PAIR BONDS IN MONOGAMOUS APES: A COMPARISON OF THE SIAMANG HYLOBATES SYNDACTYLUS AND THE WHITE-HANDED GIBBON HYLOBATES LAR

by

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Summary

Descriptions of the social systems of gibbons (*Hylobates*, Hylobatidae) have typically emphasized generically uniform attributes such as 'monogamy' and 'territoriality'. This has prevented testing of the hypothesis that pair bonds differ in the siamang (*Hylobates syndactylus*) and the white-handed gibbon (*Hylobates lar*) (Chivers, 1972). I replace a description of sociality based on mating system and group size/composition with quantitative measurement of social interactions and spatial relations between wild adult males and females in three heterosexual pairs of siamang and two pairs of white-handed gibbons studied for 2.5 years at the Ketambe Research Station (Sumatra, Indonesia). Siamang pair bonds show greater heterosexual cohesion than those of white-handed gibbon as reflected in higher rates of affinitive interactions such as close proximity, relaxed physical contact, embraces, and

communal use of sleep trees. Although males are more responsible than females for the maintenance of close proximity in both species, sex differences in intra-pair allogrooming suggest divergent mechanisms maintaining pair bonds in the two species. In white-handed gibbons, the female rarely initiates grooming and grooms her mate significantly less than he grooms her, partly because she solicits grooming from him at higher rates while simultaneously ignoring more of his 'presents' for grooming. In siamang, the contributions of the sexes to grooming are more equivalent and reciprocal. Taken together, these results suggest that investment of the sexes in maintaining the pair bond is more asymmetrical in white-handed gibbons (*i.e.* males contribute relatively more than females) and more mutual in siamang. Although mate guarding may have been the selective force behind the origin of pair bonds in both species, greater intra-group feeding competition in the gibbon and substantial paternal care in the siamang may account for the evolution of more reciprocal and stronger pair bonds in the latter. Future research on more groups is necessary to clarify the proposed species differences in light of existing intraspecific variation in social behavior.

Introduction

Until recently, the individual social behavior of monogamous animals — particularly mammals — received little attention and was assumed to be relatively invariable (Gowaty & Mock, 1985). Recognition that the term 'monogamy' specifies very little — if anything — about the social interactions of individuals (Kleiman, 1977; Wickler & Seibt, 1983) has fostered the hypothesis that the diversity of social systems in monogamous mammals "should parallel the variation seen in polygynous mammals" (Kleiman, 1981, p. 333; see also Barlow, 1984, 1986). Kleiman (1981) provided a useful preliminary framework for interpreting such variation by describing a continuum of monogamous social systems based upon systematic covariation in life history and social behavior. One end of this continuum, 'facultative' monogamy, is characterized in part by weaker or more antagonistic social relationships between adult males and females, and by reduced parental tolerance of relatively rapidly maturing offspring, as exemplified by some voles (Lambin & Krebs, 1991), small ungulates (Kranz, 1991), tree shrews (Kawamichi & Kawamichi, 1982), elephant shrews (Rathbun, 1979), and Bornean tarsiers (Niemitz, 1984). The other extreme, 'obligate' monogamy, is associated with pronounced affiliation between paired adults as well as between parents and slowly maturing off-

spring, *e.g.* canids (Kleiman & Eisenberg, 1973), dwarf mongoose (Rasa, 1987), and gibbons.

The gibbons (*Hylobates*, Hylobatidae) of southeast Asia are the most often cited example of obligate monogamy in nonhuman primates. The possibility that social structure varies among the monogamous hylobatids was first raised by Chivers (1972, 1976) for two species: the siamang (*Hylobates syndactylus*) and the white-handed gibbon (*H. lar*). Although field studies and censuses made it clear that both species lived in apparent 'nuclear families' of heterosexual adult pairs and their *putative* offspring, Chivers (1976, p. 132) argued that siamang sociality was characterized by "closer integration and greater harmony of group life" than was found in the white-handed gibbons studied independently by Ellefson (1974). On the other hand, in a more direct, quantitative comparison, Fischer & Geissmann (1990) did not find any clear differences between captive siamang and white-handed gibbons in rates of grooming, aggression, and food transfer.

The hypothesis that siamang and white-handed gibbons differ socially has not been tested adequately in the field for at least two reasons. First, interspecific comparisons have relied upon data collected by different individuals at different sites and times. Variation in the methods employed and in the scope and focus of research projects limits detailed comparison and may obscure subtle species contrasts in sociality.

Second, most quantitative field studies of siamang and white-handed gibbon have been ecologically-oriented and have described social structure primarily in terms of group-level phenomena (*e.g.* group size and composition, the presence or absence of overt dominance hierarchies). At this level there are no significant interspecific differences among the social systems of *all* hylobatids: with the possible, but currently debated exception of *Hylobates concolor* (Haimoff *et al.*, 1987; Daoying, 1989; Daoying *et al.*, 1990; Bleisch & Nan, 1990), individuals of the nine to ten species of *Hylobates* live in groups comprising one adult male, one adult female, and 0-4 immatures (Brockelman & Srikosamatara, 1984). As Brockelman (1984) points out, most field studies have focused on *intergroup* relationships, not the social interactions of individuals *within* groups. Consequently, descriptions of gibbon sociality have had to rely on the terms 'monogamy' and 'territoriality' (Leighton, 1987), which has tended to emphasize interspecific

similarities (Wrangham, 1979). This framework has led naturally to the conclusion that individual social behavior is relatively inflexible and so-cial systems uniform across *Hylobates*, possibly because of phylogenetic constraints (Martin, 1981; Kinzey, 1987).

