts *sensu stricto* do not provide information on group sizes, and hence no estimates on the density in number of individuals can be made using this technique. Data on group sizes were obtained by combining all accurate counts of gibbon groups at other times during the study in the wide surroundings of the listening points. Standard errors of the mean for individual densities were calculated following equation (3).

Biomass estimates. – Gibbon biomass was calculated based on group densities for each of the above census techniques. Geissmann (1993) tabulated weights of wild-shot animals of different gibbon taxa on Borneo. Weights of animals from the north-eastern part of Borneo (*H. m. funereus*) do not differ significantly from those in the south-eastern part (*H. m. muelleri*) (t-test, $t = 0.42$, $df = 24$, $p > 0.50$), and data are pooled in order to provide an average weight of Müller's gibbons in east Borneo. An adult female, on average, weighs 5.25 kg (SE = 0.18, $n = 16$) and an adult male 5.57 kg (SE = 0.17, $n = 12$); weights for two sub-adult females were 3.29 kg and 4.20 kg, respectively (Geissmann, 1993: 347). Neonate weights of Müller's gibbons are some 0.40 kg (Geissmann & Orgeldinger, 1995). Few data are available on weights of an 'average' immature, but for calculation of biomass this was, arbitrarily, taken as halfway between birth weight and mature weight, viz., 2.91 kg (cf. T. Geissmann, *in litt.*).

Groups always contained an adult male and an adult female (with a combined weight set at 10.82 kg), and a varying number of immatures. Since each group contains an adult pair, variation in group sizes reflects the variation in number of immatures in a group, and standard errors of group mass

Table 1. Density and biomass estimates for Müller's gibbon, *Hylobates muelleri*, obtained by three different census techniques for two areas in East Kalimantan, Indonesia.

Site [†]	Census technique	Census area (km ²)	Density (groups.km ² ± SE)	Group size (individuals ± SE)	Density (individuals km ² ± SE)	Group mass (kg ± SE)	Biomass (kg.km ² ± SE)
KMNP	Range Mapping	3.8	2.4	3.1 (±0.3)	7.4 - 7.6	14.0 (±0.8)	33.7
	Line Transects	0.46 (8.7) ^{††}	2.9 (±0.2)	3.4 (±0.2)	9.9 (±3.3)	14.9 (±0.5)	43.2 (±40.0)
	Fixed Point Counts r = 0.7 km	5.3	2.4 (±0.1)	3.3 (±0.2)	7.9 (±2.5)	14.6 (±0.5)	35.1 (±32.6)
	Fixed Point Counts r = 1.0 km	9.7	2.1 (±0.1)	3.3 (±0.2)	6.9 (±2.2)	14.6 (±0.5)	30.7 (±31.0)
SWPF	Range Mapping	5.0	2.6	3.5 (±0.3)	9.0-9.2 ^{†††}	15.2 (±1.0)	39.5
	Line Transects	0.54 (11.6) ^{††}	2.4 (±0.4)	3.3 (±0.2)	7.9 (±5.8)	14.6 (±0.7)	35.1 (±89.4)
	Fixed Point Counts r = 0.7 km	4.1	2.7 (±0.1)	3.5 (±0.3)	9.5 (±3.5)	15.2 (±0.8)	41.0 (±31.4)
	Fixed Point Counts r = 1.0 km	8.4	2.4 (±0.3)	3.5 (±0.3)	8.4 (±5.1)	15.2 (±0.8)	36.4 (±69.5)

[†] KMNP = Kayan Mentarang National Park; SWPF = Sungai Wain Protection Forest.

^{††} The first figure represents the actual census area (defined in equation 1), the figure in brackets represents this area multiplied by the number of repeats

were calculated using the variation in number of immatures multiplied by the average weight of an immature. Standard errors of total biomass were then calculated using standard errors of both group mass and group density following equation (3).

RESULTS

A summary of the results, with estimates of densities and biomass, is presented in Table 1. First the results of the individual techniques are presented, after which a comparison is made between techniques.

