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Status of Western Hoolock Gibbon (*Hoolock hoolock*) Populations in Fragmented Forests of Eastern Assam

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Abstract: A survey was carried out at 14 sites to investigate how forest fragmentation affects populations of the Endangered western hoolock gibbon. Encounter rates were used as an index of gibbon population densities, and gibbon group size and age class ratios as an index of the status of the population. The 28-day survey was carried out in May and June 2002 in the Doomdooma, Dibrugarh, Digboi and Tinsukia Forest Divisions of Upper Assam. Sites comprised 11 forest fragments in two size classes (small <5 km² and medium 20–30 km²) and three large forest-tracts (>100 km²) that served as controls. Two survey teams, each of three to five people, sampled each site over two days, walking between 6–21 km/site. Encounter rates for gibbon groups were lowest (0.09/km) in the small forest fragments, increasing as the forest size increased (0.23/km in 20–30 km² forest fragments and 0.58/km in the controls). Similar trends were recorded with group sizes. The smallest groups (mean 2.5, n = 2) were in the small fragments. Larger groups were found in the mid-size fragments (mean 3.29, n = 24) and the three large forest-tracts (mean 3.9, n = 28). Although infant-to-female ratios were similar among size classes, the total young (infant and juvenile)-to-female ratio was as low as 0.5 in the <5 km² size class forests. The ratios were higher in the 20–30 km² and 100 km² size classes; 1.28 and 1.46, respectively. Ways that forest fragmentation affects hoolock gibbons are discussed.

Key Words: Assam, forest fragments, western hoolock gibbon, *Hoolock hoolock*, population estimates

Introduction

The western hoolock gibbon (*Hoolock hoolock*) occurs in the western-most extreme of the distribution of the 16 gibbon species currently recognized (Geissmann 2007). Its range between the Brahmaputra and Chindwin rivers takes in three countries; Bangladesh, India and Myanmar. Preliminary surveys in Myanmar indicate that it occurs at least as far south as Rakhine Yoma in south-west Myanmar (Geissmann *et al.* 2008). It has been on the list of the World's 25 Most Endangered Primates since 2006 (Walker *et al.* 2007), with the global population estimated to be about 5,000 animals: 2600 to 4450 in India (Molur *et al.* 2005; Choudhury 2006), and about 200 in Bangladesh (Molur *et al.* 2005). The Myanmar population although not well known might be significant, but further surveys are needed there. Most populations of the western hoolock are isolated and small, with 80% of those assessed in India and Bangladesh harbouring fewer than 20 individuals, and over half having fewer than 10 (Walker *et al.* 2007).

The decline of the hoolock gibbon has been caused by the destruction, degradation and fragmentation of its forests for settled and shifting agriculture, plantations, logging, fuel-wood collection, and development projects such as mining, roads, and railways. Poaching of wildlife, including gibbons, for food and trade is common among the hill tribes of north-east India (Srivastava 1999; Choudhury 2006) leading to empty forests even where the habitat might be intact.

This survey was part of a longer study by the first author (Kakati 2004) to investigate the effects of forest fragmentation on the hoolock gibbon. It is recognized that the fragmentation of large, contiguous and undisturbed forests into small patches is one of the most serious threats to biodiversity. The effects of isolation into small forest patches are compounded by certain highly specialized gibbon life-history characteristics, notably frugivory, arboreality, territoriality and monogamy. The specific objective of our 14-site survey was to compare encounter rates, group sizes and age-sex ratios of western hoolock gibbon in lowland forest fragments with those in large, relatively undisturbed forest.

Study Area

We conducted the survey in lowland tropical evergreen and semi-evergreen forest fragments and continuous forest in the Digboi, Doomdooma, Dibrugarh and Tinsukia Forest Divisions of eastern Assam, north-east India, within a 40-km radius of the oil town of Digboi (Fig. 1). The original vegetation of these fragments was Assam Valley Tropical Wet Evergreen Forest (category 1B/C1) (Champion and Seth 1968), also called the Upper Assam *Dipterocarpus-Mesua* forest. The forest reserves have old mixed plantations with a number of deciduous species. Soil type is old alluvium of the Brahmaputra and Dehing rivers. The topography is flat *kurkani*, characterized by earthen mounds and dissected by seasonal streams in the Doomdooma and Tinsukia Forest Division reserves. Altitude ranges from 122 m to 475 m above sea level. The climate is tropical monsoonal characterized by high humidity and rainfall (2,226–2,372 mm). The monsoons last from June to September; July is the month of heaviest rainfall. There is a relatively dry period from November to February. Average temperature ranges from 6°C to 38°C. There are from 119 to 164 rainy days/year (Das 1965; Chand 1990; Choudhury 1995). Sympatric primates at the survey sites include the Assamese macaque (*Macaca assamensis*), northern pig-tailed macaque (*Macaca leonina*), rhesus macaque (*Macaca mulatta*), capped langur (*Trachypithecus pileatus*), and Bengal slow loris (*Nycticebus bengalensis*).

We selected the 14 forest reserves on the basis of size and similarity of habitat and topography (see Table 3 in

'Results'). They were categorized as small (<5 km²), medium (20–30 km²) and large (>100 km²). The reserves were in matrices of tea-plantations, paddy cultivation and villages. All were within the geographical coordinates given in Table 1.

Table 1. Geographic coordinates circumscribing the survey sites.

	Latitude (N)	Longitude (E)
North	27° 45' 26.4	95° 44' 41.8
South	27° 09' 23.0	95° 27' 03.8
West	27° 24' 32.0	95° 21' 01.7
East	27° 21' 43.3	96° 00' 50.3

Table 2. Characteristics used to classify hoolock gibbons into different age and sex classes.