The traditional socio-ecological approach, however, seriously underes-timates the complexity and variability of primate societies because bio-logically important elements of social structure may vary independently of overall group size and composition (Kummer, 1978; Mason, 1976; Dunbar, 1988) as well as mating system (Kleiman, 1977; Wickler & Seibt, 1983; Rowell, 1986). A biologically meaningful description of a primate social system must quantify the nature and patterning of its constituent social relationships (Hinde, 1975, 1983a). Hinde's framework for describing and analyzing social structure has provided important insights into the behavior of polygynous primates (*e.g.* Harcourt, 1979a, b, c), but has not yet been applied rigorously to comparative study of monogamous species. Social variation among free-ranging hylobatids — and monogamous nonhuman primates in general — has simply received little empirical attention. Thus, when Gittins & Raemaekers (1980, p. 72) evaluated Chivers's original hy-pothesis in light of current field data, they could state only that "there is some suggestion" of social differences between the siamang and the white-handed gibbon.

Three goals of this study were to: 1) describe quantitatively the hetero-sexual pair bonds of wild siamang and white-handed gibbons; 2) evaluate behavioral mechanisms of pair bond maintenance; and 3) use the compar-ative approach as the basis for an evolutionary analysis of male-female re-lationships in these species. Because *Hylobates syndactylus* and *H. lar* are extremely closely related phylogenetically (Bruce & Ayala, 1979; Weiss, 1987), interspecific similarities may be homologous, but differences are likely to reflect adaptations to contrasting ecological conditions (Harvey & Pagel, 1991).

Methods

Study area

Research was conducted at the Ketambe Research Station (3°40′ North, 97°40′ East) in the Gunung Leuser National Park, Aceh Tenggara (Sumatra), Indonesia. The 300-ha study area occupied a series of terraces enclosed by escarpments rising from alluvial areas along

the Alas and Ketambe Rivers in the north (*ca.* 350 m a.s.l.) to the slopes of mountains of the West Alas Range to the south (600-3300 m). The territories of the hylobatid study groups were situated on the lower terraces (< 600 m), where the mixed-dipterocarp, primary lowland rain forest was predominantly of the 'low' and 'hill' types (Laumonier, 1990). Detailed descriptions of the study area are provided by Rijksen (1978) and Palombit (1992).

Subjects

Data for five fully habituated and individually recognizable adult pairs from four groups are presented. Two of these pairs were white-handed gibbons, AS-AY and GD-GM (male and female members of these pairs are indicated by initials to the left and right of the dash, respectively), while the others were siamang, CH-CJ, PP-PN, and PM-PN. Two siamang pairs both involved the same female, PN (in group 'P'). Her first mate — the male PP — left her and their mutually defended territory after the first year of study. She simultaneously acquired a new mate, PM, which remained with her throughout the second year of study. Observations were conducted during all stages of the female reproductive cycle (*i.e.* cycling, gestation, lactation) for all females except during lactation for siamang CJ and gibbon GM. The histories of all pair bond associations, changes in group composition, and female reproduction over six years are described in detail by Palombit (1994a, 1995).

Behavioral measures

Systematic observations were made from January 1986-December 1987 after an initial period of habituation and preliminary study (August-December 1985). Each study group was followed 4-6 days/month in all months (except December, 1986 when no observations were conducted). Behavior was measured via continuous real-time measurement during half-hour focal animal samples (Altmann, 1974). I adopted the recommendation of previous investigators (Carpenter, 1945; Mason, 1971; Rowell & Olson, 1983) and particularly Hinde (1975, 1983a) that numerous diverse, complementary measures of *both* spatial relations and social interactions be considered when describing social relationships. The following measures were used to quantify pair bonds.

Close proximity or '*sitting together*': time adults spend within one meter *without* allogrooming or copulating (the primary social interactions of adult hylobatids).

Maintenance of close proximity: Hinde's index of responsibility for proximity measures which partner of a dyad is more responsible for proximity maintenance by subtracting the percent withdrawals performed by an individual from the percent approaches performed by the same individual (Hinde & Atkinson, 1970). The index ranges from +100 (complete male responsibility for maintenance of close proximity) to −100 (complete female responsibility). An individual that moved to within one meter of another was designated an 'approacher', whereas one that by moving increased the distance between itself and another from within one meter to over one meter was the 'withdrawer'. Observed approaches and withdrawals during focal sessions and *ad libitum* observations were used to calculate the Hinde index.

Approach-withdraw interaction: time within one meter with *no* specific reference to intervening behaviors.

Allogrooming: manipulation, stroking, or picking through the hair of another individual. Direct interactions between paired adult hylobatids are remarkably infrequent given the apparent opportunities, but grooming is by far the most common of these interactions (Leighton, 1987). In order to assess the symmetry of male-female grooming interactions, I calculated the cumulative duration of 'male groom female' and 'female groom male' expressed as a percentage of all grooming exchanged between them during a particular grooming session (see below for definition of 'grooming session').

Presenting: elevating of the head, limb, or torso towards or directly in front of another individual (in invitation or solicitation for grooming). If grooming is a means of investment in social relationships (Dunbar, 1991), then presenting provides a gibbon with the means to elicit this investment from its mate. 'Unanswered' or 'rejected' presents were defined operationally as any instance where an individual responded to a present by: 1) performing a present itself to the partner; or 2) withdrawing from the presenter, thereby terminating the grooming session; or 3) grooming another nearby individual.

Maintenance of grooming sessions: The Hinde index of responsibility for proximity was used to evaluate whether one sex was more responsible than the other for initiating and terminating grooming sessions. The index was calculated in the same way as described above for close proximity except that only 'grooming sessions' were considered. These were defined as any approach-withdraw bout with at least one intervening grooming event (since withdrawal of a pair-mate usually concluded ongoing grooming).

'Embrace': stationary ventral-ventral contact during which at least one individual put its arms around another (see also Baldwin & Teleki, 1976).

Nongrooming social contact: relaxed physical contact (*e.g.* huddling) that does *not* involve other social interaction (*i.e.* excludes allogrooming, embraces, copulation).

