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Group Harmony in Gibbons: Comparison Between White-handed Gibbon (*Hylobates lar*) and Siamang (*H. syndactylus*)

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ABSTRACT. The siamang (*Hylobates syndactylus*) is exceptional among gibbons in that its area of distribution almost completely overlaps those of other gibbons, namely the white-handed gibbon (*H. lar*) and the agile gibbon (*H. agilis*) of the lar group. The siamang has almost twice the body weight of the gibbons of the lar group (ca. 11 kg vs. 5–6 kg), and it has been suggested that distinct ecological and behavioural differences exist between the siamang and its two sympatric species. The siamang has been claimed to differ from the white-handed gibbon "in the closer integration and greater harmony of group life" (CHIVERS, 1976, p. 132). However, few quantitative data exist to support this hypothesis. In the present study, intra-group interactions in captive family groups of white-handed gibbons and siamangs (two groups of each species) were recorded by focal-animal sampling. These data failed to show a consistent association between species and most of the behavioural patterns recorded, such as frequency of aggression, percentage of successful food transfer, frequency of social grooming bouts, and duration of social grooming/animal/hr. A significant difference was found for only two of the variables: Individual siamangs in this study showed longer grooming bout durations, and made fewer food transfer attempts than lar individuals. Only the first of these two differences is consistent with the hypothesis mentioned above, whereas the lower frequency of food transfer attempts in siamangs is the opposite of what should be expected under the hypothesis. On the other hand, two of these behavioural patterns showed a significant correlation with the parameters group size and individual age: Both individuals in larger groups and younger individuals tended to show shorter grooming bouts and a smaller proportion of successful food transfers. Our findings indicate that social cohesion within these gibbon groups may be much more flexible according to and depending on social or ecological influences and less rigidly linked to specific gibbon taxa than previously assumed. A considerably larger number of gibbon groups would have to be compared to provide reliable evidence for or against species-specific differences in group cohesion. Another finding of this study—a positive correlation between the frequency of aggression and grooming—is discussed in the light of the functional interpretations commonly attributed to allogrooming behaviour in primates.

Key Words: White-handed gibbon; Siamang; *Hylobates lar*; *Hylobates syndactylus*; Social cohesion; Aggression; Food transfer; Grooming.

INTRODUCTION

In spite of many similarities shared by most or all gibbon species (e.g. GROVES, 1972; LEIGHTON, 1987; SCHULTZ, 1973), the siamang (*Hylobates syndactylus*) is exceptional among gibbons in that its area of distribution almost completely overlaps those of other gibbons, namely those of the white-handed gibbon (*H. lar*) and the agile gibbon (*H. agilis*) of the lar group (CHIVERS, 1971, 1972, 1974, 1977a, 1978; CHIVERS & GITTINS, 1978; GROVES, 1972; KHAN, 1970; LIAT, 1969; MARSHALL & SUGARDJITO, 1986; WILSON & WILSON, 1977). The siamang has almost twice the body weight of the gibbons of the lar group (ca. 11 kg vs. 5–6 kg) (e.g. JUNGERS, 1984; SCHULTZ, 1973), and it has been suggested that distinct differences in ecology and behaviour exist between the siamang and the two sympatric species (CALDECOTT, 1980; CHIVERS, 1972; GITTINS & RAEMAEKERS, 1980; MACKINNON, 1977; MACKINNON & MACKINNON, 1978, 1980; RAEMAEKERS, 1978a, b, 1979, 1984; RAEMAEKERS & CHIVERS, 1980).

Among other things, the siamang has been claimed to differ from the white-handed gibbon and other gibbons of the lar group "in the closer integration and greater harmony of group life" (CHIVERS, 1976, p. 132; see also CHIVERS, 1972, 1974, p. 293, 1984b, p. 418; GITTINS & RAEMAEKERS, 1980, p. 72f). However, few directly comparable data exist to support this view, which appears to be based mainly on the following three observations: (1) the members of a siamang group spent more of their time less than 10 m apart than the members of an agile gibbon group; (2) the members of a siamang group were all visible more frequently than the members of a lar gibbon group; and (3) the siamangs "sleep in one or two adjacent trees, whereas the smaller species scatter, sometimes over hundreds of metres." (GITTINS & RAEMAEKERS, 1980, p. 73).