Age Category	Sex	Distinguishing characteristic(s)
Adult (8 years+)	Male	Black coat, scrotum prominent, usually scowling expression
	Female	Light brown/blonde coat
Sub adult (6–8 years)	Male	Black coat, slightly smaller than adult male, scrotum distinct, facial expression gentler
	Female	Coat colour lightening from black to brown, smaller than adult female
Juvenile (2–6 years)	Male	Black coat, size small, small scrotal sac seen if inspected carefully
	Female	Black coat, size small, no scrotum
Infant (0–2 years)	Male & female	Carried by adult female. White to light grey coat colour (<1 year), dark grey or black (1–2 year old). Cannot determine sex in the field.

Table 3. Encounter rates for western hoolock gibbon, *Hoolock hoolock* (63 encounters of 59 different groups) at each site and in each forest size class.

Site (RF)	Size (km ²)	At Each Site			In Each Size Class		
		No. of encounters	Distance walked (km)	Encounter rate (per km)	No. of encounters	Distance walked (km)	Av. encounter rate (per km)
Forest size class <5 km² (n = 4)							
Phillobari	3.17	0	6.25	0.00	3	32.47	0.09
Nalani	3.74	0	6.05	0.00			
Tokowani	5.02	1	11.27	0.09			
Borajan	5.05	2	8.91	0.22			
Forest size 20–30 km² (n = 7)							
Tarani	20.4	1	16.05	0.06	28	123.34	0.23
Buridihing	22.95	8	20.81	0.38			
Kumsang	22.52	3	16.38	0.18			
Kakojan	23.47	9	15.2	0.59			
Doomdooma	28.81	4	16.12	0.25			
Tinkopani	30.34	0	20.39	0			
Dirok	30.42	3	18.4	0.16			
Forest size >100 km² (n = 3)							
Dehing East	129.00	16	17.85	0.90	32	55.13	0.58
Dehing West	280.00	6	21.06	0.28			
Jeypore	108.00	10	16.24	0.62			
All sites (n = 14)							
	712.90	63	210.97				

Methods

The 28-day survey was carried out in the months of May and June 2002 by two survey teams, each of 3–5 people. Observations in the previous year had shown that both fragment and large forest groups call on a similar number of days during the rainy season of fruit abundance, while there is variation in calling rates during the drier winter season (Kakati 2004). The survey was thus conducted in the rainy season to avoid this possible source of bias in the detection of groups through calls. Each team comprised the team leader, 1–2 field assistants and 1–2 forest guards. All observations were recorded by the team leaders. We sexed and classified all hoolock gibbons seen into one of four age classes (adult, sub-adult, juvenile or young) based on body size and coat color (Table 2). With interbirth intervals being 2–3 years, a group can have two juveniles of different ages (*c.* 2–4 years and *c.* 4–6 years) differing slightly in size. We included both in a single category (juvenile), however, because of the difficulty in accurately differentiating between the two during a brief sighting.

We conducted 54 census walks covering 211 km across 14 sites. Each of the 14 sites was sampled over two days, with four walks/site (except in the Kumsang and Phillobari Reserve Forests [RF], where we did only three). We used existing foot-trails or elephant-trails when possible, and roads were avoided as far as practicable. We used 24 forest roads in whole or part during 34 out of 54 walks. Of these, four had daily vehicular traffic, six were occasionally used and 14 were either unfit

for road traffic or had been abandoned. We covered between six and 21 km/site at an average speed of 1.3 km/hour. We walked shorter distances (*c.* 8 km) in the smallest fragments because of their small sizes compared to the larger fragments and the large forests (*c.* 17 km)/site. The surveys were begun at 05:05–07:55 and ended between 07:00 and 12:45. They were completed in 199 min on average (range: 50–352 min).

We located gibbons by seeing them from the trail ($n = 26$) or by homing in on calls ($n = 37$). We tried to locate all calling groups when their distance from the trail was estimated to be less than 500 m. Groups usually call for about 15 minutes; sufficient time to find them, although not all were located. Nine of the 37 calling groups were located at >500 m from the trail. The mean sighting distance from the trail for the groups we saw was $45.16 \text{ SE} \pm 5.3 \text{ m}$ (range 5–110 m, $n = 26$) (Fig. 2a). The average distance over which calls were heard and which led to their subsequent location was $336 \text{ SE} \pm 35.2 \text{ m}$ (range 68–905 m, $n = 37$) (Fig. 2b). We also recorded the time and angle from the trail, and distance was noted as <500 m (very loud), 500–1,000 m (clear), >1,000 m (faint), and >2000 m (very faint) for all groups heard calling but not located (tracked down) during the walks. The GPS Trackmaker Version 11.7 software (Ferreira 2002) was used to plot this information on maps and to carry out spatial analyses of the survey data.

A minimum estimate of groups heard calling in each reserve was arrived at by deducting from the total count of calls heard, the following categories of calls: (a) calls of groups sighted after homing in on their calls, (b) calls of groups possibly outside the reserve boundary, and (c) all possible repeat

