

# GROUP ENCOUNTERS IN WILD GIBBONS (*HYLOBATES LAR*): AGONISM, AFFILIATION, AND THE CONCEPT OF INFANTICIDE

by

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## Summary

1. Gibbons are the least studied apes and traditionally thought to live in nuclear families of 2-6 individuals including a pair of breeding adults who maintain lifelong, sexually monogamous relationships and vigorously defend territories against neighbours. The present paper challenges this view.
2. During a long-term study on white-handed gibbons (*Hylobates lar*) in Thailand's Khao Yai rainforest, 162 encounters were recorded between 3 habituated and 8 non-habituated groups. Encounters characterized 9% of the activity day (mean 8.31 h). Those between habituated groups were nine times more frequent (0.7/day) and lasted significantly longer (median 70 min) than encounters with non-habituated neighbours (median 38 min). It was also found that gibbon group home ranges (mean 24 ha) overlap extensively (64%) with neighbours', all of whom were met. However, most previous studies centered on single groups surrounded by unhabituated neighbours. This produced underreporting of the importance of inter-group interactions, particularly the affiliative aspects observed presently.
3. Encounters included many elements which seem to have a 'defensive' function. Chases occurred during 61%, contact aggression during 8-9%; each adult and subadult male chased

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all others and was chased by all others. Moreover, encounters occurred often in or near food trees and rates peaked during the early morning when ripe fruit were most abundant. However, a seasonal correlation between the rate of encounters and (crude) measures of resource availability could not be detected.

4. The study indicates that gibbon groups are structured by female resource-defense and male mate-defense because adult females led 76% of all travels into and out of fruit trees, whereas males moved to the front as soon as neighbours were encountered. Male-male interactions constituted 90% of all inter-group chases. This pattern is compatible with the idea that conflicts over food sources (which can be shared) will rarely provoke contact aggression. Control of mate access, on the other hand, has a much higher relative value for males. These explanations are more parsimonious than the traditional concepts of 'pairbonding' and 'territoriality'.

5. Contrary to earlier assumptions, encounters were nevertheless not always dominated by aggression. Groups fed, traveled or rested together for prolonged times (35% of encounters). Inter-group play between immatures was likewise common (21% of encounters; 55% dyadic, 45% triadic and quartetic play). Same-aged play partners are not present in a gibbon's natal group. However, gibbon youngsters clearly preferred age-mates during inter-group play which may indicate that play is ontogenetically important.

6. The adult female of one group copulated not only with her pair-mate, but also with two neighbouring males. The overall proportion of extra-pair-copulations (EPC) was 12% and they occurred during a period when the female conceived. Encounters thus provide opportunities for alternative mating strategies. However, philandering males are faced with the dilemma to lower their mate guard which creates a risk of cuckoldry for themselves. This could explain why subadults are often tolerated in natal groups beyond sexual maturity, because they assisted the resident adult male during agonistic encounters. Moreover, females gave solo great calls during a quarter of all encounters. These calls increase the costs of philandering for the paired male (who cannot answer without giving away that his female is unguarded) and may at the same time attract neighbouring males.

7. For the first time, close spatial proximity and body contact between intruding adult males and infants of neighbouring groups are reported, including play (during 6% of all inter-group play sessions). Immatures were at times relaxed but at other times frightened in the presence of neighbouring males. A near-zero mortality of infants at Khao Yai shows that infanticide is absent or at least not a regular occurrence. EPCs and a long period of pre-conception copulations could be strategies of females to confuse paternity and forestall infanticide. In any case, the non-monogamous mating pattern makes it likely that kin-relationships extend well into neighbouring groups. A reduced level of inter-group competition and aggression is therefore not surprising.

*Keywords:* gibbon, territoriality, monogamy, infanticide.

## **Introduction**

Aggression between groups is seen as a major selective factor in human evolution (Aiello & Dunbar, 1993). Nevertheless, behavioural studies of

primates focus overwhelmingly on social interactions within groups. Thus, the causes for friendly or agonistic group interactions are poorly understood (review in Cheney, 1987). A taxon traditionally seen as a model for aggressive territorial group encounters are the gibbons, the least studied *Hominoidea*. Our data illustrate that the concept of territorial defense as the driving force behind group encounters is too narrow. We also discuss evidence for the theory that protection from infanticide fostered the evolution of monogamy in gibbons (van Schaik & Dunbar, 1990) and perhaps permanent male-female associations amongst primates in general (van Schaik & Kappeler, 1993).

