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POPULATION DENSITY AND HABITAT OF SIAMANG AND AGILE GIBBON IN BALA FOREST, SOUTHERN THAILAND

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ABSTRACT

Siamang (*Symphalangus syndactylus*) and agile gibbon (*Hylobates agilis*) were censused and mapped in Bala Forest, part of the Hala-Bala Wildlife Sanctuary, Narathiwat Province, South Thailand. Nineteen groups of siamangs and 136 groups of agile gibbons were found in this 168-km^2 area. This is the northernmost population of the siamang in Asia. Densities of siamangs were positively related to altitude, which reaches a maximum of 953 m in Bala Forest. In comparison with agile gibbons, siamangs occurred at higher altitude, lower-slope terrain, shorter distances from ridge-tops, and on more east-facing terrain. Both species occurred mostly in areas far from villages and the forest edge. Diminished submontane forest in Thailand, as well as competition with agile gibbons, may be limiting the distribution of siamang at the northern end of its range.

Keywords: siamang, agile gibbon, population density, geographic range, Bala Forest

INTRODUCTION

The siamang (*Symphalangus syndactylus* Raffles, 1821) and the smaller agile gibbon (*Hylobates agilis* Cuvier, 1821) are found sympatrically in parts of Peninsular Malaysia and in central and southern Sumatra (Wilson & Wilson, 1975; Groves, 2001; O'Brien *et al.*, 2004; Chivers, 2013). The siamang is the largest member of the lesser ape family Hylobatidae, which contains four genera and 19 species as currently defined (Chivers, 2013). The siamang is also distinguished from members of the smaller *Hylobates* spp. on the Malaysian peninsula and mainland in being all black in body color and in having a very distinctive-sounding duet with screams and deep booming sounds (Haimoff, 1981). The body color of the agile gibbon is usually buff to dark brown, with dark fur on the hands, white eyebrows and (in males) white cheeks on the face. The duet of the agile gibbon most closely resembles that of the white-handed gibbon (*Hylobates lar* [Linnaeus, 1771]), with the females' great call consisting of a series of long, drawn-out hoots, but the males' phrases are distinctive.

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Although both species occur in South Thailand, the range of the siamang there is very small, confined to the Bala Forest part of Hala-Bala Wildlife Sanctuary (MARSHALL, 1981; TREESUCON & TANTITHADAPITAK, 1997) (Fig. 1). As do most species of gibbons, they live in small, territorial, primarily monogamous groups (CHIVERS, 1974; GITTINS & RAEMAEKERS, 1980; PALOMBIT 1994). Siamangs have generally been found at higher altitudes than agile and lar gibbons (*Hylobates lar*) in Sumatra (O'BRIEN *ET AL.*, 2004; WILSON & WILSON, 1975; YANUAR, 2009) and Malaysia (CALDICOTT, 1980; CHIVERS, 1974, 1977; MARSH & WILSON, 1981). For example, MARSH & WILSON (1981), in Peninsular Malaysia, found that the density of siamangs was higher in montane forest sites than in lowland forest sites, and that no siamangs occurred in swamp forest sites where white-handed gibbons (*Hylobates lar*) occurred. CALDICOTT (1980) found that on Gunung Benom (Krau Wildlife Reserve in Pahang, Malaysia), siamangs occurred at low density below 300 m altitude, were most abundant between 700 and 1,000 m altitude and declined with altitude to 1,500 m. White-handed gibbon density generally declined above 760 m and was zero above 1,300 m. CALDICOTT (1980) believed that siamangs occurred at higher altitudes due to their ability to exploit a greater variety of plant species, and greater reliance on leafy material, than the smaller gibbons. In Kuala Lompat, central Pahang, a lowland site (ca. 50 m a.s.l.), MACKINNON & MACKINNON (1980) found *H. lar* and the siamang to have low and nearly equal densities (siamang approximately 1.5 groups km^{-2} and *H. lar* [similar in size and ecology to *H. agilis*], about 1.8 groups km^{-2}).

Similar situations have been found on Sumatra. For example, in the area of sympatry in Bukit Barisan Selatan National Park, southern Sumatra, O'BRIEN *ET AL.* (2004) found that the density of siamangs was bimodal: it peaked at altitudes below 300 m (3.3 groups km^{-2}), was low in the mixed dipterocarp forest between 400 and 900 m, and higher above 1,000 m. The density of agile gibbons, however, peaked in mid-altitudes and was low above 1,000 m. YANUAR (2009) found a similar pattern in Kerinci Seblat National Park, central Sumatra. Densities of the agile gibbon were highest in mid-altitudes, and densities of the siamang were highest in lowland forest (<400 m) and montane forest (1,400–2,400 m), where siamangs reached average densities greater than 5 groups km^{-2}. Agile gibbons were absent from the montane forest. In the hill dipterocarp forest (400–900 m) agile gibbons were about twice as abundant as siamangs (about 4 groups km^{-2} vs. 2 for siamang). These studies suggested that siamangs and agile gibbons could be in competition with one another, and that the agile gibbon has a competitive advantage, or is in its optimal habitat, in the middle altitudes (O'BRIEN *ET AL.*, 2004). The high overlap in their fruit/fig diets in Sumatra suggests the possibility of direct competition for food.