Range mapping. – SWPF: within the 5.0 km² area, 13 groups were present, totalling 45 or 46 individuals (one group consisted of three or four individuals) (mean group size 3.5 ± 0.3, range 3-6). Of seven groups, small parts of their ranges might have been outside the boundaries of the study area. Of four other groups, small parts of their ranges possibly fell inside the study area (subsequently these groups were not included). The density was 2.6 groups km⁻² or 9.0-9.2 individuals km⁻². Accumulation of groups encountered over time was rapid (Fig. 2), with no new groups added after 15 days. The increase of groups after 17 days was due to enlargement of the study area.

KMNP: within the 3.8 km² area, nine groups were present, totalling 28 individuals (mean group size 3.1 ± 0.3, range 3-6). For three of the nine groups small parts of their ranges might have been outside the boundaries of the study area, whereas two groups that were not included might have had small parts of their range inside the study area. Once a single gibbon was encountered in the centre of the study area. It was not observed again, and may have been only temporarily present in the area, or may in fact be part of one of the resident groups. The density was 2.4 groups km⁻², corresponding with 7.4 individuals km⁻², or 7.6 individuals km⁻² when the single male is included. Fig. 2 shows an accumulation curve of the number of groups located over time. From this it becomes clear that within 9 days most groups were located at least once, and that no new groups were encountered after 10 days.

Repeat line transects with variable distances. – SWPF: Encounter rates varied between 0.08 and 0.20 groups km⁻¹, and tend to differ between directions within transect routes (t-test, t = 3.46, df = 2, p = 0.07). Since all transects were walked in both directions, data from both directions were pooled. Estimates of perpendicular distances did not differ significantly between transects (Kruskal-Wallis one way analysis of variance, p > 0.10) and data from all transects were used in order to estimate the effective distance. Using an effective distance and a group spread of 28.0 m and 11.0 m (SE=1.0, n = 20), respectively, this gives a density of 2.4 groups km⁻² (SE = 0.4, n = 3). Mean group size detected along the transect line was 3.3 (SE = 0.2, n = 15).

KMNP: Encounter rates varied between 0.14 and 0.21 groups km⁻¹, and did not differ between directions within transect

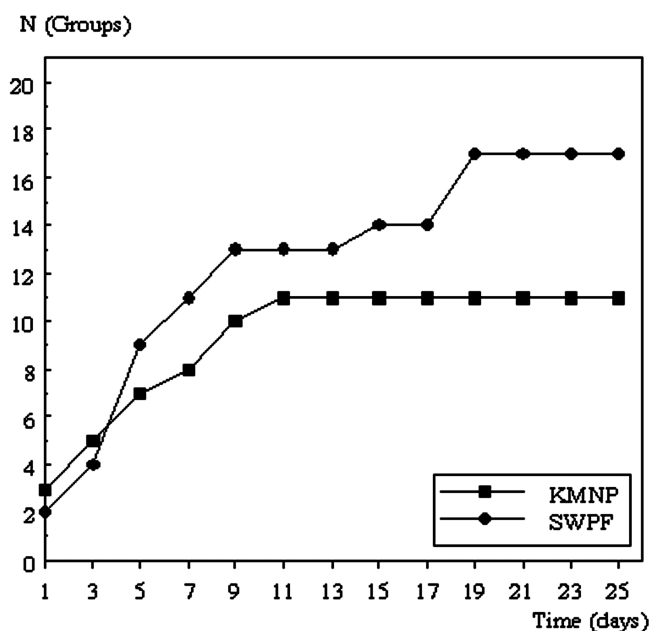


Fig. 2. Cumulative number of groups of Müller's gibbon, *Hylobates muelleri*, as observed during range mapping in Kayan Mentarang National Park (KMNP) and Sungai Wain protection forest (SWPF), East Kalimantan, Indonesia.

routes (t-test, $t = 2.0$, $df = 2$, $p = 0.18$), nor when one or two observers performed the survey (t-test, $t = 0.59$, $df = 29$, $p = 0.56$), and thus data were subsequently pooled. Estimates of perpendicular distances did not differ significantly between transects (Kruskal-Wallis one way analysis of variance, $p > 0.10$) and data from all transects were used in order to estimate the effective distance. This was estimated at 26.0 m and using a mean group spread of 9.0 m (SE = 0.9, $n = 14$), following equation (1), a density of 2.9 groups km^{-2} (SE = 0.16, $n = 3$) was reached. The mean group size of gibbons detected along the transect lines from which accurate group counts could be made was 3.4 individuals (SE = 0.18, $n = 9$).