Gibbons (*Hylobatidae*) are arboreal apes confined to South-East Asia, Northwest-India and Bangladesh (overviews on ecology and behaviour in Preuschoft *et al.*, 1984; Tuttle, 1986; Leighton, 1987). They live in groups of usually 2-6 individuals which mostly contain a single adult female, a single adult male and immatures. Gibbon females give birth about every third year. Once an infant becomes independent with about 2 years, females may cycle several months before a new conception. Until recently, gibbons were thought to form permanent pairs (*e.g.* Mc Cann, 1933; Carpenter, 1940; Tenaza & Hamilton, 1971; Ellefson, 1974; Tilson, 1979; Brockelman & Srikosamatara, 1984). However, this view of mandatory nuclear families with a socially and sexually monogamous pair has been challenged by observations of extra-pair copulations and partner changes (*e.g.* Palombit, 1994a, b; Reichard, 1995). Gibbon groups occupy relatively stable home ranges including an exclusively used core area which many researchers consider to be a territory. Suitable habitats are usually saturated with groups (*e.g.* Mitani, 1990), creating a tight mosaic pattern of closely interlocking home ranges. Edges overlap and meetings between neighbours are common.

Traditionally, group relations in gibbons are thought to deal only with territorial defense. However, actual knowledge about group encounters is scarce, for several reasons. (a) Groups often flee silently from observers which is facilitated by their small group size and arboreality. (b) Recording complex events taking place high up in the canopy is difficult. (c) Most earlier observers habituated at best a single group. (d) Life-histories and thus kin-relations of individuals in adjacent groups are unknown. We solved these problems at least partly because our data derive from the longest

field study on hylobatids, spanning about 17 years and involving several well-habituated neighbouring groups (*cf.* Brockelman *et al.*, in press).

### Material and methods

The study site was located at 730-870 m elevation inside the primary rain forest of the Khao Yai National Park, Thailand (2,168 km<sup>2</sup>; 101°22' E, 14°26' N; 130 aerial km NE of Bangkok). A population of white-handed gibbons (*Hylobates lar*) immediately west of park headquarters in the Mo Singto area has been studied by various observers since 1979 (*e.g.* Raemaekers & Raemaekers, 1984a, b; Treesucon, 1984; Brockelman, 1985; Whittington, 1990; Reichard, 1996). About half a dozen trees in the study area were illegally exploited for an incense raw-product over the last decade, but otherwise the gibbons were not threatened by poaching or forest destruction.

The authors collected data during the following periods; UR: Oct89-Jan90 (55 days, ~150 h), Jan92-May93 (259 days, ~1600 h), Oct93 (~15 days), Oct94 (~15 days), May-Jun96 (~21 days); VS: Sep94-Jul96 (110 days, ~550 h). Observations focused on three adjacent gibbon groups (A, B, C) whereas neighbours were studied opportunistically during encounters with the main study groups and surveys (Fig. 1). All these gibbons were individually identifiable. Qualitative information presented in this paper may originate from any of these observation periods. However, quantitative analysis is restricted to Jan92-May93 when UR observed groups A, B and C during 250 days for a total of 1537 h. The core data set stems from a one-year period of focal-animal sampling (Altmann, 1974) on groups A, B, C (May92-Apr93, 175 days, 1209 h; see below, Table 1). Data were collected using a battery-powered, hand-held-size computer (Psion Organiser LZ 64) connected to a bar-code reader pen. Codes were displayed on a score-board which was carried by the observer in front of the belly (*cf.* Reichard, 1996). Fast sequences were at times tape recorded. Most observation days started at dawn and ended around 16:30 after the apes had settled in their sleeping trees. Data on group encounters were recorded *ad libitum*. An *encounter* was defined to start when a group approached another within 50 m and it ended when groups had again distanced themselves further away than 50 m.