Siamangs tend to have somewhat larger group sizes than agile gibbons in Sumatra (especially in the south), but not in peninsular Malaysia. In Kerinci Seblat National Park, average group size was 3.4 for siamangs and 3.0 for agile gibbons (YANUAR, 2009). O'BRIEN & KINNAIRD (2011) found the mean size of 11 groups in Way Canguk study area, in extreme south Sumatra, to be only 2.7 individuals, which was evidently due to a high infant mortality rate. The poor survival of agile gibbons at the site was thought by these authors to be due to interference and competition from the larger siamang at fruiting trees. In Peninsular Malaysia, the siamang has been reported to have a mean group size of 3.0 ($N = 6$) at Kuala Lompat (MACKINNON & MACKINNON, 1978), and the agile gibbon 4.4 ($N = 7$) at Sungai Dal (GITTINS & RAEMAEKERS, 1980).

Both the siamang and the smaller sympatric *Hylobates* species have diets comprising mainly succulent fruits, figs, shoots and young leaves (CHIVERS, 1974; PALOMBIT, 1997;

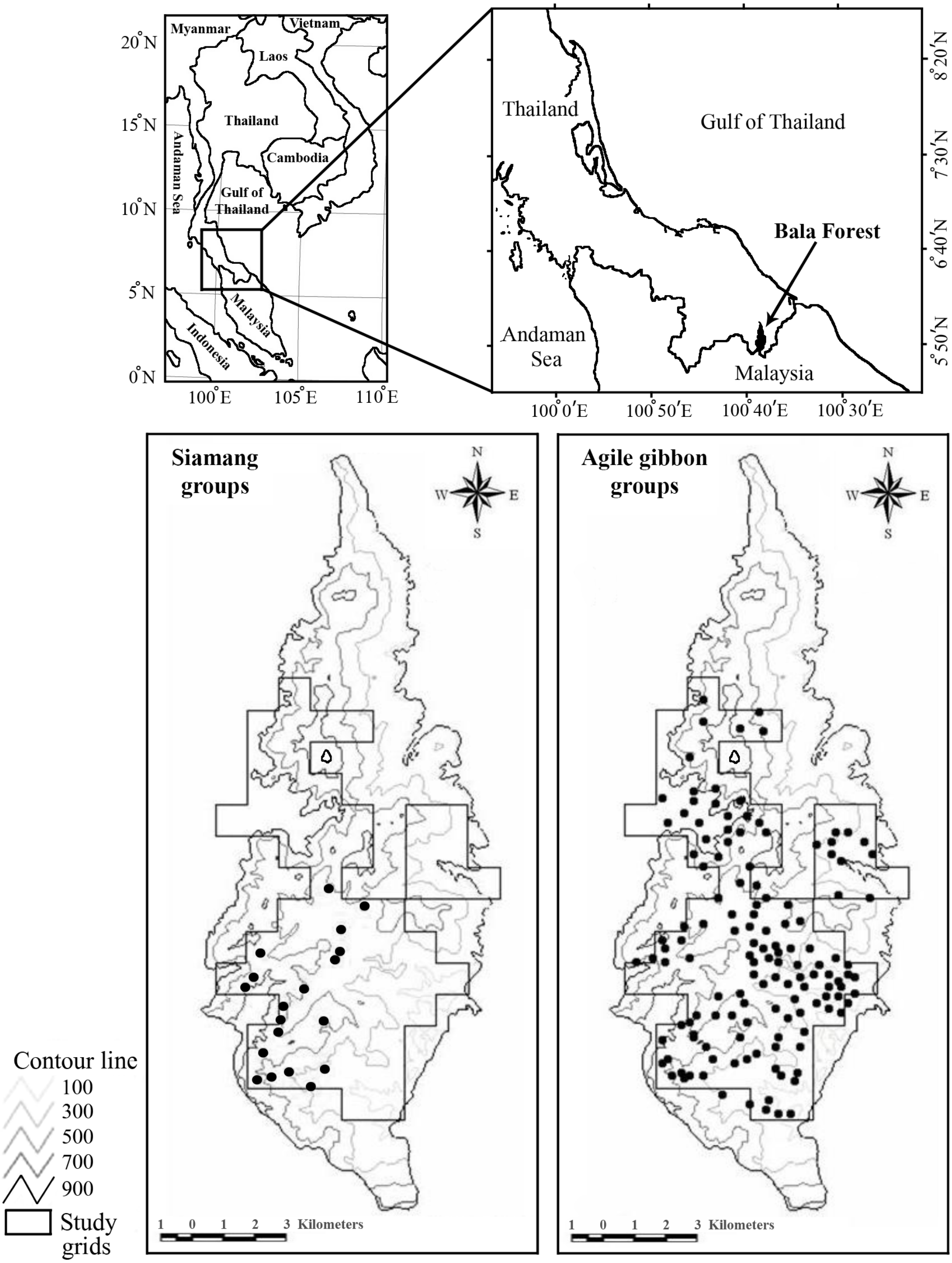

Figure 1. Maps showing the location of the Bala Forest part of Hala-Bala Wildlife Sanctuary (above), and the location of siamang groups (lower left) and agile gibbon groups (lower right) in the Bala Forest part of the sanctuary.