Fixed width transects. – When calling, gibbons have a preference for tall trees on ridges and hill tops, and are proportionally more often found on ridges and hills in the early morning hours compared to other times of the day. This preference for ridge forest at times of surveying was reflected in that encounter rates were higher on ridges compared to line transects. The encounter rate along one ridge in SWPF (0.30 groups km^{-1}) was significantly higher than along any of the transects (mean encounter rate per 12 km: transects vs. ridges equals 19 vs. 36: binomial test, $p < 0.05$). Encounter rates along two ridges in KMNP (0.25 and 0.30 groups km^{-1}) were higher than along any of the transects, approaching significance (mean encounter rate per 15 km: transects vs. ridges equals 27 vs. 41: binomial test, $p = 0.06$).

Fixed point counts. – SWPF: Male gibbons in SWPF were frequently heard vocalising prior to sunrise (05.20 hrs), often commencing at c. 04.00 hrs and occasionally females joined in at these early times as well. The average proportion of days that female gibbons were calling between 06.00 and 09.00 hrs was 0.70 (four groups were monitored over 7 days). Eleven days were spent at listening posts, at least 3 days per listening post. The areas surveyed for $r = 0.7$ km and $r = 1.0$ km were 4.1 km^2 and 8.4 km^2 , respectively. Following equation (3) the average density for $r = 0.7$ equalled 2.7 groups km^{-2} (SE = 0.1, $n = 3$, range 2.5-2.9) and for $r = 1.0$ it equalled 2.4 groups km^{-2} (SE = 0.3, $n = 3$, range 1.8-2.7). Average group size of gibbons in the study site at large was 3.5 (SE = 0.28, $n = 16$).

KMNP: Gibbon songs peaked in the first few hours after sunrise (05.00 hrs) and were occasionally heard throughout the day. The proportion of days that female gibbons were calling between 06.00 and 09.00 hrs (p_{6-9}) ranged from 0.75 (one group: 9 out of 12 days) to 0.80 (two groups: 4 out of 5 days and 11 out of 14 days, respectively). For calculation of densities, each group was given the same weight and p_{6-9} was set at 0.78. A total of 17 days were spent on listening posts, at least 3 days per listening post. The census area for $r = 1.0$ equals 9.7 km^2 . Following equation (3) the density estimates obtained from the four listening posts ranged from 1.9 to 2.5 groups km^{-2} , with an average of 2.1 groups km^{-2} (SE = 0.1, $n = 4$). For $r = 0.7$ the census area equalled 5.3 km^2 . The corresponding density equalled 2.4 groups km^{-2} (SE = 0.1, $n = 4$). Combining all accurate counts of gibbons groups throughout the study area, the average group size for Müller's gibbon was estimated to be 3.3 (SE = 0.1, $n = 18$).

Comparisons of techniques. – For comparisons between techniques (repeat line transects and fixed point counts) and for calculation of technique-site-interactions, group densities were used, as individual densities were derived from these. For fixed point counts only the estimates with a radius of 0.7 km were included, as these are probably more accurate (see discussion), and estimates from fixed point counts with a radius of 0.7 km or 1.0 km are not independent.

In a two-way Analysis of Variance neither technique nor site explain a significant proportion of variance in density ($F_{1,9} = 0.08$, $p = 0.78$ and $F_{1,9} = 0.27$, $p = 0.61$, respectively) while their interaction is approaching significance ($F_{1,9} = 3.65$, $p = 0.09$). Thus, the effects of, or differences in, one variable (site, technique) depends on the levels of the other variable. It is illustrative to compare densities obtained by the two techniques as a post-hoc test: for KMNP the difference between techniques is larger than in SWPF (t-test, $t = 2.27$, $df = 4$ vs. $t = 0.87$, $df = 2$ for KMNP and SWPF, respectively). Hence, density estimates vary more in KMNP than in SWPF, with high estimates for line transects for SWPF and low estimates for fixed point counts in KMNP.