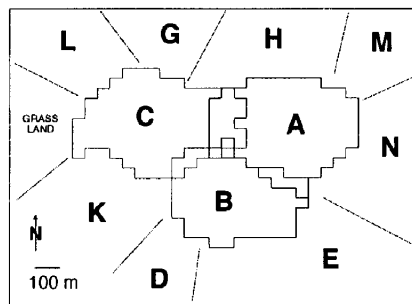


Fig. 1. Home ranges of main study groups (A, B, C) and neighbours, Khao Yai National Park, Thailand (1992-93).

TABLE 1. *Distribution of observations and encounters of main study groups with neighbours*

Period	Observation days			Observation h			Encounter rate/day <sup>1)</sup>			Mean
	Group A	Group B	Group C	Group A	Group B	Group C	Group A	Group B	Group C	
1992 May	5	11	6	51	87	48	1.2	1.3	0.3	0.9
Jun	1	3	-	4	22	-	-	1.8	-	1.8
Jul	1	-	5	1	-	37	-	-	0.4	0.4
Aug	-	-	-	-	-	-	-	-	-	-
Sep	5	-	9	50	-	78	0.5	-	0.7	0.6
Oct	8	11	9	39	74	70	1.1	0.9	0.8	1.0
Nov	3	-	-	15	-	-	0.6	-	-	0.6
Dec	7	7	7	51	53	51	0.3	0.0	1.1	0.5
1993 Jan	6	8	8	47	43	57	0.3	0.4	0.5	0.4
Feb	6	9	5	46	61	33	0.6	0.6	0.0	0.4
Mar	21	-	-	122	-	-	1.6	-	-	1.6
Apr	14	-	-	69	-	-	1.1	-	-	1.1
Subtotal	77	49	49	495	340	374				
Grand total	175			1209			0.8	0.8	0.5	0.7
Mean										

<sup>1)</sup> For months with  $\geq 15$  h of observation.

TABLE 2. *Composition of the main study groups*

Group	Sex	Color	Name	Jan92-May93		Sep94-Jul96	
				Age class	Denotation (Age/Sex/Group)	Age class	Denotation (Age/Sex/Group)
A	F	Buff	Andromeda	Adult	AFA	Adult	AFA
	M	Black	Fearless <sup>1)</sup>	Adult	AMA	Adult	AMA
	M	Black	Arnadeus	Juvenile	JMA	Subadult	SMA
	M	Buff	Aran	Infant	IMA	Juvenile	JMA
	M	Buff	Akira			Infant	IMA
B	F	Black	Bridget	Adult	AFB	Adult	AFB
	M	Black	Bard	Adult	AMB	Adult	AMB1
	F	Black	Brit	Subadult	SFB <sup>2)</sup>		
	F	Buff	Brenda	Juvenile	JFB	Subadult	SFB
	F	Black	Benedetta	Infant	IFB	Juvenile	JFB
	M	Buff	Chet			Adult	AMB2 <sup>3)</sup>
C	F	Black	Cassandra	Adult	AFC	Adult	AFC
	M	Buff	Cassius	Adult	AMC	Adult	AMC
	M	Buff	Chet	Subadult	SMC1 <sup>3)</sup>		
	M	Black	Claude	Subadult	SMC2 <sup>4)</sup>		
	M	Black	Christopher	Juvenile	JMC	Subadult	SMC
	M	Buff	Caleb	Infant	IMC	Juvenile	JMC
	M	Black	Cyrano			Infant	IMC

1) Emigrated from group F into group A in 1983.

2) Left group in about Aug92, formed new pair (group R) before Mar93.

3) Emigrated from group C into group B during 1994.

4) Emigrated from group C into group N during 1993.

Table 2 lists the composition of the main study groups which were well habituated to gibbon researchers (group A since about 1981, groups B and C since May92). Gibbons are arboreal apes. Nevertheless, they do on rare occasions descend to the ground (*e.g.* VS observed about half a dozen ground contacts of usually less than 1 min). However, they sometimes traveled in heights of less than 5 m right above observers. Visibility into the canopy was variable but often very good, particularly during the dry winter. A marked and measured trail system, often along elephant paths, transversed the study area. Day ranges of gibbon groups were reconstructed on maps with grid cells of 50 × 50 m.