RAEMAEKERS, 1978, 1979). Siamangs consume somewhat more leaves and less succulent fruit than smaller gibbons (ELDER, 2009; GITTINS & RAEMAEKERS, 1980; RAEMAEKERS, 1980), and this partly reflects a general (although weak) correlation between diet and body size in gibbons, and food availability in the habitat (ELDER, 2009; RAEMAEKERS, 1984). Siamangs have been found to be somewhat more folivorous in Malaysia than in study sites on Sumatra (CHIVERS & RAEMAEKERS, 1986; PALOMBIT, 1997).

In this study we censused siamangs and agile gibbons in Bala Forest and compared their densities and habitat distributions. Both siamangs and *Hylobates* species can be surveyed by listening for their loud songs, which in most species are performed as duets (BROCKELMAN & ALI, 1987; O'BRIEN *ET AL.*, 2004). We estimated forest attributes of the habitat within each listening area of gibbons and analyzed factors restricting the distribution and habitat selection of each species. We attempt to explain what factors limit the range of the siamang in particular.

METHODS

Study Area

The field study area covered Bala Forest which is a part of Hala-Bala Wildlife Sanctuary in Narathiwat Province, South Thailand. The Bala Forest has an area of about 168 km^2 and covers an isolated mountain range with altitudinal range of 100–953 m a.s.l. The forest, with many species of large trees of family Dipterocarpaceae, more closely resembles the Malayan mixed dipterocarp forests than the more seasonal, semi-evergreen forests farther north (WHITMORE, 1984). The area is in the first order watershed of the Kolok River and Saiburee River. The Bala Forest was continuous with the forests in Kelantan, Malaysia, a few decades ago, but is now separated by agricultural areas along the international border. Although most of the forest appears to be old-growth, local personnel have informed us that much of the forest was selectively logged before about 1990.

Gibbon Census

During April through September, 2005, we censused gibbons of both species using a point count sample method from fixed listening posts. Gibbon groups were mapped by triangulation from adjacent listening posts (BROCKELMAN & ALI, 1987; BROCKELMAN & SRIKOSAMATARA, 1993; O'BRIEN *ET AL.*, 2004). Siamangs give duets during 0800–1100 h but the peak of agile gibbon singing is within 0600–0800 h in the morning (BROCKELMAN & GITTINS, 1984; GITTINS & RAEMAEKERS, 1980; S. NONGKAEW, unpublished observations).

We attempted to cover all areas of the Bala Forest which contain siamang or gibbon groups in the survey, based on preliminary hikes into the forest and reports of local personnel (Fig. 1). The northernmost part of the sanctuary did not have many gibbons, as well as areas near the edge of the sanctuary, where the condition of the forest was partially degraded. The terrain of the mountain is divided by relatively sharp ridges into valleys of up to about 8 km^2 in area, which provided natural "listening areas" which could be surveyed by auditory means. Thirteen listening areas were selected on a 1:50,000 topographic map (Royal Thai Survey Department) and 4 listening posts (LPs) were selected on the tops of hills or ridges within each listening area which allowed the listeners to hear all groups in the valley and on the sides of the mountains, up to the ridge-top. LPs were in the range of 300–600 m apart. We assumed that the duets of gibbon groups can be heard clearly at least 1.5 km away in calm weather (O'Brien *et al.*, 2004). The "listening areas", or total areas from which gibbons could be heard and mapped from the 4 listening posts, were estimated from the topographic map. All areas were covered with pristine forest so that there were no habitats, except for scattered windthrows, where gibbons cannot occur.

We attempted to survey each area for 4 consecutive days, but some areas were surveyed for only 3 days. We did not estimate the frequency of singing (probability of singing on a given day) of individual groups, so that with 3 days of listening, some groups will have been missed. O'Brien *et al.* (2004) estimated the frequency of singing of agile gibbons in their study area to be 0.417/day, and for siamang, 0.246/day. With these frequencies, 0.80 of gibbon groups should be heard after 3 days, and about 0.88 after 4 days (Brockelman & Srikosamatara, 1993). For siamang, the corresponding estimates for 3 and 4 days are approximately 0.57 and 0.68. These numbers may be used as correction factors to correct density estimates for missed groups.