Sleep trees: I calculated the percentage of days in which the adult male and female used the same sleep tree or used different, scattered sleep trees. On a few nights, adults slept in different but adjacent trees that were so close together that their crowns intermingled and the distance between the adults at was less than 25 m. These cases were scored as 'communal' because such a dispersion is commensurate with sleeping in a single sleep tree and was much less than the > 200 m typically isolating 'separate' night positions.

Agonistic gestures: A number of ritualized, facial expressions common among catarrhines were measured: 1) the 'open-mouth' threat; 2) the 'grimace' or 'bare-teeth' submissive-appeasement gesture; 3) the 'lip-smacking' conciliatory gesture. For further details on structure and function of these displays see Andrew (1965), van Hooff (1967), Baldwin & Teleki (1976), de Waal & Luttrell (1985), Easley & Coelho (1991), and Petit & Thierry (1992).

Statistical analysis

The data were analyzed in a nested ANOVA design; species status was the primary factor and pair identity was nested within species. Half-hour focal periods were the samples in analyses of time spent in close proximity, in grooming, and in nongrooming social contact. Consecutive focal samples within half an hour of one another were not *both* included in

the nested ANOVA (one of these focal periods was randomly selected for inclusion, the other was excluded) since a 'lag' correlational analysis (*sensu* Sackett, 1978) suggested non-independence of these samples (for further details see Palombit, 1992). Data for time spent in close proximity, duration of close proximity bouts, time spent grooming, and time spent in nongrooming physical contact were log transformed to increase homogeneity of variance (the last measure was additionally square root transformed). Approach rates were square root transformed. These transformations brought variation in variances well within the 20 to 1 ratio criterion (between largest and smallest variances) suggested by Harris (1975); scattergrams of residuals versus the fitted values of the transformed dependent variables also lacked evidence of pronounced heteroscedasticity. Following the suggestion of Seitz (1980), I additionally analyzed these data with nonparametric tests (Kruskal-Wallis followed, when appropriate, by Mann-Whitney U-tests); the conclusions with respect to species differences were the same as those reported here from the nested ANOVA.

For some measures involving aspects of grooming interactions, sample sizes of grooming sessions were too small to justify a nested ANOVA design. These data were therefore analyzed with nonparametric statistics (Kruskal-Wallis, Mann-Whitney U-tests). Statistical analysis of grooming presents and responses to them excluded the siamang pair PP-PN because too few of their grooming sessions involved presents. All tests were two-tailed.

Results

Close proximity

Time in close proximity

Members of siamang pairs spent significantly more time in close proximity to one another than did gibbons (Fig. 1a) (Species: $F_{[1,3]} = 35.4$, $p = 0.009$; Pairs: $F_{[3,626]} = 2.8$, $p = 0.04$). Greater time in close proximity was primarily the outcome of higher rates of approach in siamang than in gibbons (Fig. 1b) ($F_{[1,3]} = 6004.8$, $p = 0.0001$), which did not differ among pairs intraspecifically ($F_{[3,626]} = 0.01$, $p > 0.10$). Although durations of close proximity tended to be longer in siamang than in gibbons (Fig. 1c), this difference was not significant ($F_{[1,3]} = 1.7$, $p = 0.28$).

Responsibility for close proximity

Hinde's index of responsibility for close proximity was positive for all five pairs (Table 1). No substantive species difference was apparent.
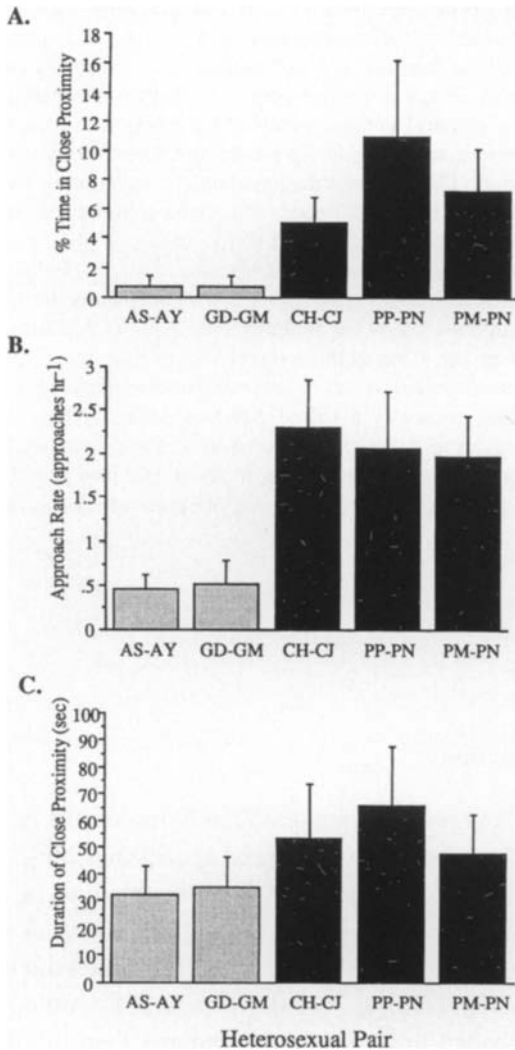
Fig. 1. Three measures (means plus 95% confidence error bars) of 'close proximity' (see text) of pair-mates: A. Percent time in close proximity; B. Approach rate; C. Duration of close proximity bouts. Black bars = siamang, light bars = white-handed gibbon. N's (number of focal samples) for A and B are: 163 (AS-AY), 112 (GD-GM), 173 (CH-CJ), 68 (PP-PN), and 115 (PM-PN) for A and B. N's (number of close proximity bouts) for C are: 79 (AS-AY), 54 (GD-GM), 334 (CH-CJ), 93 (PP-PN), and 181 (PM-PN).