DISCUSSION

Density and Biomass. – The estimates of population parameters obtained in this study are comparable with those from various other studies conducted at undisturbed lowland sites (Rodman, 1978; Leighton, 1987; Mather, 1992; Bennett & Dahaban, 1995). Group sizes in Müller's gibbon vary little, with mean group sizes around 3.0-3.8 individuals (e.g., Leighton, 1987; Rodman, 1978), although fragmentation may lead to larger group sizes and locally larger densities, as offspring are unable to migrate out of their natal forest fragments (Oka et al., 2000). However, there seem to be a few anomalous reports on densities and/or group sizes in Müller's gibbon. First, for the primary forests of Belalong, in Brunei's Temburung district, Bennett (1994) reports a density of 5.3 groups km^{-2} , and notes that "normally monogamous, associating in groups of four to five, comprising of an adult male, an adult female and their offspring, at Belalong, a high proportion (42%) of the gibbon groups have more than one female". Bennett et al. (1987), working in primary forest in a different part of the Temburung district calculated densities of 3.3 groups km^{-2} , and made no mention of an atypical social structure. Second, Blouch (1997) estimated a density of 10.2 groups km^{-2} or 31.4 individuals km^{-2} for south Lanjak Entimau, Sarawak, an estimate at least two times that of any other forest area. Similar reports come from the adjacent Betung-Kerihun National Park (J.K. Gurmaya pers. comm. 1998). These estimates may be somewhat biased by the use of ridges and spurs for many of the transects (due to the difficult accessibility of the terrain), but densities in Lanjak-Entimau seem to be generally much higher than in other sites where gibbons have been studied to date (R.A. Blouch *in litt.* 2000). Like group density estimates, reported biomass estimates of Müller's gibbon seem to vary little among (undisturbed lowland) forest sites (Mather, 1992; Suzuki, 1992; Bennett et al., 1987; Rodman,

1988; Davies & Payne, 1982). However, comparing biomass estimates directly is complicated by the limited amount of data we have on group mass. In the present study, average group mass ranged from 14.0 to 15.2 kg, largely depending on the average number of immatures in the group. However, Rodman (1988) estimated group mass at 12 kg (mean group size 4.0 individuals; Rodman, 1978), Suzuki (1992) at 14.5 kg (mean group size 3.6 individuals), and Davies & Payne (1982) and Bennett et al., (1987) at 16 kg (mean group size 4.0 individuals).

Range mapping. – Range mapping is methodologically less demanding than either line transect walks or fixed point counts. There are few underlying assumptions, it is possible to deviate from the route to check anything uncertain and it can be done at all times of the day. Gibbons can be located by sight, hearing and even smell. Range mapping is facilitated by a number of social characteristics of gibbons: groups are relatively stable and cohesive and live in permanent territories, groups are relatively easy to recognise individually by their age and sex composition, and mated pairs sing regularly. Brockelman & Ali (1987) stated that, under favourable weather conditions, an experienced observer can roughly map the ranges of all gibbon groups within an area of 1-2 km² within a 10 day period. Precision of range mapping increases with the number of observers and the length of the study period. However, intense censusing may create too much disturbance and as a result some animals may move away from the observer to other parts of their home range. We think that within the 10-week study periods all gibbon groups present within the study area were identified with an accuracy sufficient for the aims of the study, while disturbance levels were kept low.