During the auditory survey, 1 or 2 persons went to each LP and listened for siamang and agile gibbon calls from 0600 h to noon. Listeners noted the exact times of all calls and estimated the compass directions. Only days of good weather were used for estimation of density. If most of the morning was windy or rainy, that day's data were not used. The compass directions from adjacent LPs were used to determine each group's location by triangulation whenever possible.

We mapped the locations of groups of siamang and agile gibbon within each listening area manually, using the daily records of exact singing times and compass directions. Nearly all groups were heard from more than one LP and could be mapped to within a few hundred meters by triangulation. First, we mapped each day's data separately, and later combined them on a single map for each area, and circled the singing locations believed to be from the same groups. As groups may duet more than once during a morning (or not at all), a method must be found to avoid multiple counting of groups. Duets were attributed to different groups if they overlapped in time on any day (allowing us to infer boundaries between mapped groups), mapped too far apart (> ca. 500 m) to likely be within the same territory, or were acoustically distinguishable based on song pattern, pitch, or presence of singing offspring. The total "listening area" (LA) could be estimated from a topographic map of the area and a knowledge of the distance that gibbon songs usually carry (assumed to be about 1.5 km). Finally, the densities of agile and siamang groups were determined by dividing the number of mapped groups of each species by the total LA in km^2. Previous studies have shown that these methods are conservative and are more likely to underestimate rather than overestimate the density of the population (Brockelman & Srikosamatara, 1993; Phoonjampa & Brockelman, 2008; Brockelman *et al.*, 2009).

Habitat Characteristics

Habitat characteristics measured included forest condition (density of trees and canopy height), terrain characters, and a variety of distance measurements. Forest condition was measured on plot transects within each LA. A point in the middle of the LA was selected and four 250-m long transects were established extending north, south, east and west from the point. On each line we set 25 circular plots with 5.6-m radius (0.01 ha in area) spaced at 20-m intervals. There were thus 100 plots in each LA, totaling 1 ha. Forest characters measured in these plots included: upper canopy surface height directly over the point (measured with an optical rangefinder) (BROCKELMAN, 1998), basal area of trees >10 cm in DBH (diameter at breast height), and numbers of trees >10 cm, >20 cm, >40 cm and >80 cm DBH. These measures were designed to provide a crude indication of forest condition within the listening area for comparison with estimated gibbon densities, and they serve to document the forest condition in this habitat.

The part of the study area used for purposes of habitat preference analysis (terrain and distance characters) consisted of all 1-km^2 grid squares on the 1:50,000 map which contained at least one gibbon group of either species. There were 60 such squares containing gibbons (Fig. 1). We described habitat attributes determined at the approximate geometric mean location of each mapped gibbon group, including: altitude, distance from nearest ridge, slope direction (estimated in the forest by standing on the slope), slope value (measured with a hand-held clinometer), distance from nearest road, distance from nearest village, distance from nearest stream, and distance from edge of the forest. Down-slope direction angle in degrees (a) was transformed to the index d = (1+sin a), which varies from 0 (directly west) to 2 (directly east). The index measures differences between slopes in the east-west direction but not the north-south direction; we believe that in the tropics, differences in the east-west direction reflect greater changes in irradiance and habitat than differences in the north-south direction)

For both siamangs and agile gibbons, the grid points at gibbon locations were compared with the grid square points that did not contain gibbons; then the points containing agile gibbons were compared with those containing siamangs. There were 42 grid squares that did not contain siamangs and 22 that did not contain agile gibbons. A random sample of 150 points in these grid squares was selected for comparison of each variable with the points occupied by gibbon groups (for purposes of sampling, the 1-km^2 grid squares were divided into 100 sample points, one in each ha). Points lying on the highway crossing the Bala forest and the developed area around headquarters without forest were excluded.

Statistical Analysis

All habitat attributes were tested for normality with the Kolmogorov-Smirnov test. Means of characteristics that were normally distributed were compared using t-tests. Characteristics that were not normally distributed were compared using the Mann-Whitney U test. Siamang and agile gibbon densities in each LA were correlated with habitat characters in each LA with the product moment correlation coefficient, r, by converting r to a t value (dividing r by its standard error). A discriminant analysis of sites with and without gibbons and siamang was carried out by the senior author, but is not reproduced here; readers are referred to NONGKAEW (2010). Statistical significance was judged at the level of $p = 0.05$.

RESULTS

Density of Groups

Nineteen groups of siamangs and 136 groups of agile gibbons were found in 60-km^2 of the sanctuary contained within listening areas (Table 1). Our estimates of density of groups apply only to the listening areas surveyed, not the whole sanctuary. The siamang occurred mostly in the southwestern part of Bala Forest, closest to the Malaysian border, while agile gibbons were more evenly distributed throughout Bala Forest (Fig. 1).