TABLE 1. *Responsibility for close proximity between pair-mates*

Heterosexual pair	% Male approaches	% Male withdraws	N	Hinde index
Siamang				
CH-CJ	54.7	36.3	380	18.4
PP-PN	64.5	21.3	141	43.2
PM-PN	52.8	38.7	212	14.1
White-handed gibbon				
AS-AY	51.9	38.9	108	13.0
GD-GM	51.4	27.8	73	23.6

Allogrooming — overall patterns of occurrence

Time spent grooming

Time adults spent grooming each other differed among heterosexual pairs ($F_{[3,626]} = 3.2$, $p = 0.02$), but these differences were not related to species status (Fig. 2a) ($F_{[1,3]} = 0.03$, $p > 0.10$). As with close proximity bouts, there were no significant differences among pairs of both species in the duration of 'grooming sessions' (Kruskal-Wallis $H = 7.4$, df $= 4$, $N = 208$, $p = 0.12$), which was 11.7 ± 0.86 min (Mean $\pm$ SE, Range $= 0.35$-69.8 min; $N = 208$) (Fig. 2b). Thus, grooming sessions were on average about ten times the duration of close proximity bouts (*cf.* Fig. 1c).

Grooming and approach-withdraw interactions

The absence of a species difference in overall time spent grooming is striking because approach-withdraw interactions of the adult white-handed gibbon pairs more often involved allogrooming than those of the siamang pairs. I evaluated this in two ways. First, I determined what proportion of the time adults spent within one meter of each other ('approach-withdraw' interaction) was devoted to grooming. To control for any species differences in the frequency of approach-withdraw bouts that were too brief to permit the initiation of allogrooming, I considered only bouts in which the time between an approach and a withdraw was at least 13 s. This criterion was the median latency for adults to begin grooming after an approach, which did not differ among pairs (Kruskal-Wallis $H = 6.421$, df $= 4$, $N = 204$, $p = 0.17$). Under these conditions, the proportion of time during a male-female approach-withdraw interaction that was occupied by allogrooming was about 3-4 times greater
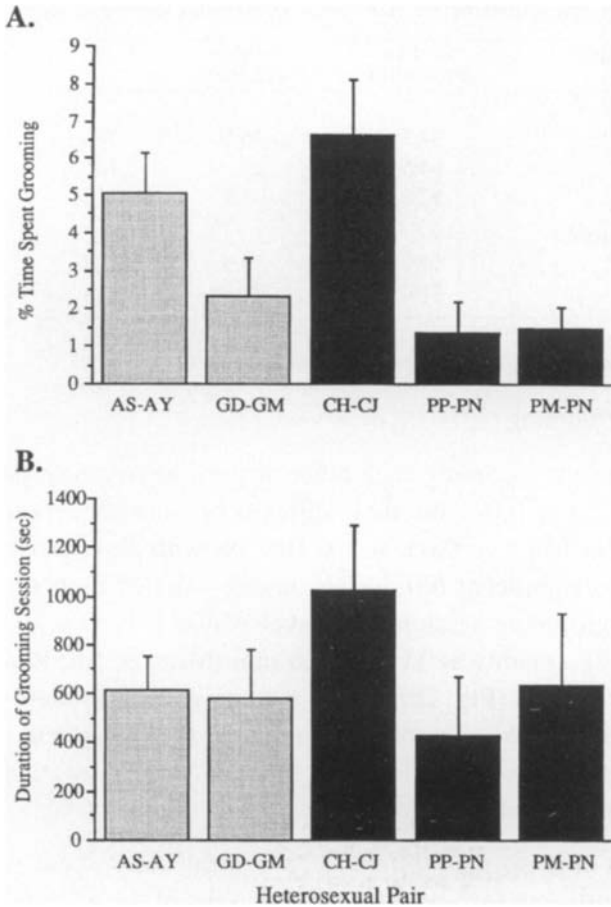
Fig. 2. Allogrooming of pair-mates: A. mean percent time (with 95% confidence error bars) pair-mates spent grooming one another. N's (number of focal samples) for each pair are: 163 (AS-AY), 112 (GD-GM), 173 (CH-CJ), 68 (PP-PN), and 115 (PM-PN). B. Duration (seconds) of 'grooming sessions' (see text) (mean with 95% confidence error bars). N's (number of complete grooming sessions) for each pair are: 78 (AS-AY), 26 (GD-GM), 58 (CH-CJ), 19 (PP-PN), and 27 (PM-PN). Black bars = siamang; light bars = white-handed gibbon.

in gibbons than in siamang (Fig. 3) ($F_{[1,3]} = 90.2$, $p = 0.003$), and did not differ among pairs of the same species ($F_{[3,735]} = 0.94$, $p > 0.10$).
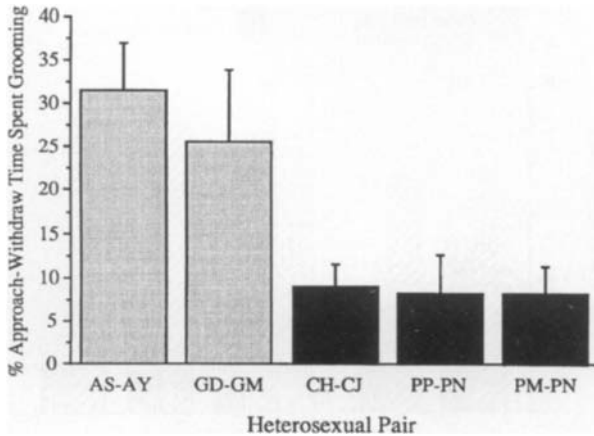
Fig. 3. Percentage of 'approach-withdraw' time (within 1 m — see text) pair-mates spent grooming one another (mean with 95% confidence error bars). Black bars = siamang; light bars = white-handed gibbon. N's (number of approach-withdraw bouts) for each pair are: 127 (AS-AY), 65 (GD-GM), 307 (CH-CJ), 90 (PP-PN), and 151 (PM-PN).