Gibbons are peculiar amongst *Hominoidea* because of their vocalizations (review in Haimoff, 1984; Raemaekers *et al.*, 1984; Cowlishaw, 1992) which can be heard from 1-2 km away. Males and females sing loud duets, mostly from 07:00-11:00. Duets consist of a warm-up phase by both individuals, followed by a high-pitched female 'great call' and a male 'reply/coda'; the sequence may or may not be repeated many times. Male gibbons also sing 'solos', mostly around dawn. A typical call during encounters is the 'male encounter vocalization', a series of low-key hoots. Other observers termed the calls 'conflict vocalization' (Brockelman & Srikosamatara, 1984) or 'conflict hoo(t)s' (Ellefson, 1974; Gittins, 1980). A more neutral term is preferred in this paper to avoid implications about the calls' function.

## Results

### *Home range use and group cohesion*

The following section describes general features of group life to provide the necessary backdrop against which the role of encounters has to be viewed.

Home ranges of groups A, B and C as measured from Aug-Dec92 (Neudenberger, 1993) comprised on average 24 ha. Non-overlapping areas between the 3 groups constituted 71% (group A, 64.3% of 24.5 ha; group B, 74.4% of 21.5 ha; group C, 73.6% of 26.5 ha). However, all groups had 5-6 neighbours and overlap existed with all of them. The length of borders amongst groups A, B and C and the proportion of overlap was used to calculate the expected overlap with other neighbours, yielding a mean of 63.7%. Thus, only about one third of a group's range was exclusively used (*cf.* Fig. 1). Both successive and simultaneous use of overlap areas occurred, the latter of which being the basis for encounters. Adult females tended to enter and leave food sources as the first group member whereas adult males tended to travel behind them (Table 3; binomial test,  $z_{\text{enter}} = -6.83$ ,  $x = 15$ ,  $p < 0.001$ ,  $z_{\text{leave}} = -3.67$ ,  $x = 39$ ,  $p < 0.001$ ). This progression order clearly contrasts the pattern during group encounters (male in front, female in the background; see below). The decision to treat 'groups' as

'units' that encounter each other is justifiable because members maintained close spatial proximity throughout the day. (An exception was SMC2 who sometimes left for days to unknown places. He was then considered as not being with the group.) The median distance to the nearest neighbour was between arms' reach and 10 m (Fig. 2). Distances between the female and infant in group B, which was carried for most of the time were excluded from the sample. Only during 0.8% of the time was any group member (nearly always a subadult or adult male) found to be further away than 50 m from others. But such periods of peripherization were usually short (<45 min). In almost all cases did groups reunite if neighbours were encountered.

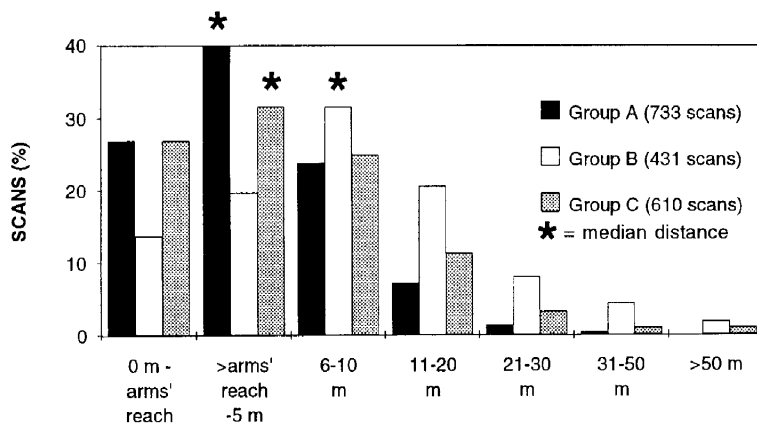


Fig. 2. Intra-group spatial distributions. Based on distances to the nearest neighbour of focal animals sampled in 15-min intervals, with equal distribution over daytime and individuals.