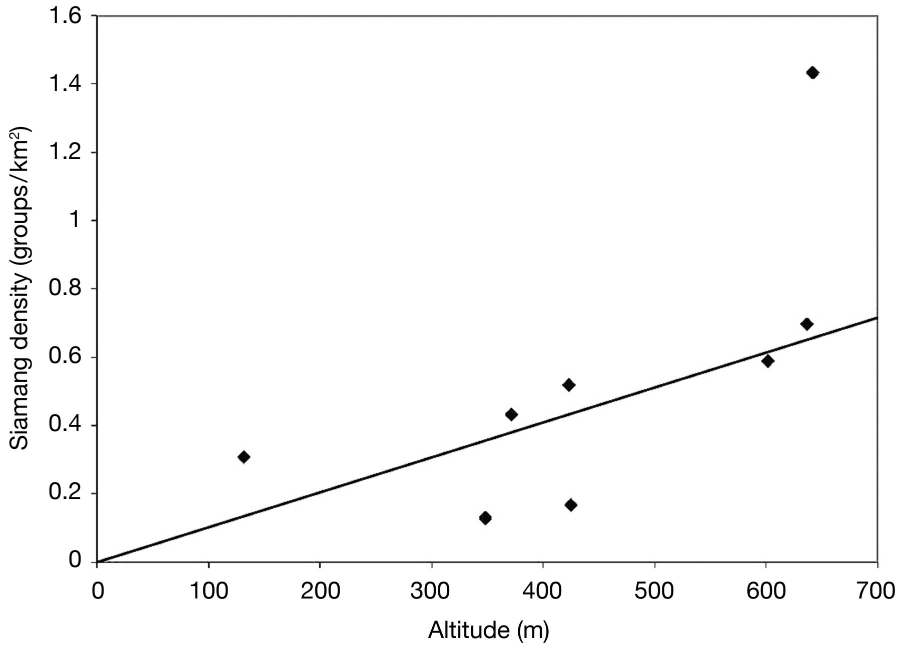

Figure 2. Relationship between altitude and siamang density in listening areas where siamangs were heard.

The density of siamangs ranged from 0 to 1.43 groups km^{-2} (average = 0.32, standard error (SE) = 0.08 groups km^{-2}). In the eight LAs where siamangs were found densities of groups ranged from 0.13 to 1.43 km^{-2} (average = 0.53, SE = 0.08 groups km^{-2}). Agile gibbons were found in all 13 sites, and densities ranged from 1.05 to 3.27 groups km^{-2}. Mean density of agile gibbons in Bala Forest was 2.27 groups km^{-2} (SE = 0.18).

The density of siamangs was positively related to altitude ($r = 0.435$) but was not significantly related with most forest characteristics. When density of siamangs was considered only in grid squares where they were found, it was correlated with altitude ($r = 0.810$, $P = 0.015$) (Fig. 2).

Habitat Occupancy

Habitat characteristics of grid points without gibbons were compared with those with gibbons. Seven habitat characters, including altitude, distance from ridge, slope direction index, slope value, distance from road, distance from village, and distance from edge, were significantly different between grids with and without siamangs (Table 2). For the agile gibbon, six habitat characters (altitude, distance from ridge, distance from road, distance from village, distance from stream, and distance from edge) were significantly different between grids with and without groups (Table 3). Siamangs tended to occur more at higher elevations and on east-facing slopes, and agile gibbons at lower elevations, than the average of those

Table 1. List of census listening areas, showing numbers and densities of agile and siamang groups, and characteristics of each area.

No.	Date (2005)	Mean altitude (m)	Area (km^2)	Agile groups	Density (km^{-2})	Siamang groups	Density (km^{-2})	Mean canopy surface height ± SD (m)	No. trees/ha by cm DBH class				Basal area ($m^2\ ha^{-1}$)
									10–19	20–39	40–79	80+	
1	22 Apr.	424	5.8	15	2.59	3	0.52	25.3 ± 10.4	286	133	44	12	23.7
2	4 May	134	7.5	21	2.80	0	0	27.6 ± 9.9	222	109	30	6	15.0
3	9 May	123	5.8	16	2.76	0	0	23.6 ±10.6	331	154	50	9	25.1
4	6 June	748	7.6	8	1.05	0	0	24.8 ± 9.9	302	161	53	10	28.5
5	10 June	348	7.9	16	2.03	1	0.13	28.0 ± 12.1	420	205	61	14	32.8
6	8 July	583	5.4	12	2.22	0	0	28.5 ± 12.2	367	175	51	20	36.9
7	13 July	372	7.0	22	3.14	3	0.43	27.9 ± 11.4	430	207	46	7	27.9
8	19 July	642	4.9	16	3.27	7	1.43	28.9 ± 12.7	351	178	60	18	38.5
9	10 Aug.	132	6.5	13	2.00	2	0.31	19.2 ± 8.5	264	122	34	5	16.0
10	16 Aug.	425	5.8	11	1.90	1	0.17	29.5 ± 13.9	294	135	40	17	31.2
11	24 Aug.	636	4.3	10	2.33	3	0.70	22.5 ± 13.3	244	118	29	7	19.1
12	7 Sept.	231	5.2	10	1.92	0	0	25.8 ± 13.9	316	140	38	9	26.9
13	21 Sept.	601	6.8	10	1.47	4	0.59	31.3 ± 12.8	302	149	58	15	33.8
Total/ave.			80.5	180	2.24	24	0.30	26.4 ±11.7	317.6	152.8	45.7	11.5	30.1
Total[1]			60.2[1]	136[1]	2.27	19[1]	0.32		Total: 527.6				

[1] Areas of overlap between listening areas and their groups have been subtracted out.