Second, allogrooming between pair-mates occurred in a higher proportion of approach-withdraw interactions bouts in gibbon than in siamang pairs. In all pairs, bouts of close proximity ('sitting together' without interacting directly) were more common than grooming sessions, but this difference was more pronounced among siamang than in gibbons (Fig. 4). In the vast majority (almost 90%) of cases in which siamang pair-mates came within one meter of one another, *no* grooming occurred at all; in gibbons this happened only 50 or 70% of the time. The two types of approach-withdraw interactions were independent of pair identity ($G = 93.5$, df $= 4$, $p < 0.001$); bouts of close proximity were much rarer than expected in the gibbon pairs, but grooming sessions were somewhat rarer than expected in siamang.

Given that in gibbons a higher proportion of approach-withdraw interactions involved grooming and that a larger proportion of the time paired adults spent within one meter was devoted to grooming, greater time spent grooming is expected relative to siamang. The lack of such a species difference underscores the fact that siamang mates approached one another much more often than the gibbons did.
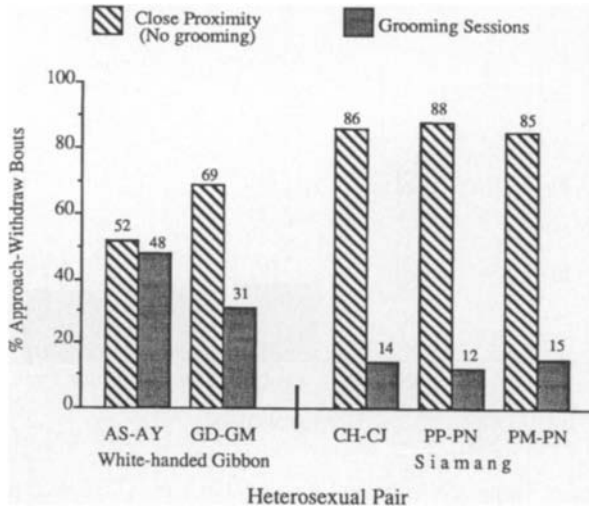
Fig. 4. Relative frequency of 'approach-withdraw' interactions (within 1 m — see text) with and without grooming. Bars indicate the percentage of approach-withdraw bouts that involved: allogrooming (shaded bars); and sitting together ('close proximity') without grooming (hatched bars).

Allogrooming — male and female contributions

White-handed gibbons exhibited a number of sex differences in the patterning of grooming, but these were generally less apparent among siamang pairs.

Reciprocity of grooming

Males consistently groomed females more than females groomed males in both gibbon pairs and in one siamang pair (Wilcoxon's test, pair AS-AY: $T = 132$, $N = 76$, $p \ll 0.001$; pair GD-GM: $T = 0$, $N = 26$, $p \ll 0.001$; pair PP-PN: $T = 13$, $N = 18$, $p < 0.001$). In these pairs, male grooming of females accounted for over 80% of grooming exchanged between the sexes (Fig. 5). In contrast to these three pairs, there was no sex difference in grooming investment in the other two siamang pairs (Fig. 5) ($p > 0.10$; pair CH-CJ: $T = 734$, $N = 54$; pair PM-PN: $T = 110$, $N = 26$). Indeed, the siamang male CH and his mate CJ showed almost perfect reciprocity of grooming.

Fig. 5. Sex differences in reciprocity of grooming between pair-mates. Bars indicate the mean percent (± SE) of total grooming time exchanged by partners within 'grooming sessions' (see text) that was performed by the adult male *versus* the adult female. Hatched bars = male groom female; shaded bars = female groom male. *N*'s (number of complete grooming sessions) for each pair are: 76 (AS-AY), 26 (GD-GM), 54 (CH-CJ), 18 (PP-PN), and 27 (PM-PN).

Within grooming sessions, cumulative durations of male and female grooming were positively correlated with one another in all five hylobatid pairs (Fig. 6). As indicated by the steeper slope of their regression lines, however, adjustments in male and female grooming of one another corresponded more closely in siamang pairs than in gibbon pairs.

Initiation and termination of grooming sessions

As with close proximity (Table 1), the Hinde indices were positive for all pairs (Table 2). The species did not differ significantly.

Another measure of a predisposition for one sex to initiate grooming bouts is the identity of the first adult to begin grooming. The sex of the approacher and the sex of the first groomer were independent in all five pairs (χ^2 = 1.22 (AS-AY), 0.39 (GD-GM), 0.0 (CH-CJ), 0.01 (PP-PN), 0.08 (PM-PN), df = 1, $p > 0.10$). This situation can arise in two ways:
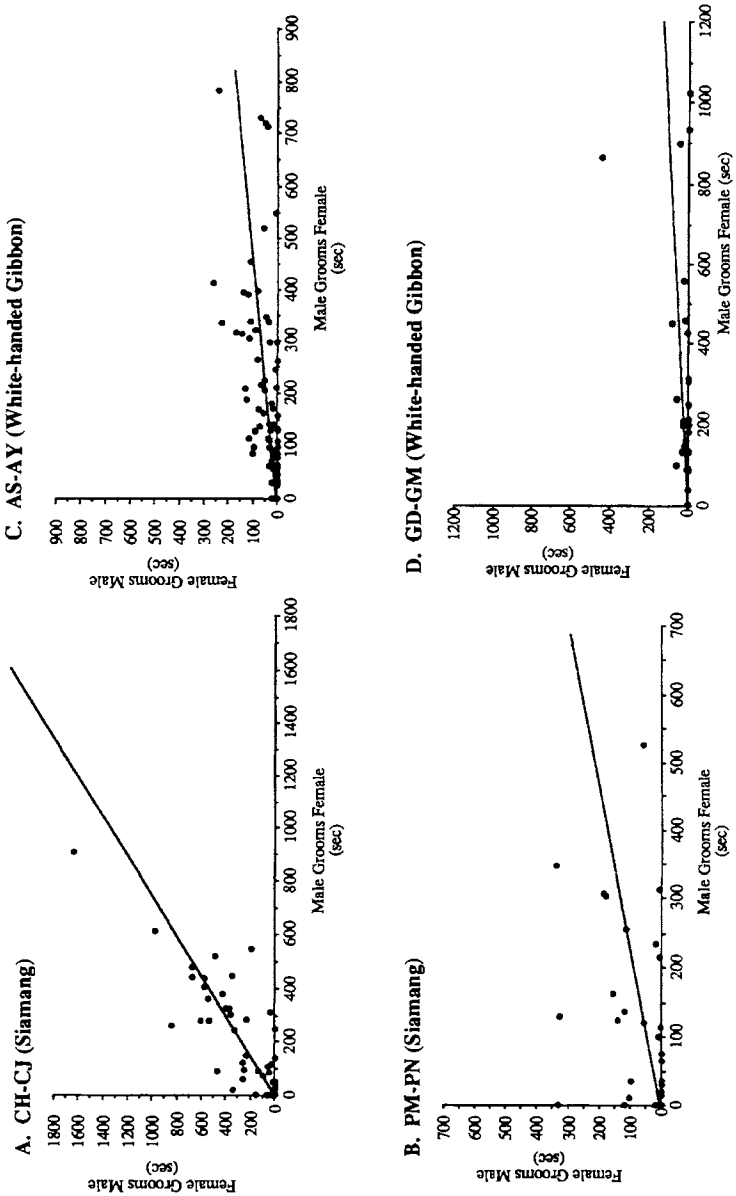
Fig. 6. Covariation of total 'male groom female' time and total 'female groom male' time within grooming sessions.