In small census areas, the ratio of edge to area increases, so that there is a greater chance of error per unit area in determining whether groups (or individuals) on the edges of the census area are inside or outside the boundary (Krebs, 1998). For gibbon studies, Brockelman & Ali (1987) recommended the census area to be at least five times larger than the average home-range size in order to reduce the edge effect. Home-range sizes of Müller's gibbon average 36 ha (range 33-43 ha) (Leighton, 1987). In the present study the census areas were some ten (KMNP) and 14 (SWPF) times larger than the average home range size and at least eight times larger than the largest home-range size reported. Although the study areas were large enough to contain a fair number of groups and in part had sharp boundaries (KMNP: the Bahau River; SWPF: boundary between burned and unburned forest), it is anticipated that the edge effect introduces the largest problem in establishing densities when range mapping. In both study areas groups that had small parts of their ranges outside the boundaries of the study area (and thus were included) were more numerous than those with small parts inside the boundaries (and hence were excluded). This difference may reflect a preference for including a group rather than excluding it.

Repeat line transects. – Line transects proved to be an effective method for estimating population densities. While

conducting line transect censuses, problems can arise when collecting data on group size and group spread. Gibbons live in tightly clustered groups that are dispersed over rather small distances (a small group spread), and the chance of detecting all individuals in a group is large. Problems with grouping, as elucidated by Brockelman & Ali (1987), are less apparent in gibbons than in most other primates on Borneo. For east African forest primates, Plumptre (2000) showed that group spread varies between different times of the day and between months, and recommended that survey techniques that used group spread not to be used. Yet, Fashing & Cords (2000) also working with east African forest primates, concluded that Whitesides et al.'s (1988) method, which incorporates species-specific group spread for estimating transect width (equation 1), provide the most accurate density estimates. We feel that variation in group spread in the present study introduced less of a problem compared to Plumptre's (2000) study. Gibbons live in tightly clustered groups, the line transect censuses were conducted in the mornings only, and seasonal variation in group spread in Müller's gibbons is expected to be generally small and unimportant given the short duration of the present study.

It has been suggested that for gibbons, since at least some groups escape observation, line transects will tend to systematically under-estimate true densities (Marsh & Wilson, 1981). We are confident that relatively few groups were missed during transect walks as sighting angles >90° (reflecting groups that were initially 'missed') were uncommon (KMNP: 4% and SWPF: 6% of groups within the effective sighting distance). Density estimates from line transects in KMNP were just higher than from the other two methods, whereas in SWPF it was in line with estimates from the fixed point count. Hence, there is no indication that the line transect technique systematically under-estimates density.

Estimation of sighting distances and/or perpendicular distances inevitably introduces error in calculation of the census area. Mitani et al. (2000) found that inter-observer variability in estimating sighting distances might be high. Measuring perpendicular distances might reduce this error to some degree, but we feel that given that gibbons live at great heights (e.g. the average height of Müller's gibbons upon encounter in KMNP was 25.4 m, range 10-52 m, n=14) and the observer has to measure the projection of the gibbon's location at ground level, in practise, the error will be reduced little. Since in the present study only one observer estimated perpendicular distances, inter-observer variability is absent, but distances could have been systematically over- or underestimated.

Fixed-width transects. – Steep slopes may introduce problems in estimation of perpendicular distances. Following Blouch (1997), we estimated perpendicular distances assuming that the animals were on a plane with the observer's eye. In hilly terrain this will lead the area censused to be larger than the effective strip width indicates, and will create an over-estimation of true densities. In the present study a comparison was made between encounter rates at permanent line transects, and trails following ridges. In both areas,

encounter rates from the ridges were 25-60% higher than from the transect lines. In hilly areas, gibbons use ridges disproportionately for singing and also spent incommensurate more time on ridges than in valleys (SWPF: V. Nijman, unpubl. data; Whitten, 1982) or along rivers (KMNP: Nijman, unpubl. data). Preference for ridges is more pronounced in the morning than in the afternoon (Whitten, 1982), coinciding with the period most researchers conduct their transect walks. The probability of seeing primates is, furthermore, greater from ridge vantage points as the observer looks down across the top of the forest canopy or horizontally through the tops of crowns. It is easier to spot primates from a ridge than from line transects that largely run underneath the canopy where visibility in an upward direction is obscured. Hence, positioning of transect routes along ridges is therefore not recommended as it introduces a bias and will lead to an over-estimation of true densities.