In the present study, intra-group interactions in captive family groups of white-handed gibbons and siamangs (two groups of each species) were observed. Three different classes of interactions were recorded by focal-animal sampling. They will be referred to in this study as aggression, food transfer, and grooming. Intra-group aggression is thought to be relatively rare among gibbons and siamangs (BERNSTEIN & SCHUSTERMAN, 1964; CHIVERS, 1977b, p. 96; KAWATA, 1980; RIESS, 1956), as compared to Old World monkeys, whereas food transfer appears to be relatively common (BERKSON & SCHUSTERMAN, 1964; BERNSTEIN & SCHUSTERMAN, 1964; FOX, 1977, 1984; ORGELDINGER, 1989; RIESS, 1956; SCHESSLER & NASH, 1977). For the third class of interactions studied here, it has been reported "that gibbons spend only a small part of their day grooming. There is some suggestion that siamang may groom more than the smaller gibbons, this may be related to the more cohesive nature of the siamang group" (GITTINS & RAEMAEKERS, 1980, p. 72). All three classes of interactions are generally thought to provide information on the strength of bonds within primate groups.

It appears reasonable to assume that strong bonds should reduce the amount of aggression and enhance the likelihood of successful food transfers to be observed within a gibbon group. If the hypothesis is correct that siamang groups show a "closer integration and greater harmony of group life" (CHIVERS, 1976), then the following predictions can be formulated and tested: (1) In siamang groups, the incidence of aggression should be lower than in lar gibbon groups. (2) In siamang groups, more attempted food transfers should occur, and relatively more attempts should be successful than in lar gibbon groups.

Grooming appears to be a more problematic parameter: Social grooming (allogrooming) has been observed to occur in many primate species (e.g. GOOSEN, 1987). Although the functions of grooming are not well understood, it is generally accepted that there is "a relationship between grooming and something like a social bond" (GOOSEN, 1980, p. 13, but see BARTON, 1985; HUTCHINS & BARASH, 1976). If this is true, then, irrespective of the nature of the connection between grooming and a social bond, a third prediction concerning the comparison between siamang and lar gibbon groups can be made: (3) If siamang groups do have a different intensity of family bonds than lar gibbon groups, then there should be a consistent difference in the amount of social grooming occurring in siamang and lar gibbon groups.

The present study was carried out in order to test the three predictions presented above.

MATERIALS AND METHODS

The age classes as proposed by Gittins and Raemaekers (1980, p. 70) for gibbons and siamangs were used in this report. The four groups studied here were composed as follows:

Group 1, *H. lar*, Zoologisch-Botanischer Garten Wilhelma, Stuttgart, Germany: *1-1*: adult male, in Stuttgart since 7 May, 1972, at least 16 years old; *1-2*: adult female, in Stuttgart since 7 May, 1972, at least 16 years old; *1-3*: juvenile-II, female, born on 29 July, 1983, 5 years old; *1-4*: juvenile-II, female, born on 14 April, 1984, 4.2 years old; *1-5*: juvenile-I, probably male, born on 17 July, 1986, 2 years old; *1-6*, infant, female, born on 31 August, 1987, 0.9 years old, usually carried by mother (*1-2*).

During observations made on this group, the adult male (*1-1*) was temporarily separated from the group for medical treatment of the skin. The observations made on this group before and after removal of *1-1* were analyzed both separately and pooled. During the separation period, the group had no visual contact with the adult male. During this time, the male was kept in a sleeping box adjacent to that of the group, within hearing distance to the group, which had free access to the sleeping boxes during the day.

Group 2, *H. lar*, Tierpark Bochum, Germany: *2-1*: adult male, "*Marco*," in Bochum since 1975, at least 14 years old; *2-2*: adult female, "*Marika*," in Bochum since 1975, at least 14 years old; *2-3*: juvenile-II, female, born on 4 January, 1985, 4.4 years old; *2-4*: juvenile-I, male, born on 24 April, 1987, 2.1 years old.