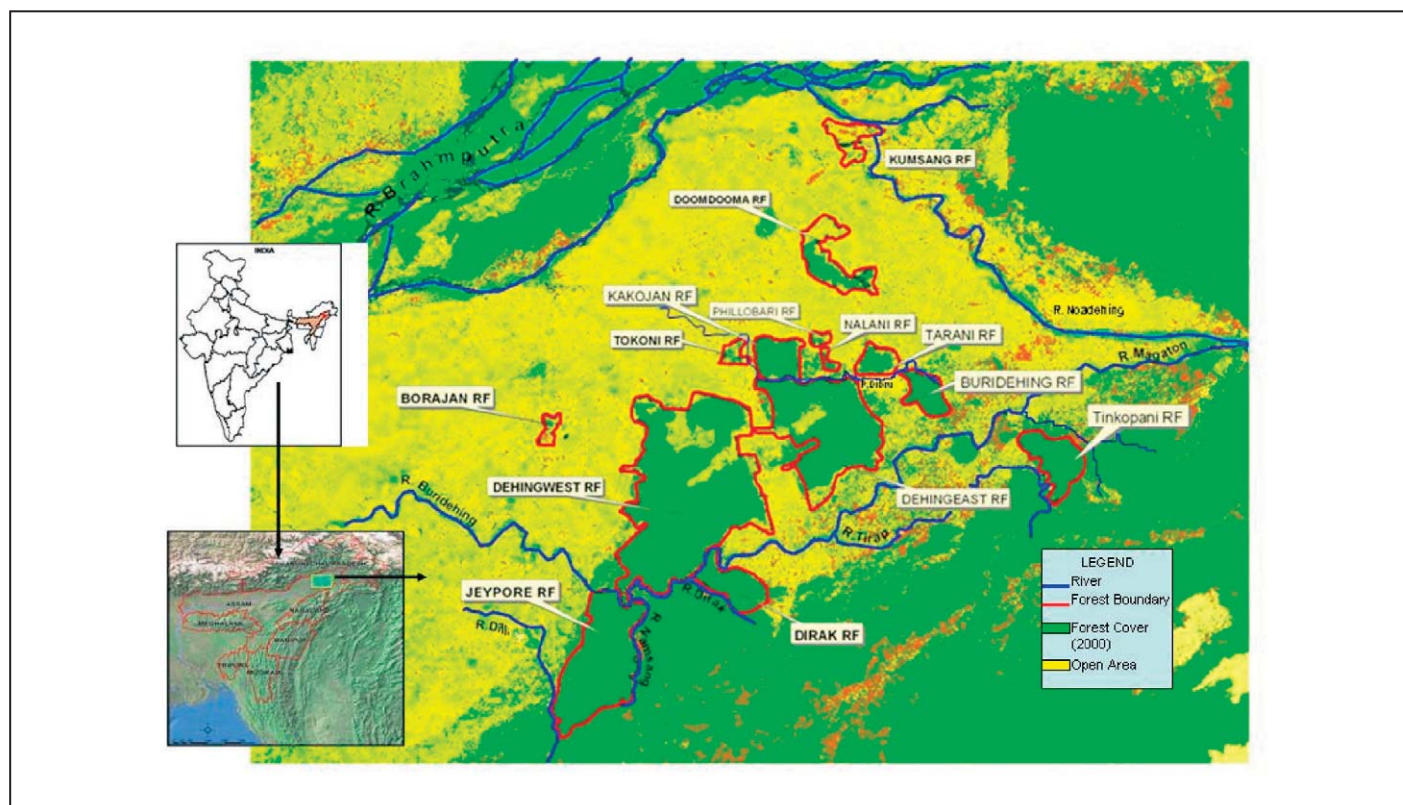


Figure 1. Satellite image (2000) of eastern Assam showing the forest patches surveyed for western hoolock gibbons, *Hoolock hoolock*.

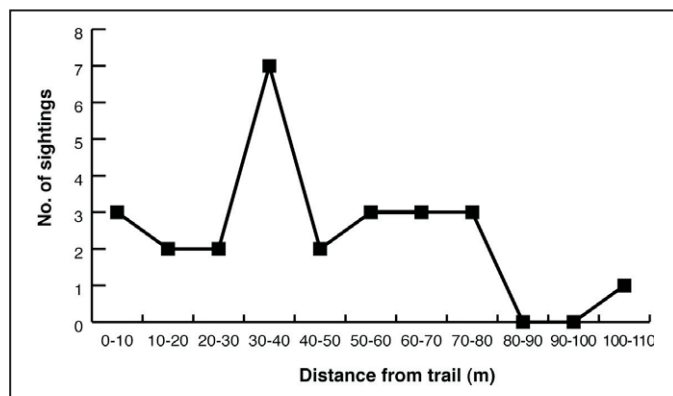


Figure 2a. Detection distance from trail for gibbon groups that were directly sighted from the trail (n=26).

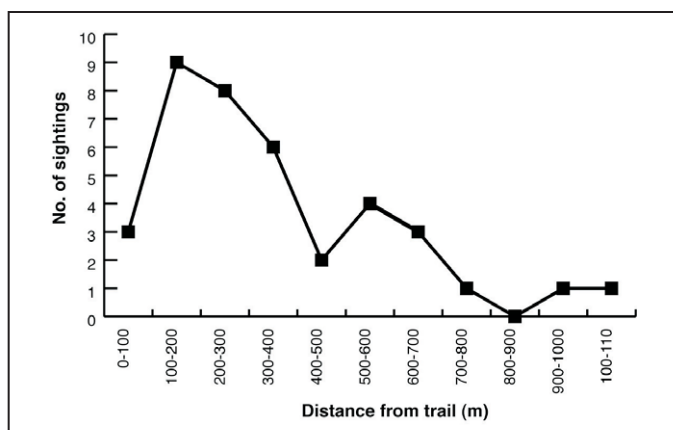


Figure 2b. Detection distance from trail of gibbon groups located by homing in on their calls (n=37).

calls (likely to have originated near the point where a group was encountered or likely to have originated from near where another call had been pin-pointed previously).

Survey of India maps and Assam Forest Department maps of the reserves were used for reference. All routes walked and the locations of all gibbon groups sighted (n=63) were recorded with a hand-held Garmin 12 Global Positioning Systems (GPS) and mapped with the software GPS Trackmaker (Ferreira 2002).

Waypoints along the route were marked on the GPS units at distances of every 140 m on average (n = 1495). We assessed tree-cover in a roughly 20-m-radius at each waypoint, scoring it on a broad scale of four categories: Open—no trees, scrub with ferns, weeds or bamboo; Low—scattered trees, crown of nearest tree to observer not connected to another tree or to only one other tree crown at most; Medium—middle-storey trees, and crown of nearest tree to observer connected to crowns of two or more trees; Good—three-tiered forest with large emergent trees and dense middle storey, and crown of nearest tree to observer connected to other crowns on all sides. The medium and good cover categories were combined for analysis since both classes represented adequate canopy continuity for gibbon movement. Forest cover change at all the sites was analysed from satellite images of the years 1990 and 2000 using the ERDAS Imagine (5th edition, 1999) software.