Fixed point counts. – Density estimation by means of fixed point counts was the most time-efficient technique, and covered the largest survey area. The largest source of error is estimation of the distance between the observer and the location from where gibbons are calling. Accuracy decreases with increasing distance (Brockelman & Srikosamatar, 1993) and the error introduced in estimating density increases with increasing distance (Buckland et al., 1993). In the forest, calls can carry as far as 2 to 3 km and estimation of distance for calls given at the farther end of the range are inevitably inaccurate (V. Nijman, unpubl. data). More distant groups, when calling simultaneously, can be recorded as one calling group. This may lead to underestimation of true densities. Again the error arising increases with increasing distance. As air heats up in the morning groups become harder to locate (D.J. Chivers *in* Duckworth et al., 1995), and thus accuracy of density estimation is greatest in the early morning. Calls carry poorly through vegetation and can best be heard from high vantage points, away from noisy rivers.

By censusing in the early hours of the day and by taking the topography of the area into account bearings and distances can be estimated with more accuracy, whereas by limiting the analysis to the nearest calls only, inaccuracies in density estimation can be reduced. Censusing at times of low activity will lead to under-estimating densities (Buckland et al., 1993). There are inherent difficulties in calculating the proportion of groups calling on a particular morning. This proportion varies with species, populations, and season (Brockelman & Ali, 1987). Both study sites are situated near the equator and compared to other parts of the gibbon's range, seasonal variation is relatively small. The studies were furthermore short in duration making it unlikely that seasonal variation in the proportion of groups calling on an individual morning introduced a source of error. Calling frequency can be altered under the influence of various kinds of habitat disruption, such as sounds of chain saws, logging, or hunting (Johns, 1985, 1986; Nijman, 2001ab). Both SWPF and KMNP are relatively secure from logging and hunting and it is unlikely that during the two study periods levels of disturbance substantially changed.

Gibbons appear to have consistent individual differences in their call, and with practise, neighbouring groups can be distinguished in the field (Dallmann & Geissmann, 2001). Most studies that used fixed point counts did not distinguish between individual groups (or at least did not reported that they did), but Geissmann & Nijman (in press) demonstrated that density estimation can be more accurate when these individual differences are taken into account.

Comparison between techniques and recommendations. –

The variation in density estimates as obtained by the different techniques compares well with similar primatological studies (Green, 1978; Whitesides et al., 1988; Defler & Pintor, 1985; Mitani et al., 2000; Fashings & Cords, 2000; Brugiere & Fleury 2000). Nevertheless, we feel there is considerable variation in density estimates among the three different census techniques. For group densities, the lowest estimate was 28% (KMNP) and 11% (SWPF) lower than the highest; for individual densities these figures were 30% and 17%, respectively. In comparing temporal changes of gibbon populations or in comparing habitats with different degrees of disturbance, changes in the order of 10 to 30 % can be quite significant. Methodology did not explain a statistical significant proportion of the variance in density estimation, nor did site. The interaction between site and technique explained the greatest proportion of variation, albeit not significant. The site-technique interaction is probably best explained by taking into account the differences of topography between KMNP and SWPF, and diel habitat preferences of gibbons in relation to time of surveying. More rugged topography with transects proportionally including more ridge might lead to a positive bias in density estimation for transects (as gibbons prefer ridges above flat parts during the early hours of the day) and a negative bias in fixed point counts (if there are indeed more listening shadows behind ridges).

There are few other studies that have used different methodologies to estimate gibbon densities in one area, but data from different studies conducted in the Kutai National Park (Table 2) do allow a comparison with the present study. The studies by Rodman (1978), Mitani (1984), Chivers (1984), Leighton (1987), Robbins et al. (1991) and Suzuki (1992) were all conducted on the roughly the same research site, were collected during the same general period (between 1973 and 1985), and were based on range mapping of several gibbon groups. Yet reported group density estimates vary by 32% and individual density estimates by as much as 37%. These differences may be due to differences in methodology employed by the researchers, differences in the precise location where the animals were surveyed, or may indicate temporal changes in densities. Interestingly, the three studies by Chivers (1984), Leighton (1987), Robbins et al. (1991) all seem to refer to the same data set, yet reported densities differ 0.5 groups km⁻², or almost 20%. In Suzuki's (1992) study, the low densities may be due to deterioration of the available habitat (as a result of forest fires associated with the 1982-1983 El Niño Southern Oscillation (ENSO) Event). The line transect studies by Wilson & Wilson (1975) in Kutai National Park generally provide much lower estimates.