Group 3, *H. syndactylus*, Zoologischer Garten Zürich, Switzerland: *3-1*: adult male, "*Dagobert*," born on 4 October, 1979 (Dortmund Zoo), 9.3 years old; *3-2*: adult female, "*Chandra*," born on 25 December, 1976 (Zürich Zoo), 12 years old; *3-3*: juvenile, male, "*Luang*," born on 23 July, 1985, 3.5 years old; *3-4*: infant, female, "*Mias*," born on 10 January, 1987, 2 years old; *3-5*: infant, male, "*Oleng*," born on 23 September, 1988, 0.3 years old, always carried by mother (*3-2*).

Group 4, *H. syndactylus*, Zoologischer Garten der Stadt Frankfurt am Main, Germany: *4-1*: adult male, "*Ulli*," in captivity since 23 March, 1972 (Antwerp Zoo), at least 15 years old; *4-2*: adult female, "*Tilly*," in captivity since 12 December, 1961, at least 28 years old; *4-3*: infant, female, "*Vera*," born on 26 October, 1988, 0.3 years old, mostly carried by mother (*4-2*).

Table 1. Duration of observation for each study group.

Group No.	Species	Zoo	Composition of group[1]	Date of observation	Duration of observation (h)
1	*Hylobates lar*	Stuttgart	1, 3, 2[2]	6–12 July, 1988	38.5
			0, 3, 2[3]	13–19 July, 1988	36.5
2	*H. lar*	Bochum	2, 2	22–28 May, 1989	40
3	*H. syndactylus*	Zürich	2, 2, 1	2–8 January, 1989	40
4	*H. syndactylus*	Frankfurt	1, 1, 1	5–11 February, 1989	40

1) Figures in this column indicate, from left to right: number of males, females, and unsexed individuals; 2) before removal of adult breeding male *1-1* (on 13 July, 1988); 3) after removal of adult breeding male *1-1*.

The total duration and dates of observation for each study group are listed in Table 1. The behavioural data for this study were collected with the focal-animal sampling method (ALTMANN, 1974). All occurrences of specified interactions of an individual were recorded by one of us (J.O.F.) during 30-min sample periods. The order of observation of group members was altered each day. The observations were restricted to those periods of the day when the group was active; no observations were carried out when the group was inactive or sleeping.

The following three classes of interactions were recorded: (1) *Aggression*: This class includes all occurrences of open mouth threat ("Drohverhalten," ORGELDINGER, 1989, p. 128–133; "open-mouth threats," FOX, 1977, p. 429–430). More severe forms of aggression (such as grappling, biting, aggressive lunging, and aggressive chasing) were not observed to occur. For all occurrences, the individuals involved and the direction of threat were recorded. If it was not possible to distinguish whether an interaction occurred in an agonistic or playful context, the interaction in question was not counted. (2) *Food transfer*: This class includes all attempts of an individual to take food which was carried in hand, foot, or mouth of another individual (also includes "request," see BALDWIN & TELEKI, 1976, p. 44). No "active" or "overt" food transfer (with one animal deliberately *giving* food to another one, see e.g. ORGELDINGER, 1989, p. 150) was observed during the present study. (3) *Grooming*: This class includes only social grooming (allogrooming) and excludes self-grooming (autogrooming). For each class of social interactions and for each animal, the frequency per hour was determined. For the second class (food transfer), records specified not only the frequency of *attempts* to take food from another individual, but also the percentage of *successfully* completed food transfers. For the third class (grooming), the mean duration of grooming bouts and the mean total duration per animal per hour were also determined. Grooming bouts were separated by an arbitrarily established minimal interval of 10 sec. When determining the frequency of social interactions, each occurrence was counted for only one of two animals involved, i.e. for the aggressor (in aggressive interactions), for the food-owner (in attempted or successful food transfers), or for the groomer (in grooming).

No quantitative information on food transfer was collected for the three infants (individuals *1-6*, *3-5*, and *4-3*) of the study groups. Infants *1-6* and *3-5* (but not infant *4-3*) were repeatedly seen to touch the mother's hand or mouth when she was eating, but it was often not clear whether or not the infant had actually taken bits of food away from the mother. Detailed descriptions and definitions of the behavioural patterns mentioned above are given by BALDWIN and TELEKI (1976) for white-handed gibbons and by FOX (1977) and ORGELDINGER (1989) for siamangs. These studies also provide useful criteria for the distinction between playful and aggressive contexts of some of the behavioural patterns.