We used the SPSS 11.0 for Windows software for statistical analysis. Spearman's Rank correlation test was used to test for the relationship between fragment size class and encounter rates. The Kruskal-Wallis One-Way Anova and

Table 4. Western hoolock gibbon, *Hoolock hoolock*, group sizes (n = 54 complete group counts) at each site and in each forest size class.

Site (RF)	At Each Site		In Each Forest Size Class		
	Av. group size	Range	No. of different groups	No. of groups Full counts	Av. group size
					(n=54)
Fragment size class <5 km² (n=4)					
Phillobari	0		2	2	2.5*
Nalani	0				
Tokowani	1.00				
Borajan	4.00				
Fragment size class 20–30 km² (n=7)					
Tarani	3.00		26	24	3.29 ± 0.22
Buridihing	3.42	2–5			
Kumsang	3.00				
Kakojan	3.44	1–4			
Doomdooma	4.00	3–5			
Tinkopani	0				
Dirok	1.50	1–2			
Fragment size class >100 km² (n=3)					
Upper Dehing East	4.14	3–5	31	28	3.96 ± 0.13
Upper Dehing West	3.80	3–4			
Jeypore	3.77	2–5			

*Standard error on this value was not calculated because the number of groups in the sample was inadequate.

Mann-Whitney U test were used to examine differences in encounter rate and group size among the three forest size classes. Means are reported with standard errors.

Results

Encounter rates

Hoolock gibbons were seen in 11 of the 14 reserves surveyed. Two of the three reserves where no gibbons were seen were small, and the third was a medium-sized fragment where just two groups were heard calling during our survey, and we suspect that poaching has wiped out most of the gibbons here.

The encounter rate was significantly correlated with forest size class (Spearman's $r_s = 0.69$, $p = 0.006$, $n = 14$), being lowest in the small fragment size class at 9 groups/100km, intermediate in the medium fragment size class with 23 groups/100km, and highest in the large forest size class ($>100\text{km}^2$) at 58 groups/100km (Table 3). The encounter rates were significantly higher in the large forests than in the small fragments (Mann-Whitney U = 0.00, $Z = -2.14$, $p = 0.032$, $n = 7$).

Group sizes

Group sizes differed among the three forest size classes (Kruskal-Wallis one-way ANOVA, $\chi^2 = 6.67$, $df = 2$, $p = 0.036$, $n = 54$). The smallest mean group size (2.5, $n = 2$) was in the smallest forests, intermediate group sizes (3.29 ± 0.22 , $n = 24$) were in the medium-sized forests, and the largest groups (3.9 ± 0.13 , $n = 28$) were in the largest forests (Table 4). The difference was significant between the medium and large forest size classes (Mann-Whitney U, $Z = -2.416$, $p = 0.016$, $n = 52$). The groups in the small forest fragments were smaller than the large forest groups by more than one individual/group—a potentially important discrepancy for a species with naturally small group sizes (mean 3.8, range 2–5, $n = 6$ [Kakati 2004]) and a long period (6–8 years) to maturity. The composition of each of the 59 groups seen are given in Table 5.

Age and sex ratios

Hoolock gibbon groups in the small fragment size class had the lowest numbers of immature animals (infant, juvenile and sub-adult)-to-adult animals ratio, i.e., only 0.66 immature/adult, whereas in the large forest size class, there were 0.98 immature/adult. The infant-to-adult female ratios were similar among the three forest size classes (Table 6). There were no juveniles in the small fragments surveyed. We combined the juvenile and infant categories into 'young' and re-calculated the young-to-adult female ratio. There was 0.5 young/adult female in the small fragment size class compared to 1.46 young/adult female in the large forest size class, indicating that juvenile survival has been severely affected in the small fragments. The adult male-to-female sex-ratios in the small, medium and large forest size classes were 1:2 ($n = 2$ groups), 1:0.91 ($n = 24$ groups) and 1:1.03 ($n = 28$ groups), respectively.

Minimum estimate of number of groups

The minimum number of hoolock gibbon groups in each forest was calculated based on actual encounters of groups and the most conservative, minimum estimate from the number of other groups heard calling (Table 7). A total of 178 calls were recorded across sites, from which 79 counts were deducted. It was estimated, therefore, that there were at least 99 other gibbon groups at the sites, apart from the 59 groups sighted during the survey. The highest estimate was for Jeypore Reserve Forest (RF) (at least 38 groups), followed by Upper Dehing East Block RF (at least 30 groups). The middle-size (20–30 km^2) category of forests showed high variation, ranging from just two groups in the extensively encroached and degraded Kumsang RF to as many as 25 groups in the relatively less disturbed Kakojan RF. The estimates of two groups from Tinkopani RF and seven from Dirok RF, both bordering the Arunachal Pradesh state border, were unexpectedly low since both areas contained a high proportion of medium/good tree cover suitable for gibbons. Indications were that hunting has lowered the hoolock gibbon populations at these sites. It is possible that gibbons may call less in hunted areas and in sites