TABLE 3. Progression orders of adults while entering and leaving fruit trees

Group	Entries			Departures		
	Female enters before male	Male enters before female	N	Female leaves before male	Male leaves before female	N
A	81.1%	18.9%	37	81.8%	18.2%	44
B	76.5%	23.5%	17	52.0%	48.0%	25
C	91.1%	8.9%	45	62.0%	38.0%	50
Average	82.9%	17.1%		65.3%	34.7%	

*Frequency and duration of group encounters*

Out of 21 possible combinations of group encounters, 86% were observed (Fig. 3). The habituated main study groups A, B, C met all their neighbours. It is thus very likely that every group encountered all neighbours and that the few non-recorded combinations were a mere consequence of too limited observation time. Encounters between the habituated groups accounted for 77% of all 162 recorded meetings. Habituated groups met significantly more frequently with each other (every 11.1 hours) than with non-habituated neighbours (every 100.0 h; Mann-Whitney *U*-test;  $U = 0.01$ ;  $N_{1,2} = 8$ ;  $p < 0.001$ ). Meetings of group A with habituated groups lasted significantly longer than those with non-habituated groups (Mann-Whitney *U*-test;  $U = 251.5$ ,  $N_1 = 71$ ,  $N_2 = 14$ ,  $p < 0.01$ ; Table 4). The overall median of complete encounters was 70 min (Fig. 4). Encounter durations did not differ between the study groups (Kruskal-Wallis one-way analysis of variance,  $H = 4.161$ ;  $N_1 = 36$ ,  $N_2 = 35$ ,  $N_3 = 14$ ;  $p > 0.05$ ). Clearly, detailed information on inter-group relations can only be deduced from meetings between individuals tolerant to observers, to which most of the further analysis is restricted.

Encounters usually followed if two groups were aware of each other within distances of 100-150 m. In only 10% of all cases when groups had come within 50 m did they not approach further below 20 m. Encounters occurred every 1.7 days during 98 full-day follows of the main

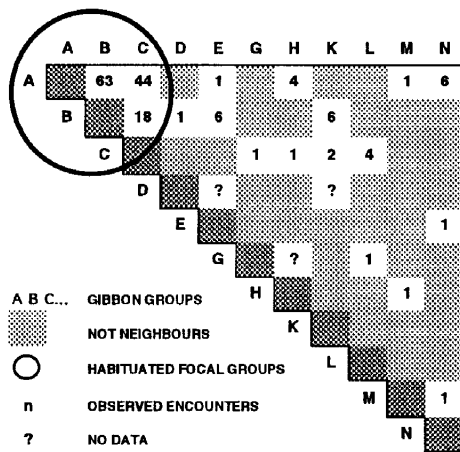


Fig. 3. Encounters between 11 gibbon groups at Khao Yai ( $N = 162$ ; Jan92-May93).

TABLE 4. *Duration of encounters of group A*

	Groups	Encounters		
		Duration (min)		
		N	Median	Range
<b>Non-habituated groups</b>				
Feb92-Apr92 (before habituation of groups B & C)	A-B	8	27	3-46
	A-C	1	51	
Feb92-Apr93	A-N	3	56	15-69
	A-M	1	71	
	A-H	1	38	
	Total	14	38	
<b>Habituated groups</b>				
May92-Apr93	A-B	36	71	2-231
	A-C	35	75	11-195
Total	71	70		