TABLE 2. *Responsibility for grooming sessions between pair-mates*

Heterosexual pair	% Male approaches	% Male withdraws	N	Hinde index
Siamang				
CH-CJ	67.1	39.7	73	23.5
PP-PN	62.5	30.0	40	32.5
PM-PN	48.9	34.0	94	14.9
White-handed gibbon				
AS-AY	45.7	30.0	70	15.7
GD-GM	56.3	32.8	64	26.7

one sex may consistently initiate grooming (regardless of which animal performed the approach), or, conversely, both sexes may be equally likely to initiate grooming once an approach has been made. The distribution of first groomer identity demonstrated that the former applied more to gibbons and the latter to siamang (although there was some interspecific overlap). The two male gibbons initiated grooming sessions much more frequently than their female mates did (Fig. 7). In two of the siamang pairs a sex-bias in grooming initiator was either absent or far less obvious. The third siamang pair (PP-PN), however, showed the same pattern as the gibbons of a distinctly greater likelihood for male performance of the first grooming bout. This result for PP-PN is consistent with the sex difference
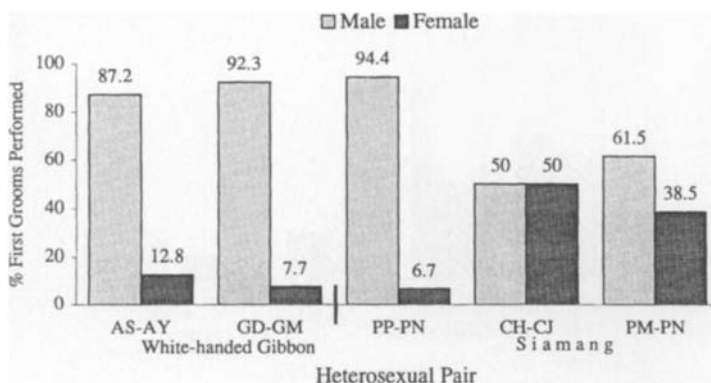

Fig. 7. Sex differences in initiation of grooming between pair-mates. Bars indicate the percent of cases in which the male or female of a pair was the first to begin grooming its mate following an approach. N's (number of grooming sessions) for each pair are: 78 (AS-AY), 26 (GD-GM), 56 (CH-CJ), 18 (PP-PN), and 26 (PM-PN).

in grooming time described above for this pair (in contrast to reciprocal patterns for the other two siamang pairs).

Solicitation of grooming

Solicitation of grooming from a mate was more common among white-handed gibbon pairs than among siamang (Fig. 8): this species difference was significant both for the overall rate of presenting (Kruskal-Wallis $H = 72.0$, df $= 4$, $N = 167$, $p \ll 0.001$; Mann-Whitney U-tests, $p < 0.05$) and for the frequency of presents relative to the number of individual grooming bouts exchanged within a session ($H = 72.1$, df $= 4$, $N = 167$, $p \ll 0.001$; Mann-Whitney U-tests, $p < 0.05$). Intraspecific differences among pairs were not significant (U-tests, $p > 0.10$).

Sex differences in presenting behavior were a potential proximate cause of the variation in female and male grooming investments described above. In those grooming sessions where one sex presented more than the other, the rate of female presenting during such grooming sessions consistently
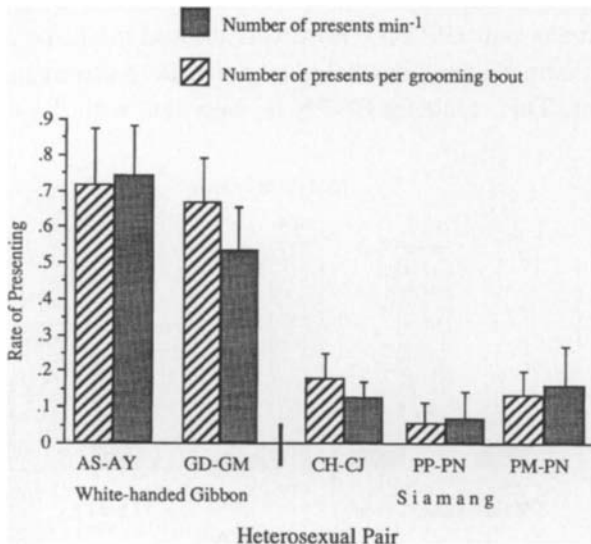

Fig. 8. Solicitation of grooming by pair-mates. Two rates of presenting are provided: shaded bars indicate mean number of presents performed per minute of 'grooming session' (see text); hatched bars indicate mean number of presents per individual grooming bout exchanged within grooming sessions. 95% confidence error bars accompany means.

exceeded that of male pair-mates in gibbons ($p \ll 0.001$; AS-AY pair: Wilcoxon $T = 120$, $N = 47$; GD-MA pair: $T = 0$, $N = 20$). In siamang pairs, neither sex was more likely to perform higher rates of presenting ($p > 0.10$; CH-CJ pair: $T = 118$, $N = 15$; PM-PN pair: $T = 16$, $N = 10$).