Table 2. Characteristics of 1-ha grids without and grids with siamangs.

No.	Characteristic	Mean		Kolmogorov-Smirnov test		Mann-Whitney *U* test and *t*-test		
		Grids without siamang	Grids with siamang	Statistic	*P*	Statistic	*P*	Test
1	Altitude (m)	414	478	0.061	0.200	–2.099	0.044	*t*-test
2	Distance from ridge (m)	188	90	0.134	0.000	–3.530	0.000	*U* test
3	Slope direction	1.152	1.596	0.209	0.000	–2.596	0.009	*U* test
4	Slope value (deg.)	36.5	18.4	0.094	0.001	–4.530	0.000	*U* test
5	Distance from road (km)	3.72	1.71	0.082	0.008	–3.703	0.000	*U* test
6	Distance from village (km)	4.05	5.94	0.097	0.000	–4.180	0.000	*U* test
7	Distance from stream (m)	285	204	0.079	0.011	–1.692	0.091	*U* test
8	Distance from edge (km)	0.94	1.62	0.094	0.001	–3.300	0.001	*U* test

Table 3. Characteristics of 1-ha grids without and grids with agile gibbons.

No.	Characteristic	Mean		Kolmogorov-Smirnov test		Mann-Whitney *U* test and *t*-test		
		Grids without agile	Grids with agile	Statistic	*P*	Statistic	*P*	Test
1	Altitude (m)	437	361	0.05	0.083	3.786	0.000	*t*-test
2	Distance from ridge (m)	183	119	0.11	0.000	–5.007	0.000	*U* test
3	Slope direction	0.936	0.955	0.12	0.000	–0.191	0.848	*U* test
4	Slope value (deg.)	20.1	20.2	0.092	0.000	–0.119	0.905	*U* test
5	Distance from road (km)	3.43	2.21	0.103	0.000	–4.462	0.000	*U* test
6	Distance from village (km)	4.26	4.75	0.063	0.008	–2.435	0.015	*U* test
7	Distance from stream (m)	293	239	0.08	0.000	–2.369	0.018	*U* test
8	Distance from edge (km)	0.99	1.40	0.095	0.000	–3.581	0.000	*U* test

available within the study area. Siamangs tended to be located near the tops of ridges whereas agile gibbons appeared to show a preference for valley areas. Both species appeared to be negatively affected by human-related factors distance from villages and edge of forest, but not by distance from road. However, the human-related factors are correlated to a degree with the terrain factors (especially elevation and distance from ridge, so that it is not clear from this analysis which factors most strongly affect gibbon distribution. Distance from forest edge was positively related to gibbon density and altitude was negatively related; distance from edge therefore could not be responsible for the altitude effect, or it would have produced a positive relation between density and altitude. Therefore both factors must have affected gibbon density independently. Distance from villages and from streams had much weaker effects, so that we may discount these factors for agile gibbons. In the case of siamang, altitude, distance from the forest edge and distance from nearest village had positive relations with density, so the effects of these three factors are difficult to separate. For both species, distance to nearest road had a negative relation with density (more groups near the road than farther away), so that the effect of this factor is spurious. There are more groups in the southern part of the sanctuary where the road happens to be located, so that it seems that the single road that crosses the sanctuary has had little effect on their distribution.

Differences in habitat distribution between siamangs and agile gibbons were also compared directly, by comparing points with siamangs and points with agile gibbons. It was found that four factors (altitude, slope direction, slope value, and distance from village) were significantly different between siamang and agile gibbon points (Tables 4, 5). No siamang groups occurred below 200 m, but 21% of agile gibbon groups did so (Fig. 3). Half of the siamang groups, but only 21% of agile gibbon groups, occurred above 650 m. Agile gibbons did not tend to favor east-facing slopes as did siamangs.

No forest characteristics were significantly related to either siamang or agile gibbon density. Forest condition was good to excellent for gibbons throughout the forest. Average canopy height in the 13 LAs was 26.4 m (range 19.2–31.3 m) (Table 1). These averages include points that happened to fall in canopy gaps; many emergent trees in the Bala Forest exceed 50 m in height, and the highest exceeded 60 m. The average standard deviation of the individual point canopy heights per LA, a measure of canopy roughness (or rugosity), was 11.7 m (range 8.5–13.9 m; $N = 13$). The average number of large trees > 80 cm in DBH ha^{-1} was 11.5 (range 5–20), indicating a relatively old-growth forest in healthy condition. The basal area of trees >10 cm DBH averaged 30.1 m^2 ha^{-1} (range 17.0–41.2 m^2 ha^{-1}) (Table 1).