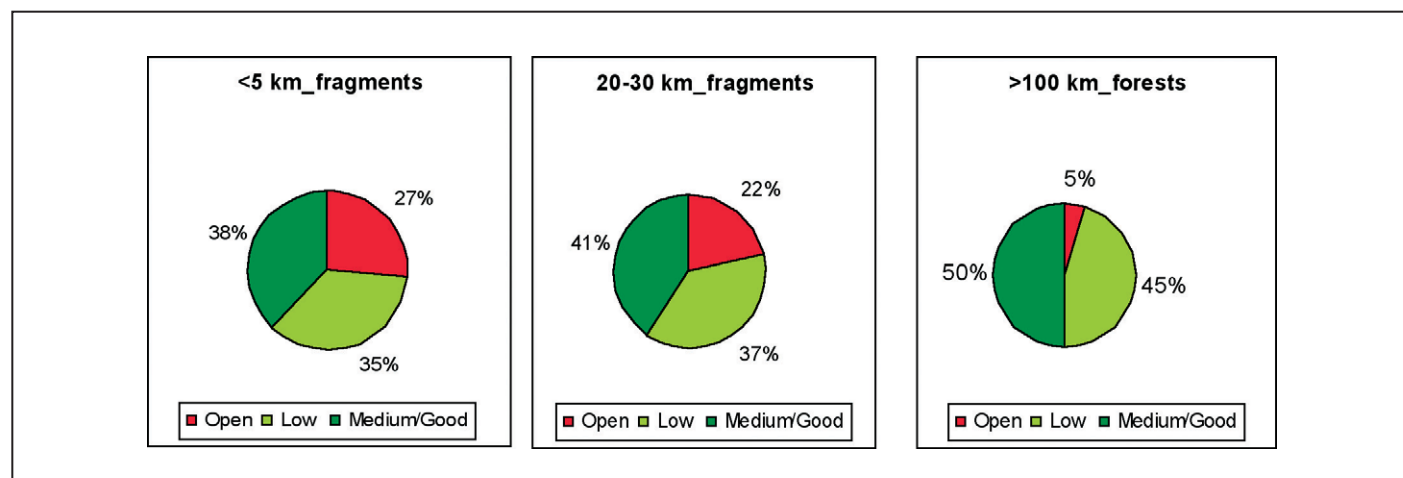


Figure 3. Proportion of points ($n = 1495$) in different tree-cover categories in each forest size class.

Table 5. Locality, group size and group composition of western hoolock gibbons, *Hoolock hoolock*, in eastern Assam (n = 59 groups; complete counts for 54 groups).

		No. of groups	Adult		Sub-adult			Juvenile			Infant	Group size
			Male	Female	Male	Female	?	Male	Female	?		
Forest size class <5 km²												
1	Tokowani	1	-	1	-	-	-	-	-	-	-	1
2	Borajan	1	1	1	-	1	-	-	-	-	1	4
Forest size class 20–30 km²												
3	Tarani	1	1	1	-	-	-	-	-	1	-	3
4	Buridihing	8	1	1	-	-	-	-	-	-	-	2
5			1	1	-	-	-	-	-	-	1	3
6			1	1	-	-	-	-	1	1	1	5
7			1	1	-	-	-	-	-	1	1	4
8			1	1	-	-	-	-	-	-	-	2
9			-		-	1	-	-	-	1	-	2+
10			1	1	-	-	-	1	-	1	1	5
11			1	1	-	-	-	-	-	-	1	3
12	Kumsang	2	1	1	-	-	-	1	-	-	-	3
13			1	1	-	-	-	-	1	-	-	3
14	Kakojan	9	1	1	1	-	-	-	-	1	-	4
15			1	1	-	-	-	-	1	-	1	4
16			1	1	-	-	-	-	-	1	1	4
17			1	1	-	-	1	-	-	1	-	4
18			1	1	-	-	-	-	-	-	1	3
19			1	1	-	-	1	-	-	-	1	4
20			1	1	-	-	-	-	-	1	1	4
21			1	1	-	1	-	-	-	-	-	3
22			-	-	1	-	-	-	-	-	-	1
23	Doomdooma	3	1	1	-	-	-	-	-	1	-	3
24			1	1	-	1	-	-	-	1	-	4
25			1	1	-	-	1	-	-	1	1	5
26	Dirok	3	1	1	-	-	-	-	-	1	-	3+
27			1	-	-	-	-	-	-	-	-	1
28			1	-	-	1	-	-	-	-	-	2
Forest size class >100 km²												
29	Upper Dehing East	15	1	1	-	-	1	1	-	-	-	4
30			1	1	-	-	-	-	-	1	1	4
31			1	1	-	-	-	-	-	1	-	3
32			1	1	1	-	-	-	-	1	1	5
33			1	1	-	1	-	-	-	1	1	5
34			1	1	-	-	-	-	-	1	1	4
35			1	1	-	-	1	-	-	2	-	5
36			1	1	-	-	-	-	-	1	1	4
37			1	1	-	1	-	-	-	1	1	5
38			1	1	-	-	-	1	-	1	-	4
39			1	1	-	-	-	-	1	-	-	3
40			1	1	-	-	-	-	-	-	-	2+
41			1	1	-	1	-	-	-	1	-	4
42			1	1	-	-	-	-	1	-	1	4
43			1	1	-	1	-	-	-	-	1	4

Table 5 continued on next page

Table 5, continued

		No. of groups	Adult		Sub-adult			Juvenile			Infant	Group size
			Male	Female	Male	Female	?	Male	Female	?		
44	Upper Dehing West	6	1	1	-	-	-	-	1	-	1	4
45			1	1	-	-	-	-	-	-	-	2+
46			1	1	-	-	-	-	-	1	1	4
47			1	1	1	-	-	-	-	1	-	4
48			1	1	-	-	-	-	-	-	1	3
49			1	1	-	-	-	-	-	1	1	4
50	Jeypore	10	1	1	-	-	-	-	-	-	-	2
51			1	1	-	1	-	-	-	1	-	4
52			-	1	-	-	1	-	-	1	-	3+
53			1	1	-	-	-	-	-	-	1	3
54			1	1	-	1	-	-	1	-	-	4
55			1	1	-	1	-	-	-	-	1	4
56			1	1	-	1	-	-	-	-	1	4
57			1	1	-	-	-	-	-	1	1	4
58			1	1	-	-	1	-	-	1	-	4
59			1	1	-	1	-	-	-	1	1	5
Total	n=11	59	55	55	4	14	7	4	7	32	29	207+

? Sex not identified

Table 6. Ratios of age and sex classes in 54 western hoolock gibbon, *Hoolock hoolock*, groups in the different forest size-classes.