For comparisons of social interactions between lar gibbon and siamang, the two-tailed Mann-Whitney *U*-test was used (SIEGEL, 1956).

RESULTS

Figure 1 presents mean values and standard errors of the behavioural patterns observed in this study for the lar groups (Groups 1 and 2) and siamang groups (Groups 3 and 4). The graphs suggest a difference between both species for two variables: "food transfer attempts" appear to be less frequent, and "grooming bout duration" appears to be longer in the siamang than in the white-handed gibbon (Figs. 1b & 1e). "Grooming duration/animal/h" (a third variable) also appears to be slightly longer for the siamang groups, but in this case, the difference is less pronounced (Fig. 1f).

Table 2. Mean frequency and duration of selected behavioural patterns for each individual.[1)]

		Aggression	Food transfer[2)]		Grooming		
Species	Individual No.	Threats/ animal/h	Attempts/ animal/h	% successful	Bouts/ animal/h	Bout duration (sec)	Duration (sec)/ animal/h
Hylobates lar	*1-1*	0.4	0.9	69.2	2.4	32.9	105.9
H. lar	*1-2*	1.3	1.8	87.5	1.1	24.5	31.8
H. lar	*1-3*	0.9	1.3	37.9	3.5	24.6	90.8
H. lar	*1-4*	1.0	1.6	27.8	2.9	24.9	80.7
H. lar	*1-5*	1.2	0.3	16.7	0.9	21.3	25.2
H. lar	*1-6*	0.3	—	—	0.0	17.3	0.8
H. lar	*2-1*	0.8	0.6	100.0	4.8	25.6	115.6
H. lar	*2-2*	0.5	1.1	100.0	5.4	23.4	171.1
H. lar	*2-3*	0.9	1.2	100.0	14.0	35.2	380.5
H. lar	*2-4*	2.4	0.8	80.0	4.0	18.7	69.9
H. syndactylus	*3-1*	1.9	0.6	50.0	14.5	64.4	1004.2
H. syndactylus	*3-2*	7.8	0.0	—	3.2	84.7	269.0
H. syndactylus	*3-3*	2.2	0.9	33.3	17.7	48.9	1035.3
H. syndactylus	*3-4*	0.9	0.0	—	16.0	31.6	536.3
H. syndactylus	*3-5*	0.0	—	—	0.0	—	0.0
H. syndactylus	*4-1*	1.6	0.1	97.1	3.9	101.0	370.9
H. syndactylus	*4-2*	0.2	0.2	96.9	1.3	148.4	195.0
H. syndactylus	*4-3*	0.0	—	—	0.0	—	0.0

1) Observations made before *and* after removal of adult breeding male *1-1* from Group 1 have been pooled for this table; 2) no observations on food transfer were collected for infants (see MATERIALS AND METHODS).

Table 2 lists mean values of the behavioural variables for each *individual*. A comparison between the values for the lar- and siamang-individuals revealed a statistical significance for the two variables "food transfer attempts" (Mann-Whitney $U = 5$, $N_1 = 9$, $N_2 = 6$, $p = 0.0095$), and "grooming bout duration" ($U = 2$, $N_1 = 10$, $N_2 = 6$, $p = 0.0024$).

Correlations between the behavioural variables were first calculated with the group means of Figure 1. In order to obtain the minimum necessary sample size of $N = 5$, the values of Group 1 before and after the removal of the breeding male (*1-1*) were entered separately. This over-representation of Group 1 may have influenced the calculated correlations. Therefore, the same correlations were also calculated with the means for each *individual*. Here, the data for the situation before and after removal of male *1-1* from Group 1 were pooled. The correlation coefficients for both sets of calculations are shown in Tables 3 and 4.