Table 4. Characteristics of 1-ha grids with siamangs and grids with agile gibbons.

No.	Characteristic	Mean		Kolmogorov-Smirnov test		Mann-Whitney *U* test and *t*-test		
		Grids with agile	Grids with siamang	Statistic	*P*	Statistic	*P*	Test
1	Altitude (m)	361	478	0.078	0.022	–3.244	0.001	*U* test
2	Distance from ridge (m)	119	90	0.153	0.000	–1.167	0.243	*U* test
3	Slope direction	0.955	1.596	0.188	0.000	–7.075	0.000	*U* test
4	Slope value (deg.)	20.2	18.4	0.485	0.000	–7.075	0.000	*U* test
5	Distance from road (km)	2.21	1.71	0.107	0.000	–1.009	0.313	*U* test
6	Distance from village (km)	4.75	5.94	0.068	0.078	–3.593	0.000	*t*-test
7	Distance from stream (m)	239	204	0.091	0.003	–0.567	0.57	*U* test
8	Distance from edge (km)	1.40	1.62	0.076	0.030	–1.113	0.266	*U* test

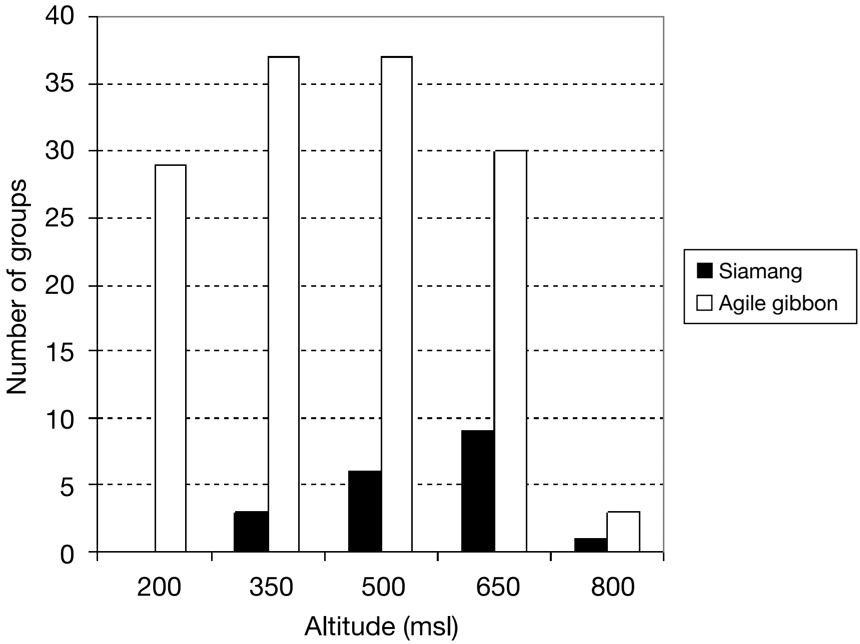

Figure 3. Numbers of groups of gibbons of each species in altitude classes in Bala Forest (number indicates upper limit of altitude class).

Table 5. Differential characters between habitats with and without agile gibbons, habitats with and without siamang, and siamang and agile gibbon habitat (from Tables 2, 3 and 4) in Bala Forest.

No.	Factors	Agile		Siamang		Siamang and agile gibbon	
		Habitat of agile	Habitat without agile	Habitat of siamang	Habitat without siamang	Habitat of siamang	Habitat of agile
1	Altitude	< (**)	> (**)	> (*)	< (*)	> (**)	< (**)
2	Distance from ridge	< (**)	> (**)	< (*)	> (**)		
3	Slope value			< (**)	> (**)	> (**)	< (**)
4	Distance from road	< (**)	> (**)	< (**)	> (**)		
5	Distance from village	> (*)	< (*)	> (**)	< (**)	> (**)	< (**)
6	Distance from stream	< (*)	> (*)				
7	Distance from edge	> (**)	< (**)	> (**)	< (**)		