The most pronounced difference in presenting rates was that female gibbons presented for grooming more frequently than both their conspecific mates and more than female siamang (Fig. 9). The rate of presenting in gibbon females was nearly seven times greater than in siamang females (Kruskal-Wallis $H = 69.3$, df $= 4$, $N = 167$, $p \ll 0.001$; pairs did not differ intraspecifically; differences among pairs were consistent with species status (Mann-Whitney U-tests, $p \ll 0.01$)).

Rates of presenting differed among males ($H = 27.2$, df $= 4$, $N = 167$, $p < 0.001$), but varied more than female rates and overlapped interspecifically (Fig. 9). The gibbon male AS exhibited a rate of presenting significantly higher than the conspecific male GD as well as the two siamang males CH and PM (Mann-Whitney U-tests, $p < 0.05$). These last three
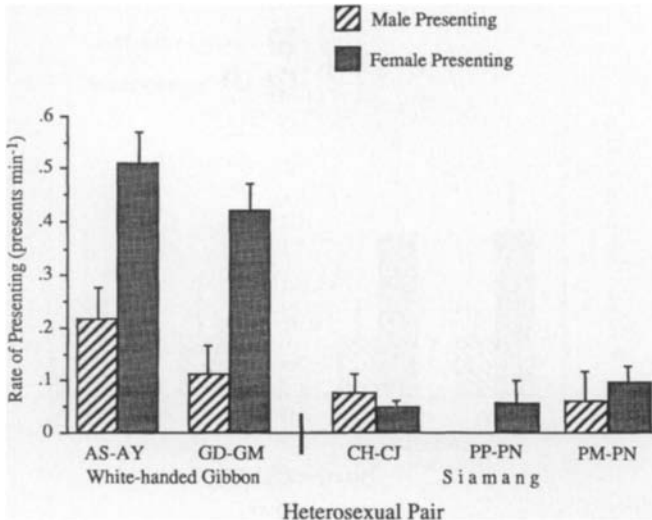

Fig. 9. Sex differences in solicitation of grooming by pair-mates. Bars indicate mean rates of presenting (per minute of grooming session) of males (hatched bars) and females (shaded bars) (95% confidence error bars). N's (number of grooming sessions) for each pair are: 60 (AS-AY), 25 (GD-GM), 47 (CH-CJ), 15 (PP-PN), and 20 (PM-PN).

males did not diverge significantly from one another. The siamang male PP never presented to his female mate during the focal sessions (although he did so infrequently at other times and presented to immatures in the group). Thus, male siamang tended to present at lower rates than male gibbons, but this species difference was smaller than that for females.

The latency for a female to respond to the present of her mate by grooming him was similar for both species, *i.e.* 5.6 ± 0.72 s (Mean ± SE) (Kruskal-Wallis $H = 2.5$, df $= 3$, $N = 190$, $p > 0.10$). Likewise, male latency to groom in reply to a female's present did not differ among males: 5.3 ± 0.66 s (Mean ± SE) ($H = 1.3$, df $= 4$, $N = 374$, $p > 0.10$). Thus, individuals of both species responded to a pair-mate's present with equivalent alacrity, *when* they responded at all.

Rejection of grooming solicitations

The percentage of female presents (per grooming session) that went unanswered by males did not differ significantly among pairs of both species: the overall Mean ± SE was 14.2% ± 2.2% (Kruskal-Wallis $H = 1.6$,

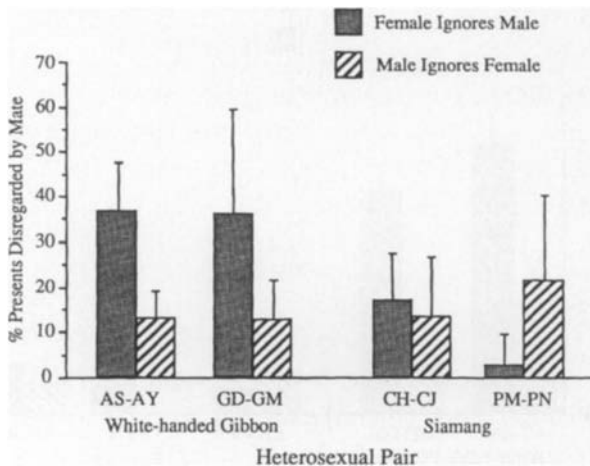Fig. 10. Sex differences in rejection of pair-mate's solicitation for grooming. Bars indicate mean percent of mate's presents not 'answered' (see text) (with 95% confidence error bars). N's (number of grooming sessions) for each pair are: 57 (AS-AY), 27 (GD-GM), 25 (CH-CJ), and 10 (PM-PN) for analysis of female presents; 44 (AS-AY), 18 (GD-GM), 28 (CH-CJ), and 8 (PM-PN) for analysis of male presents.