Using the group means, significant correlations were found between the following three pairs of behavioural variables: (1) "Aggression"—"Grooming bouts/h"; (2) "Aggression"—"Grooming duration/animal/h"; and (3) "Grooming bouts/h"—"Grooming duration/animal/h" (in all cases, $0.88 < r < 0.91$, $p < 0.05$, $N = 5$, see Table 3). Using individual means instead of group means, significant correlations between two pairs of behavioural variables were found: (1) "Food transfer attempts"—"Grooming bout duration"; and (2) "Grooming bouts/h"—"Grooming bout duration" ($r = -0.551$, $p = 0.033$, $N = 15$, and $r = 0.883$, $p = 0.0001$, $N = 16$, respectively) (see Table 4). In addition, two of the variables representing social interactions ("% successful food transfers," and "Grooming bout duration") each correlated with group size ($r = -0.745$, $p = 0.035$, $N = 13$, and $r = -0.612$, $p = 0.012$, $N = 16$, respectively) and with individual age ($r = 0.618$, $p = 0.024$, $N = 13$, and $r = 0.686$, $p = 0.003$, $N = 16$, respectively) (see Table 4).

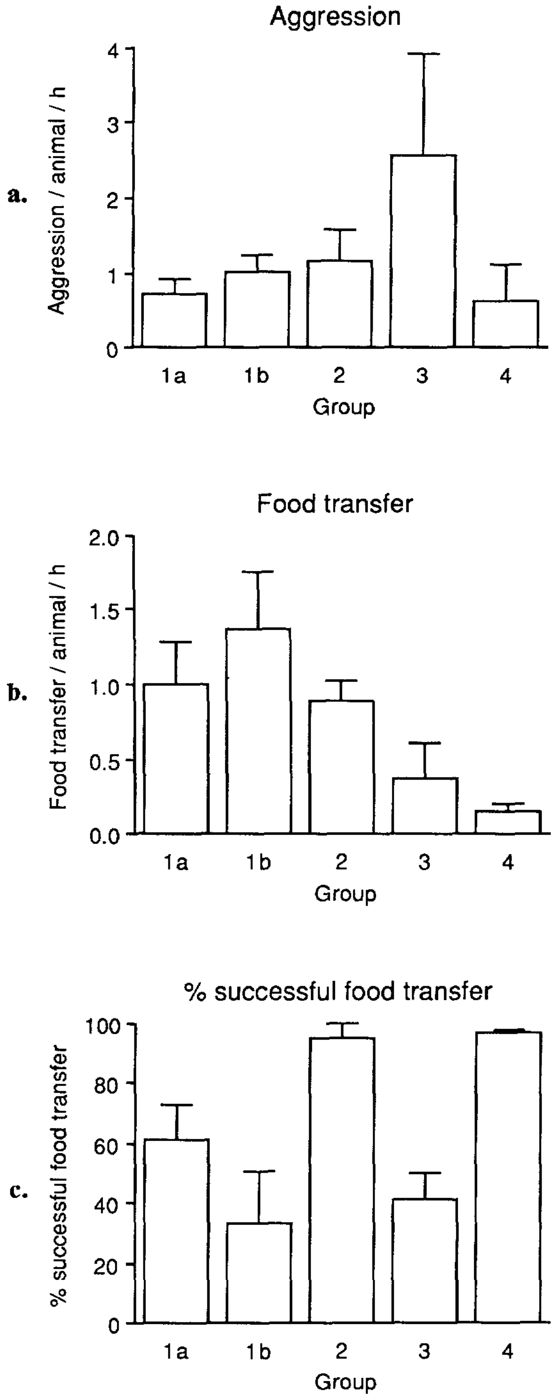

Fig. 1. Mean frequency and duration of selected classes of social interactions for each study group. Groups 1 and 2 are *Hylobates lar*, Groups 3 and 4 are *H. syndactylus*. Observations on Group 1 before and after removal of the adult breeding male are represented by bars 1a and 1b, respectively. Error bars indicate standard error of the mean.