Ratios	Forest Size Class (km ²) (No. of gibbon groups)		
	<5 (2)	20–30 (24)	>100 (28)
Immature (infant, juvenile, subadult): Adult	0.66	0.79	0.98
Infant : Female	0.50	0.52	0.60
Juvenile : Female	0.00	0.76	0.85
Young (Juvenile and Infant) : Female	0.50	1.28	1.46
Male : Female	0.50	1.09	0.96

Table 7. Estimate of minimum number of western hoolock gibbon, *Hoolock hoolock*, groups in each reserve from groups located and from calls only.

Area (RF)	No. of groups seen	No. of groups heard calling, but not tracked down	Minimum Estimate
Forest Size Class <5 km² (n=4)			
Phillobari	0	0	0
Nalani	0	0	0
Tokowani	1	1	2
Borajan	1	0	1
Forest Size Class 20–30 km² (n=7)			
Tarani	1	2	3
Buridihing	8	12	20
Kumsang	2	0	2
Kakojan	9	16	25
Doomdooma	3	4	7
Tinkopani	0	2	2
Dirok	3	4	7
Forest Size Class >100 km² (n=3)			
Upper Dehing East	15	15	30
Upper Dehing West	6	15	21
Jeypore	10	28	38
Total	59	99	158

where shortage of food may influence energy costs of calling. No groups were seen or heard in the two smallest fragments (Phillobari RF and Nalani RF), although a group was later found living in some village trees outside Nalani RF, with no canopy connection to the RF.

Forest cover

All the reserve forests had between 35% and 45% of the points sampled in the low tree cover category, indicating extensive disturbance due to logging in the past or from illegal logging more recently. The small and medium fragments had a high proportion of open areas without trees (22–27%) compared to the large forest (5%), while the largest forest-size class had the highest proportion of medium to good tree cover (50%) (Fig. 3). Assessments of tree cover for each of the reserves are represented graphically in Figure 4.

It is significant that 87% of the gibbon groups were found at medium to good cover locations, when only 42% of the total tree-cover scores fall in this category. No gibbons were seen in the open areas, and only 13% of the sightings recorded were in areas of low tree cover (Fig. 5).

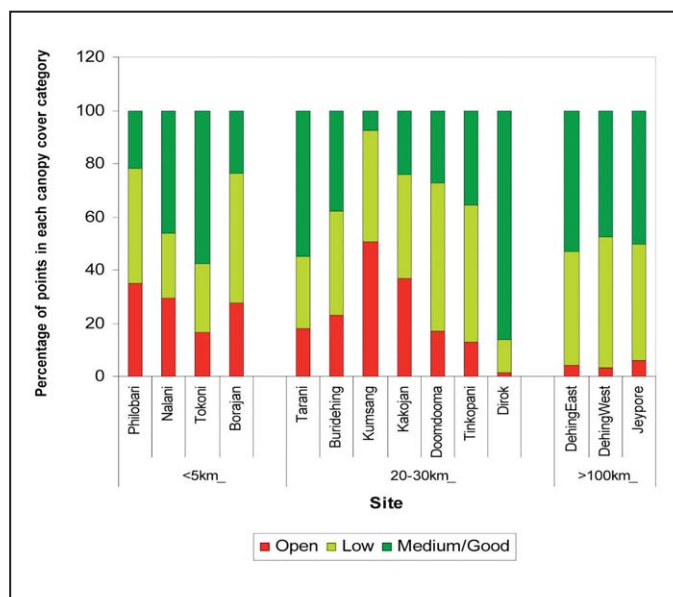


Figure 4. Percentage of points ($n=1495$) in three tree cover categories at each of the 14 sites.

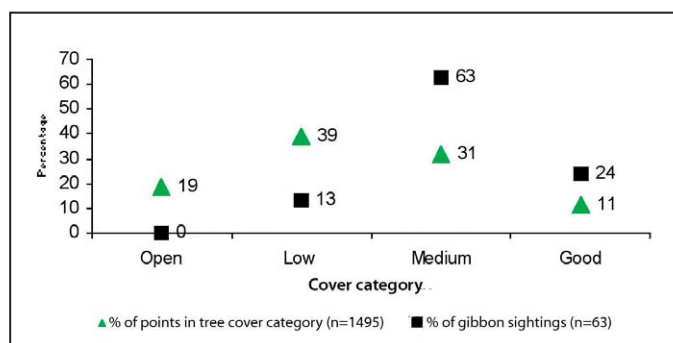


Figure 5. Proportion of gibbon sightings in the different cover classes plotted against the total proportion of points in each cover class.

A comparison of satellite images for the area between the years 1990 and 2000, a span of 10 years preceding the study, showed that the actual areas of forest cover lost in the small, medium and large forests were 0.5 ± 0.4 km², 1.3 ± 0.4 km² and 3.7 ± 1.0 km² respectively (Fig. 6a). As a proportion, however, the figures are 23.7 ± 15.7 , 16.1 ± 11.3 and $2.3 \pm 0.4\%$ for the small, medium and large forests respectively, indicating that the decadal rate of loss has been highest in the smallest fragments (Fig. 6b).

Discussion

Degradation in forest fragments was indicated by decreased canopy continuity, tree density, hoolock gibbon food tree density, and food species richness (Kakati 2004). This loss of food sources and the changes in the habitat structure are strongly implicated in the low encounter rates and smaller group sizes found in forest fragments during this survey.

All gibbons are fruit-pulp specialists (Chivers 1984) with simple stomachs and a very limited ability to digest leaf material. Unlike monkeys, they cannot cope with secondary compounds and toxins in leaves, and they prefer animal to plant protein in times of fruit-shortage (Vellayan 1981). Prolonged dependence on leaves can thus cause severe nutritional stress, especially in the juveniles. Although adults might persist and breed for a time in sub-optimal habitats, a sudden die-off may occur when eventually their nutritional tolerance threshold is breached.