*= $P < 0.05$, ** = $P < 0.01$

DISCUSSION

A small population of at least 19 groups of siamangs still exists in Bala Forest (range 0–1.43 groups km^{-2}, average 0.32 groups km^{-2} in the 60 ha that was intensively surveyed). In peninsular Malaysia and Sumatra siamang group density ranges from about 1.5 to 3 groups km^{-2}. The highest densities were in the eastern part of Hala-Bala Wildlife Sanctuary, occurring at higher altitudes of 500–700 m. This would be considered middle altitudes in mountainous habitats farther south in Malaysia and in Sumatra. The density of agile gibbons in Hala-Bala, ranging up to 3.3 groups km^{-2}, is comparable to densities of agile gibbons elsewhere, although it does not reach the maximum densities of over 4 groups km^{-2} reported at Sungai Dal, Malaysia (GITTINS & RAEMAEKERS, 1980). The mean density of agile gibbons in Sumatra estimated by O'BRIEN *ET AL.* (2004) of 0.67 groups km^{-2} seems likely to be an underestimate, with their assumption that all groups within 2 km from listening posts could be heard (in unobstructed terrain). We have found that, for white-handed and pileated gibbons, duets can be heard that far only under ideal weather and terrain conditions (e.g. BROCKELMAN & SRIKOSAMATARA, 1993; SRIKOSAMATARA & BROCKELMAN, 1983).

O'BRIEN *ET AL.* (2004) pointed out that densities of agile gibbons tend to increase from southern to northern latitudes on Sumatra, Borneo and peninsular Malaysia, but siamang densities tend to decline from south to north. Densities of siamangs in our site suggest that Bala Forest is the northernmost limit of this species on the peninsula, as the low number of groups remaining suggests a relict distribution that peters out in the middle of the sanctuary. There is no evidence that any physical barrier has limited the dispersal of siamangs (except for recent agricultural development and a road now crossing the sanctuary east to west). The agile gibbon, on the other hand, occupies most of the sanctuary and is probably limited by habitat degradation and human disturbance in the northern part of the sanctuary. The distribution of agile gibbons extends north into Yala Province west of the Hala-Bala range, and is in southern Thailand and Malaysia limited by the Tepha River in Thailand and the Muda River in Malaysia (BROCKELMAN & GITTINS, 1984; MARSHALL, 1981). The agile gibbon would doubtless disperse farther north were it not for these rivers and the presence of its ecological equivalent, the white-handed gibbon *Hylobates lar*, on the other sides of them.

What habitat characteristics might affect the distribution of siamangs in Bala Forest? No measures of forest condition (DBH of trees, canopy cover, height) in the listening areas were significantly related to the density of either species. This does not mean that these variables are not important, but only that they did not vary sufficiently to adversely affect the gibbons in the sanctuary, or that the forest condition on the transects was not necessarily representative of that in the gibbon home ranges. Several other habitat and site factors were significantly correlated with gibbon density. Altitude was positively related to siamang density but negatively related to agile gibbon density. In comparison with agile gibbons, siamangs tended to occur on sites closer to the ridge or hilltop, on east-facing slopes and on less steep slopes, and also farther from the forest edge and local villagers. Neither species was affected by distance to the nearest road, and gibbons in Bala habituate to the presence of roads and human activity there (as long as they are not hunted), just as white-handed and pileated gibbons do in Khao Yai National Park farther north (unpublished observations). Siamangs were more distant from villages than were agile gibbons. It is not likely that siamangs near villages were selectively hunted or chased away by villagers; their more remote distribution is most likely due to a preference for higher altitudes.

Local people were not found hunting gibbons in Bala Forest; however, the gibbons may be affected by local people in villages around Bala Forest who collect non-timber products such as fruits of *Baccaurea* spp., *Dialium* spp., and *Garcinia atroviridis* (Tohdam, 2001), species which are also foods for siamang and agile gibbons (Chivers, 1974; Chivers, 1980). About 9 percent of people collected these fruits by cutting down trees (Tohdam, 2001) which will also reduce available food sources for the gibbons.

The preference for high altitudes is characteristic of siamangs in most areas in Malaysia and Sumatra (Caldicott, 1980; Marsh & Wilson, 1981; O'Brien *et al.*, 2004; Wilson & Wilson, 1976; Yanuar, 2009). In Thailand, gibbons do not occur above about 1000 m in altitude, above which lower montane (or "hill evergreen") forest occurs. The lower montane forest zone occurs somewhat lower in Thailand than it does in the central tropics. Thus, siamangs, which thrive at high altitudes in the central tropics, may find lower montane forest less suitable farther north, and find themselves more forced into competition with the smaller *Hylobates* gibbons. In Bala Forest, their distributions are largely non-overlapping, with the agile population densest in the lower valleys. Without more detailed floristic analysis and behavioral observations, however, we will not be able to determine exactly what limits siamang distribution in Thailand, although we suspect that it has to do with the quality of the habitat, and possibly also competition with the agile gibbon. The structure, density and height of the forest in Bala appear to be entirely suitable for any species of gibbons, although it is unclear to us how much the gibbons were disturbed by the logging activities of several decades ago.

There is not enough terrain at sufficiently high altitude in the Bala range to allow siamangs to maintain a very large population. With only 19 documented groups, the siamang population in the sanctuary (and in Thailand) is critically endangered, and will only survive with diligent protection. Reducing use of the forest by villagers, particularly the cutting of fruit trees, will be essential to allowing both species to survive in this relatively small forest area.

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