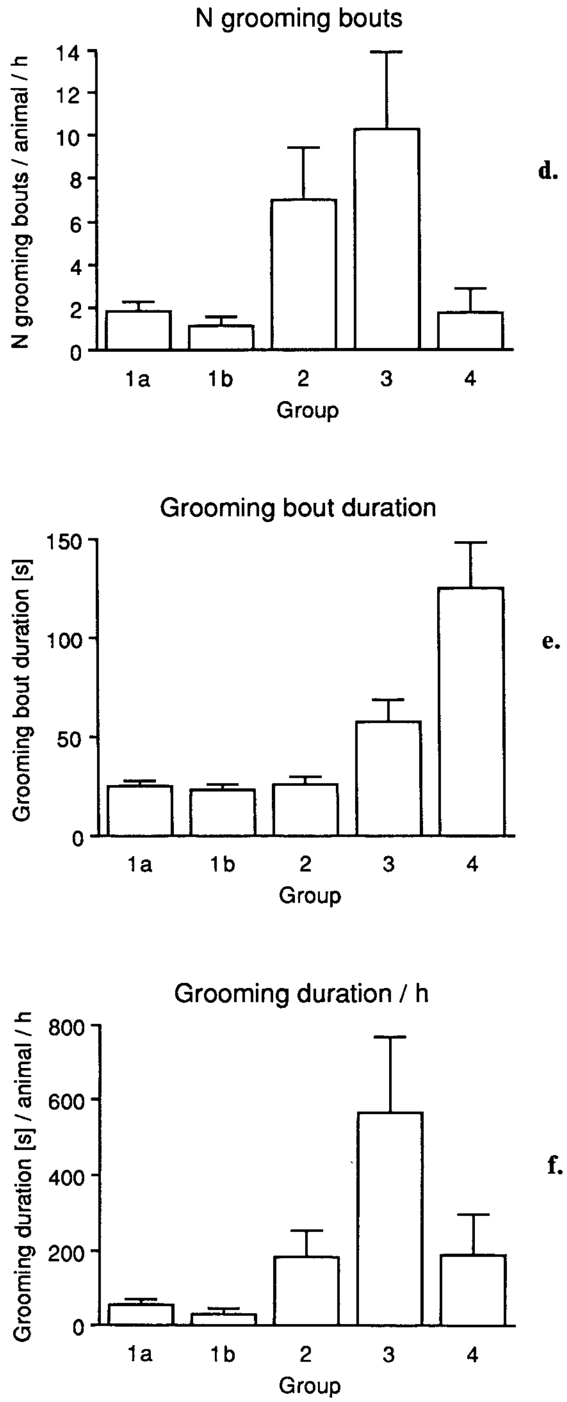

Fig. 1. (For captions, see the opposite page.)

Table 3. Correlation matrix for group size and selected behavioural patterns in the four study groups.1)

		1.	2.	3.	4.	5.	6.	7.
1. Group size		—						
2. Aggression	Bouts/animal/h	0.216	—					
3. Food transfer	Bouts/animal/h	0.592	−0.264	—				
4.	% successful	−0.72	−0.473	−0.460	—			
5. Grooming	Bouts/animal/h	0.002	0.886*	−0.365	−0.057	—		
6.	Mean bout duration (sec)	−0.743	−0.116	−0.867	0.475	−0.094	—	
7.	Duration (sec)/animal/h	−0.099	0.902*	−0.651	−0.134	0.881*	0.277	—

1) Observations made on Group 1 before *and* after removal of adult breeding male *1-1* were entered separately. $*p<0.05$.

Table 4. Correlation matrix for individual age, group size, and selected behavioural patterns in all study animals.1)

		1.	2.	3.	4.	5.	6.	7.	8.
1. Individual age		—							
2. Group size		−0.339	—						
3. Aggression	Bouts/animal/h	0.069	0.134	—					
4. Food transfer	Bouts/animal/h	−0.135	0.395	−0.348	—				
5.	% successful	0.618*	−0.745**	−0.288	−0.128	—			
6. Grooming	Bouts/animal/h	−0.169	0.044	0.123	−0.097	−0.103	—		
7.	Mean bout duration (sec)	0.686**	−0.612*	0.243	−0.551*	0.302	−0.027	—	
8.	Duration (sec)/animal/h	0.001	0.008	0.244	−0.224	−0.194	0.883***	0.27	—

1) Observations made before *and* after removal of adult breeding male *1-1* from Group 1 have been pooled for this table. $*p<0.05$; $**p<0.01$; $***p<0.001$.

DISCUSSION

Based on a hypothesis provided by Chivers (1976, p. 132) suggesting that the siamang differs from the white-handed gibbon "in the closer integration and greater harmony of group life," one should expect to find: (1) less aggression; (2) a higher frequency of attempted and a higher percentage of successful food transfers; and (3) a consistent difference in the amount of social grooming among members of family groups in siamangs as compared to white-handed gibbons.