Reductions in fruit supply and species richness of fruit trees due to disturbance and fragmentation have been documented in forest habitats (Johns 1986; Tabarelli *et al.* 1999). Reduced fruit supply in turn has been linked to low population densities and declines of primate frugivores in fragments in Mexico, the Atlantic forest of Brazil, and the Central Amazon (Estrada and Coates-Estrada 1996; Chiarello and Melo 2000; Gilbert and Setz 2001). The survival ability of several other rain-forest primates, including gibbons, has been negatively correlated to its degree of frugivory (Johns and Skorupa 1987). In undisturbed areas, the natural seasonal cycles of fruit shortage in tropical habitats may be offset by the presence of keystone species. For example, one study showed that <1% of the tree species sustained the entire frugivore community through a period of three months of low fruit availability in Cocha Cashu, Peru (Terborgh 1983). In a fragment forest, however, this vital availability might be easily disrupted. Across five intensive study sites in Assam, Kakati (2006) found that during the dry, winter season gibbon groups in all the forests shifted from a predominantly fruit diet to eating leaves. Even then, the gibbon groups in the medium-sized and large forests continued to eat at least 14–28% fruit (as percent time spent feeding), whereas the small fragment groups had practically no fruit at all for two months (January–February). Such extreme shortage of high-energy fruit could be the critical point on which hinges the survival of gibbons in small fragments.

Although the proportion of infants to adult females was similar between forest size classes (i.e., breeding rates were similar), groups in the small and medium-sized fragments had fewer juveniles/adult female than in the larger forests, suggesting that juvenile survival is compromised by fragmentation. Gibbon females in fragments probably suffer very high lactation costs because of inadequate diets in terms of both quality and quantity. Many mammals under conditions of seasonal food shortages are known to rear a reduced litter or females may not survive to breed again (Moir 1994). Weaning is thought to be the critical time that foods of particularly high nutrient density are required (Ofstedal 1991), and hoolock

gibbon infants might be surviving the entire two-year period of dependency on the mother at this high cost to her, only to die when they stop suckling.

Dispersal may be the time of greatest danger of mortality for sub-adults or displaced adults in fragments. Fragmentation causes deterioration of the habitat and the consequent attrition of suitable territories. Also, canopy discontinuity can prevent dispersing gibbons from accessing potentially suitable areas and make them vulnerable to injury or death from falls. Alfred and Sati (1990) recorded the disappearance of hoolock gibbons from 168 forest patches (0.14–2.7 km²) in *jhum* (slash and burn agriculture) matrices in the Garo Hills of

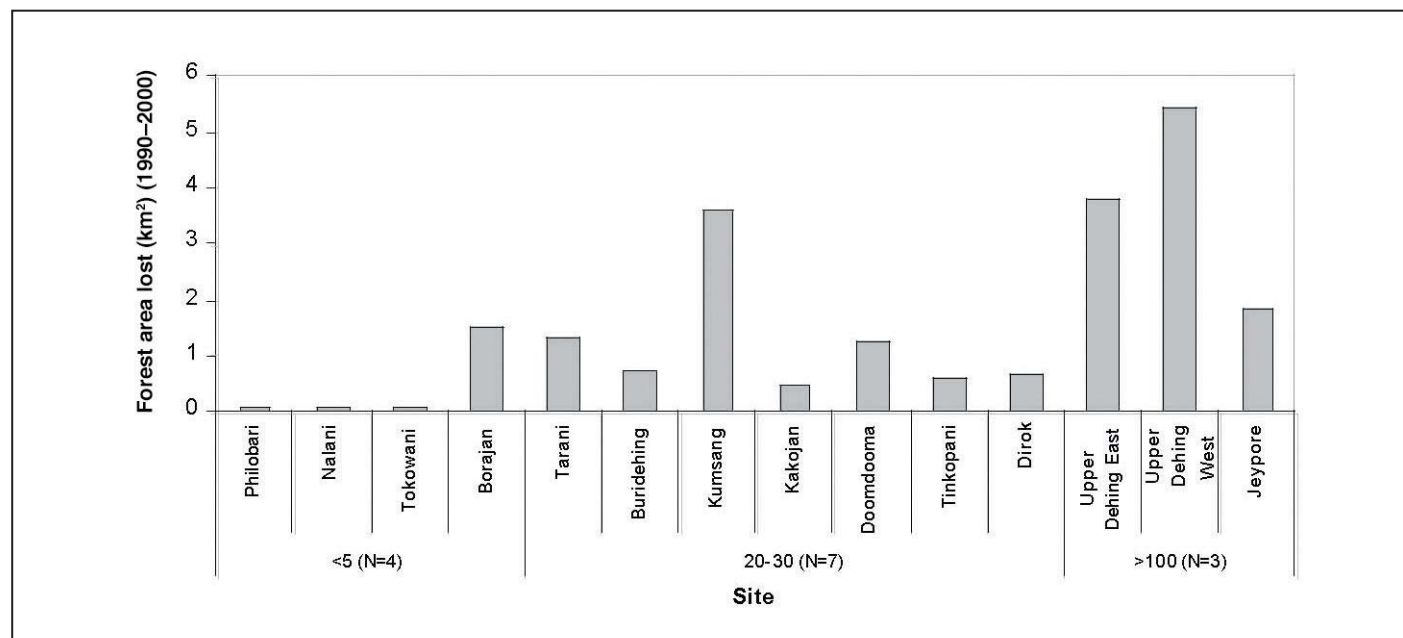


Figure 6a. Area of forest lost (km²) between 1990 and 2000, assessed from satellite images, in the 14 survey sites.