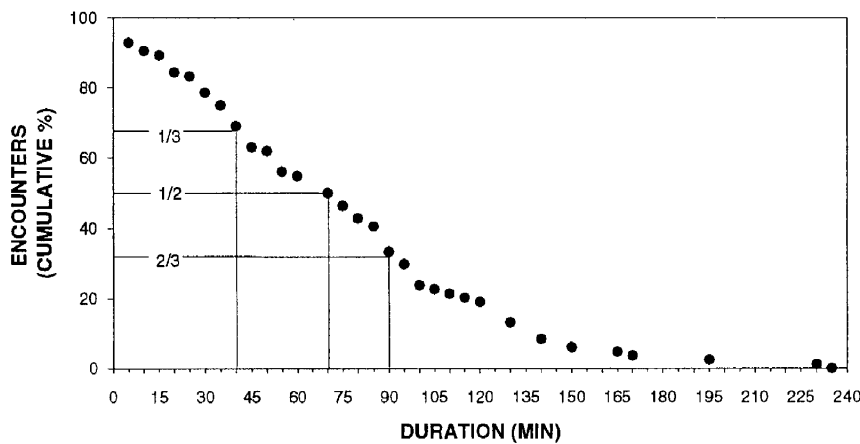


Fig. 4. Durations of 84 encounters observed from onset to end in main study groups A, B, C. 71 encounters were between A, B, and C and 14 encounters involved non-habituated groups which, however, did not detect the observer by all likelihood.

study groups. No encounter was recorded during 41.8% of these days, one encounter during 35.7% (every 2.8 days), two during 17.3% (every 5.8 days), three during 3.1% (every 32.7 days), four and the maximum of five during 1.0% each (every 102.0 days). It was often (but not always)

the same group that was met repeatedly during the same day. Overall, the main study groups met neighbours every 1.4 days (A = 1.3 days, B = 1.3 days, C = 2.0 days; Table 1). Monthly rates did not differ between the groups (Mann-Whitney *U*-test, A&B:  $U = 26$ ;  $N_1 = 9$ ;  $N_2 = 6$ ;  $p > 0.9$ ; A&C:  $U = 49$ ;  $N_1 = 9$ ;  $N_2 = 11$ ;  $p > 0.9$ ; B&C:  $U = 32.5$ ;  $N_1 = 6$ ;  $N_2 = 11$ ;  $p > 0.9$ ). Thus, group size (A,  $N = 4$ ; B,  $N = 5$ ; C,  $N = 6$ ) seemed to have no influence on encounter frequencies. The average activity day of gibbons of groups A, B and C lasted for 8 h 31 min from 06:16-14:47 (range 05:27-07:36 for  $N = 163$  records of focal individuals except infants leaving night-trees; range 13:15-16:17 for  $N = 270$  records of entering night-trees). Encounters occurred at all but the last hour of activity (Fig. 5) but were unevenly distributed throughout the day (Kolmogoroff-Smirnov test;  $K-S = 1.897$ ,  $N_1 = 20$ ,  $N_2 = 20$ ,  $p = 0.001$ ). Rates peaked between 06:30 and 07:59 and again shortly after 09:00. Half of all encounters began during the first third of the day and only about 12% during the last third. Groups spent 9% of their daytime activity in encounters with no differences between groups (A, 8 h 53 min,  $N_1$  [leave sleeping tree] = 67;  $N_e$  [enter sleeping tree] = 119, 1.3 encounters/day, average 70 min = 10.1%; B, 8 h 40 min,  $N_1 = 32$ ;  $N_e = 43$ , 1.3 encounters/day, average 67 min = 9.9%; C, 7 h 58 min  $N_1 = 72$ ;  $N_e = 109$ , 2.0 encounters/day, average 64 min = 6.7%).

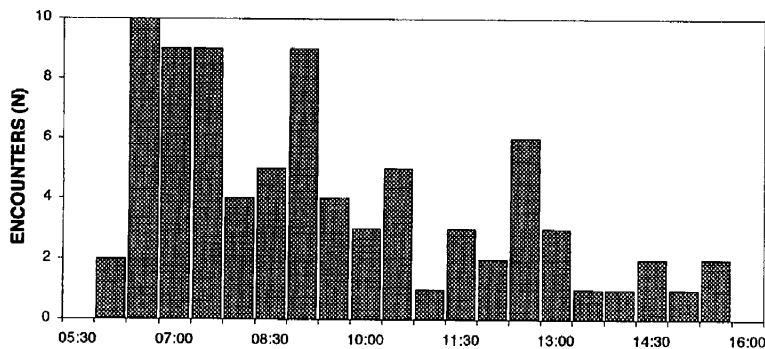


Fig. 5. Diurnal distribution of encounters in main study groups A, B, C ( $N = 82$ ). Based on 98 follows from night tree to night tree. Encounters were scored only once at the beginning; those with unknown onset ( $N = 4$ ) were scored to the nearest hour.