This study tried to test these predictions in two family groups of white-handed gibbons and two family groups of siamangs. This was done by quantitative comparison of six behavioural variables representing the types of social interactions described above. However, a significant difference was found for only two of the variables: The siamang individuals of this study had longer "grooming bout durations," and made fewer "food transfer attempts" than the lar individuals. Only one (the first) of these differences is consistent with the predictions, whereas the lower frequency of "food transfer attempts" in siamangs is the opposite of what should be expected under the hypothesis mentioned above. Our failure to find consistent differences between the two species probably indicates that a considerably larger number of gibbon groups ought to be compared in order to seek reliable evidence for species-specific differences in group cohesion.

Two of our behavioural variables, on the other hand, showed a significant correlation with the parameters group size and individual age: Both individuals in larger groups and younger individuals tended to show proportionally fewer successful food transfers, and shorter grooming bouts. Our findings indicate that social cohesion within these gibbon groups may be much more flexible according to and depending on social or ecological influences and less rigidly linked to specific gibbon taxa than previously assumed.

As a consequence of this study, other proposed differences between the siamang and other gibbons also deserve careful reassessment. Several differences regarding behavioural ecology have also been reported to exist between the two species considered here. In Malayan siamangs, home ranges were smaller than in sympatric lar groups (on average 15–48 ha vs. 54–59 ha), and day ranges were shorter (on average 738 m vs. 1,490 m). In addition, siamangs were more folivorous (monthly dietary proportion of leaves: about 43%; fruits: about 36%), whereas lar gibbons were more frugivorous (leaves: about 29%, fruits: about 50%). The data cited were extracted from Gittins and Raemaekers (1980), but similar data have been provided by several other studies (Chivers, 1972; MacKinnon, 1977; MacKinnon & MacKinnon, 1978, 1980; Raemaekers, 1979, 1984; Raemaekers & Chivers, 1980). These authors commonly came to the conclusion that important ecological differences existed between white-handed gibbons and siamangs, and it has been suggested that "the difference in body weight is the obvious clue to their ecological separation" (Gittins & Raemaekers, 1980, p. 100). However, it should be noted that these data were all collected in Malaysia, mainly in one locality (Kuala Lompat), and much of the observation was apparently carried out on one group of white-handed gibbons (see Gittins & Raemaekers, 1980, p. 66), and two neighbouring groups of siamangs (one of which constantly changed its composition and finally disappeared, see e.g. Chivers & Raemaekers, 1980).

Although the conclusions of these authors may apply to siamangs and sympatric smaller gibbon species in general, studies carried out in other areas of sympatry found less distinct differences. For instance, fruits, not leaves, were reported to be the main dietary item of siamangs in Ketambe, northern Sumatra (CANT, 1988; RIJKSEN, 1978; WEST, 1982). The same appears to be true for Maninjau, west Sumatra, where the siamang lives sympatrically with the agile gibbon, *H. agilis*, although the latter species was reported to occur at low density (NORIKOSHI, 1986). Interestingly, at Maninjau, siamangs were found to use home ranges of about 8.8 ha ($N = 17$), which apparently is much smaller than home ranges reported so far from any other gibbon locality (e.g. CHIVERS, 1984a; LEIGHTON, 1987), with the possible exception of Tei-tei Peleigei on Siberut Island, where TENAZA (1975, p. 61) and TILSON and TENAZA (1982, p. 365) found a mean *territory size* of 7 ha for 13 groups, and of 7–11 ha for 16 groups of Kloss gibbons (*H. klossii*), respectively.

A qualitative difference between the siamang and other gibbons was reported in paternal behaviour: Whereas feral siamang fathers were observed to carry their offspring during the 2nd year (e.g. CHIVERS, 1972, 1974), infants of other gibbon species were carried by their mothers (e.g. GITTINS & RAEMAEKERS, 1980, p. 70). The reasons for this apparent difference are not well understood (KLEIMAN, 1977). "The largest of the hylobatids, siamangs are an exception to the general rule that male care is most elaborate in the monogamous species that are smallest and that have the largest infants" (WHITTEN, 1987, p. 345).