Table 2. Density estimates of Müller's gibbon, *Hylobates muelleri*, in Kutai National Park, East Kalimantan, Indonesia.

Site	Year	Method*	Density		Reference
			groups km ⁻²	individuals km ⁻²	
Sangata River, Lindburg's site**	1973	LT	1.4	4.1	Wilson & Wilson, 1975
Sangata River, Mentoko	1970-1975	RM	3.6	14.6	Rodman, 1978
Sangata River, Mentoko	1977-1979	RM	3.2	-	Chivers, 1984
Sangata River, Mentoko	1977-1979	RM	3.0	10.2	Leighton, 1987
Sangata River, Mentoko	1977-1979	RM	2.7	9.4	Robbins et al., 1991
Sangata River, Mentoko	1982	-	-	c. 10	Mitani 1984
Sangata River, Mentoko	1985-1989	RM	2.5	9.0	Suzuki, 1994

* RM = range mapping; LT = line transect surveys

** Lindburg's site is situated 12 km east of Mentoko.

Like in many other studies the 'true density' or 'actual density' in KMNP and SWPF is not known. Range mapping probably approaches the true density best, but as the decision of what to do with groups ranging on the boundary of the study area can, by definition, only be resolved arbitrarily, we chose to compare techniques only relative to each other. The different estimates may reflect differences in methodologies, but may also reflect non-homogeneous densities. Although the three techniques were employed in the same general area, the actual area sampled did differ in size and partially in location. For both study areas the smallest area was sampled by the line transects, and this area was completely included in the range mapping area. The largest area was sampled during the fixed point counts. For this method hill tops and ridges were chosen, and since gibbons tend to have a preference for ridges this may introduce a bias. If gibbons are not distributed evenly, estimates at different spatial scales are expected to differ. This will be in part related to the differences that exist in crude density, i.e., the density in the study area as a whole, and ecological density, i.e., density in the habitat types actually occupied. The greater variation in micro-habitats present in KMNP and its greater altitudinal range than SWPF may account for the larger variation in density estimates in KMNP.

The results of this study indicate that the interaction between site and technique explains the greatest proportion of the recorded variation and that different census techniques employed by the same observer can explain some 10 to 30% of the variation in density estimates. In our view, this result seriously questions the validity of directly comparing estimates obtained by different techniques from different areas often collected by different observers. Yet, this is precisely how comparisons (between densities and any other parameter) are done. The large variation reported from Kutai National Park (Table 2) and that in inter-observer variability in estimation of sighting distances, as reported by Mitani et al. (2000), clearly adds and subscribes to our viewpoint.

Despite all problems, biases and pitfalls, we need data on densities and derived parameters (e.g., biomass) and primates and other animals need to be censused. It thus seems useful to make a few comments on what can be done, even if it is by default only. For all techniques, it accounts that rapid surveys may be a good way to obtain an indication of density

(low, moderate, high), but that for accurate estimates to be made sufficient time in the field is needed. In hilly terrain fixed point counts are by far the best applicable technique. However, for gibbons spending several days per listening post seems advisable and knowledge of song organisation and prior training in distance estimation is required. Line transects are possibly best employed when the study is aimed not only at gibbons but other wildlife as well. Transects should be of sufficient length (>2km) and the start of the transects should be sited randomly or through a stratified random technique (and hence not follow ridges or other geographical features). Range mapping, by default, seems only applicable in areas that are highly accessible; if the method is employed to obtain density estimates, the census area needs to be relatively large (including the ranges of several groups).

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