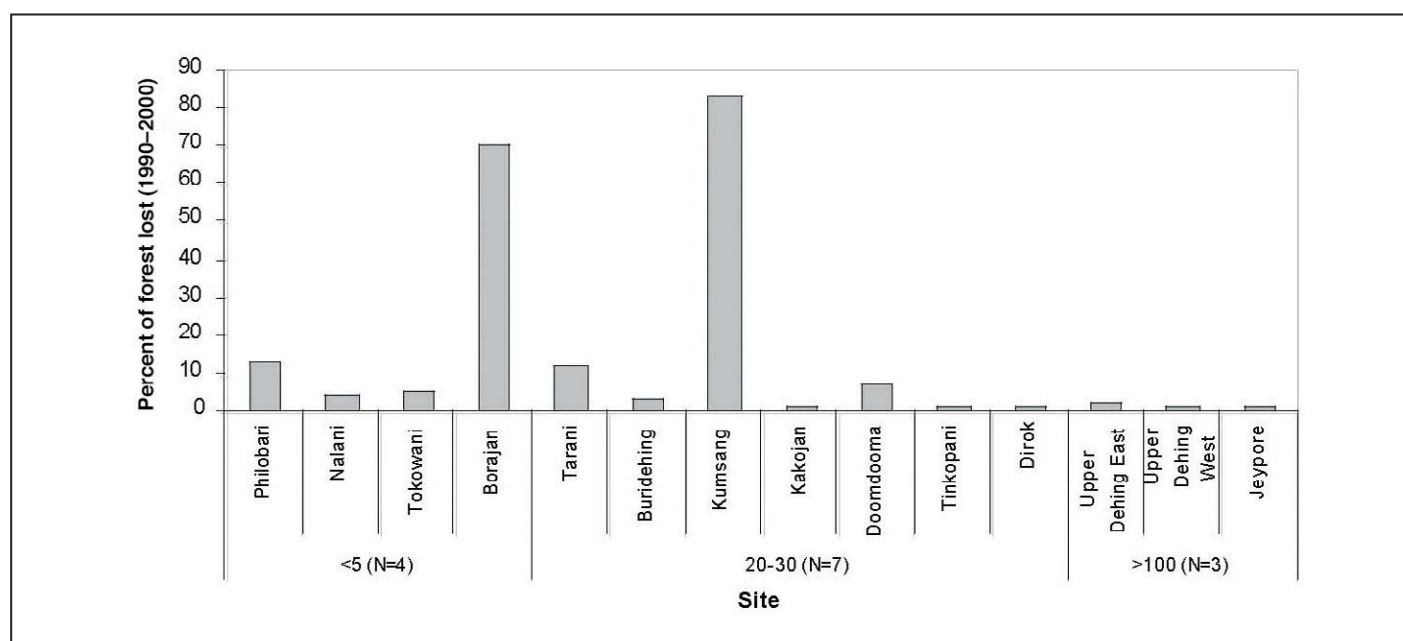


Figure 6b. Percentage of forest cover lost between 1990 and 2000, assessed from satellite images, in the 14 survey sites.

Meghalaya mostly in the 10 years preceding their study, and mainly because *jhum* cycles had shortened to <10 years and gibbon dispersal corridors (secondary forests and old growth bamboo) were no longer available. In the Upper Assam landscape studied, the sharp edges with the settled agriculture matrices leave no scope at all for gibbons to move between sites.

The extensive habitat degradation seen in fragments results from a number of factors. The reserve forests have a long history of logging (>70 years) which, although halted in 1996 by a region-wide ban by the Supreme Court of India, continues illegally and gives the forests little respite to recover. The effects are less clear in the large forests because relative to their size the damage is limited. Edge effects include hotter and drier micro-climates through exposure to the sun and wind and increased tree mortality on the periphery of the fragments (Ferreira and Laurance 1997). There are invasions of weeds and successional species (Laurance *et al.* 1998), reduction in genetic variation and vigour (Cascante *et al.* 2002), and changes in plant communities due to altered predator-prey relationships (Rao *et al.* 2001). Compared to continuous forest, fragments have also been found to have lower seedling abundance and seedling species diversity of the non-pioneer tree species (Benitez-Malvido 1998; Benitez-Malvido and Martinez-Ramos 2003). They also tend to have lower tree densities and tree species diversity and fewer large trees (Menon and Poirier 1996, Kakati 2004). Again, many forest trees depend on frugivores for dispersal and regeneration (Hamann and Curio 1999; Chapman and Onderdonk 1998). The disappearance of frugivores due to human activities such as logging or hunting will invariably affect recruitment of tree species, and the sooner and more severely in fragments.

The occurrence of most of the gibbon groups in areas of medium or good tree cover emphasizes their strong dependence on tall trees and closed canopies, not just for their food, but also in providing for adequate arboreal pathways to move around their home ranges and for protection from predators. Although they may persist in degraded habitats for a time, the outlook for their long-term survival in these areas is grim, as presaged by the series of recent local extinctions reported in Walker *et al.* (2007). One of the most impressive examples of gibbon population declines caused by rapid habitat degradation is in the Borajan fragment, which lost 70% of its forest cover between 1990 and 2000. Its gibbon population declined from 34 animals in 1995 (Srivastava 2006) to just nine in 2000 (pers. obs.).

In conclusion, it is valid to suppose that an intact 5 km² forest fragment can support 15–20 groups of hoolock gibbons, assuming each group had a home range of *c.* 25 ha (the average home range size in relatively undisturbed sites [*n* = 3, Kakati 2004]). Given that fragmented populations of the western hoolock gibbon make up a significant part of the surviving numbers of this endangered species, it is necessary to conserve these populations through forest restoration and the establishment of dispersal corridors wherever feasible. It

is also important to manage the commonly seen canopy disruptions within the forest, due for example, to roads, railways or power lines, by the establishment of canopy bridges, either natural or artificial, at distances of 50–100 m along the gap. Translocation to suitable, available habitats, to areas where they have been hunted out but where hunting can now be effectively prevented, can be a last resort for gibbons in completely degraded fragments.

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