In captive groups, however, this difference appears to be less distinct. Although some siamang fathers were actually observed to carry their offspring at some time during ontogeny (ALBERTS, 1987; Ms. S. FOWMES, pers. comm.; Dr. Dr. U. HOLLIHN, pers comm.; Mr. R. OPITZ, pers. comm.), others were never observed to do so (Ms. S. FOWMES, pers. comm.; ORGELDINGER, 1989, p. 70f; own observations on three pairs), or only in exceptional situations (FOX, 1972, p. 125, 1977, pp. 145, 561f; ORGELDINGER, 1989, p. 71). Some captive males of other gibbon species (such as *H. lar*), on the other hand, were repeatedly reported to have shown a "determined effort" to take the infant offspring from the female (e.g. CRANDALL, 1945; BERKSON, 1966). In most cases, females would not allow the father to take the infant. However, in those cases, where the male was successful (*H. concolor*, *H. lar*, *H. leucogenys*, *H. muelleri*, and *H. klossii*), it was actually observed to carry the infant around, albeit in most groups for short distances only (ADLER, 1984, 1986; BERKSON, 1966; DITTRICH, 1979; Ms. S. FOWMES, pers. comm.; LANG, 1975). In addition, there are several reports on males (*H. agilis* and *H. klossii*) which apparently had adopted unrelated infants being kept in the same cage, and which carried them around for much of the day (CARPENTER, 1940, p. 135; LANG, 1971, 1973).

Finally, in a study on feral hoolock gibbons (*H. hoolock*), a group of three animals was observed, which apparently had lost the adult female. "One day I came across a small party of three, consisting of one adult male, one partially grown young one, and a baby about 4 (?) months old. I secured all of them. All were black and both the large ones were males. The baby was clinging to the older one as though it were its mother. The baby was a female. I searched the neighbourhood to see if there was a light-coloured female about, but without success. This incident goes to confirm the Naga belief that in the event of death of the mother, the other members of the family help to look after the baby" (MCCANN, 1933, p. 402). These observations suggest that the similarity in parental behaviour between the siamang and other gibbons may be closer than has previously been assumed. It is possible that future studies will eventually reveal that infants are not carried by all siamang fathers in the wild, whereas the behaviour may occur, albeit infrequently, in other gibbon species as well.

A comparison of all the reports cited suggests considerable flexibility of gibbon behavioural ecology. Our own findings, presented above, probably reflect this flexibility.

Another finding of this study—positive correlations between the frequency of "aggression" and the number of "grooming bouts/h," and between the frequency of "aggression" and the "grooming duration/animal/h" occurring in the study groups—possibly bears on the function of grooming in gibbons. Among the social functions commonly attributed to allogrooming behaviour in primates, some kind of tension- or aggression-reducing effect has frequently been proposed (BOCCIA, 1983, 1987; MCKENNA, 1978; SCHINO et al., 1988; see also reviews by GOOSEN, 1981, 1987). However, it is not clear to what degree grooming actually reduces existing tensions and to what degree it is merely a reflection of already low tension (see e.g. OKI & MAEDA, 1973). For white-handed gibbons, CARPENTER (1940, p. 191) advocates what appears to be a combination of both interpretations: "Grooming is important from the viewpoint of group integration; not only does it depend, seemingly, upon a previous state of positive conditioning in the participating animals, but the behavior further enhances and strengthens the social relationship."

If animals in groups with a large amount of aggression engage more frequently in grooming bouts and spend more time grooming than animals in "less aggressive" groups (as our data suggest), this would favour the interpretation that grooming is used to reduce tensions. On the other hand, if grooming would occur as a *result* of already low tensions, we should have found it more frequently in the groups with less frequent aggression.

However, the evidence remains ambiguous. Although a significant correlation between grooming and aggression was also found within a group of feral siamangs (CHIVERS, 1974, pp. 231, 234, 298), such a relationship was not obvious in the captive group studied by FOX (1977, p. 387f), and in the present study, a significant correlation was found only for group means, not for individual means. Allogrooming may have much more complex, and probably multiple social functions. Several authors have suggested that allogrooming in gibbons acts as a pair-bonding device (e.g. CARPENTER, 1940, p. 191; CHIVERS, 1977b, p. 96; ELLEFSON, 1974, p. 94). "The reciprocal activity with its common incentives, like copulation, serves to form attachments between animals" (CARPENTER, 1940, p. 191). However, such a pair-bonding function remains to be demonstrated.

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