$df = 3$, $N = 119$, $p > 0.10$) (Fig. 10). In contrast, unacknowledged male presents were more common in gibbons than in siamang ($H = 11.5$, $df = 3$, $N = 98$, $p < 0.01$) (differences among pairs were consistent with species status ($p < 0.01$); study pairs did not differ significantly intraspecifically ($p > 0.10$)) (Fig. 10). In siamang, about 13.4% ± 4.3% (Mean ± SE) of male presents failed to elicit grooming from the female, which is roughly as numerous as unanswered presents of females in both species. On the other hand, 36.7% ± 4.6% (Mean ± SE) of male presents in gibbons were disregarded by females. Thus, the primary difference between the two species was a considerably higher rate of rejection of male grooming solicitations by females in white-handed gibbons than in siamang. It was common for a present from a male gibbon to elicit an immediate present from his mate, whereupon he usually groomed her. Sometimes a 'volley' of alternating presents was exchanged back and forth for some time until one adult (usually the male) finally groomed the other.

'Mutual' or 'reciprocal' grooming

Sometimes two individuals groomed one another simultaneously. Rowell *et al.* (1991) argue that mutual grooming interactions are especially effective in establishing and maintaining cooperative social relationships. Mutual grooming was observed in only one study pair, the siamang CH-CJ and accounted for 1.4 ± 0.4% (Mean ± SE, range = 0-10.6%, $N = 47$) of all grooming exchanged between the sexes during a grooming session.

Nongrooming physical contact

Members of siamang pairs were in nongrooming social contact with one another 10-30 times more than gibbons (Fig. 11) ($F_{[1,3]} = 15.0$, $p = 0.03$); pairs did not differ intraspecifically ($F_{[3,626]} = 2.2$, $p = 0.09$). This form of touching was negligible in gibbons, but siamang pair-mates often sat or lay resting in relaxed physical contact in a manner reminiscent of the 'huddling' of titi monkeys (*Callicebus* spp.) (Mason, 1971, 1974; Kinzey, 1981), except, of course, for the absence of cebid 'tail-twining'.
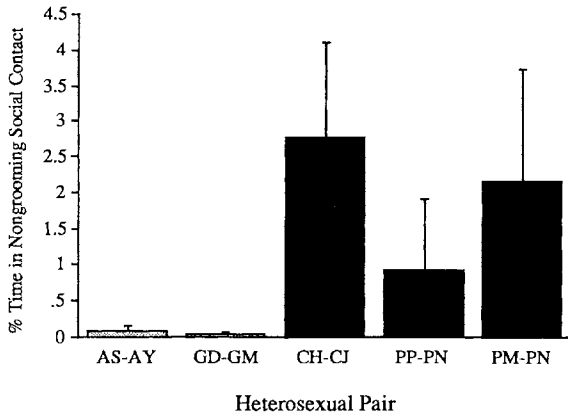
Fig. 11. Time pair-mates spent in relaxed (nongrooming) affiliative physical contact with one another (mean percent time with 95% confidence error bars). Black bars = siamang, light bars = white-handed gibbon. *N*'s (number of focal samples) for each pair are: 163 (AS-AY), 112 (GD-GM), 173 (CH-CJ), 68 (PP-PN), and 115 (PM-PN).

Embraces

Embraces occurred very rarely, but a qualitative difference in their occurrence was discernable. Adult white-handed gibbons were never observed to embrace one another (although adult females were observed to embrace immatures). Embraces among siamang, though infrequent, were sufficiently recurrent and stereotyped to suggest stability of performance. Ten embraces between pair-mates were observed during focal sessions, which constituted 63% of all embraces observed among siamang of all ages. All but one of these embraces were initiated by the adult male. All three males (PP, PM, and CH) were observed to embrace their mates. The male PM did not do so until his status in the group changed from unmated resident subadult to the new mate of the female PN. The duration of these embraces was 31.3 ± 9.4 s (Mean $\pm$ SE, range $= 4\text{-}86$ s, $N = 10$) (*cf.* 2-s embraces of gibbon females with immatures).

Sleep trees

Members of siamang pairs were much more likely than gibbons to use the same sleep tree (Fig. 12). Coordinated use of sleep trees by males and females did not vary substantively within species.
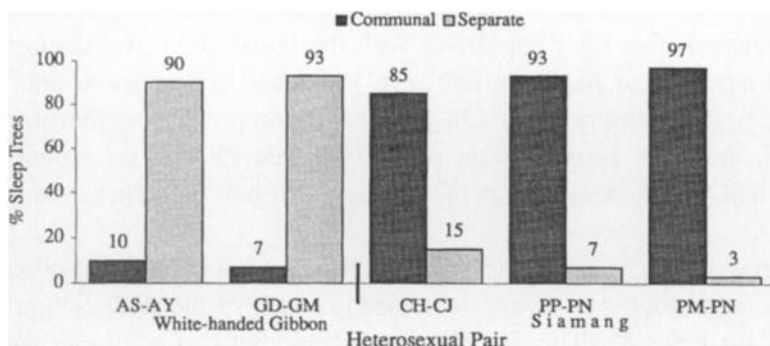
Fig. 12. Communal *vs* separate sleep tree use by pair-mates. Percentage of sleep trees (*i.e.* nights) in which paired adults slept communally in the same tree (dark-shaded bars) *vs* separately in different, widely-spaced trees (light-shaded bars). *N*'s (number of days) for each pair are: 51 (AS-AY), 67 (GD-GM), 62 (CH-CJ), 56 (PP-PN), 75 (PM-PN).

Agonistic behavior

Paired adults rarely exchanged open-mouth threats at one another (but did direct them at resident immatures). Directionality was consistent, however: all of the few threats observed were performed by adult females. The quantity and general context of open-mouth threats during focal animal sessions (*i.e.* excluding *ad libitum* observations) were: 1) the gibbon female AY directed one open-mouth threat at her mate during a grooming session; 2) the gibbon GM gave one open-mouth to her mate GD during grooming; 3) the siamang female CJ performed one threat while feeding; 4) the siamang female PN threatened her mate PM twice (once during feeding and once during grooming); and 5) siamang female PN directed six open-mouth threats at her mate PP (usually during grooming sessions). Hinde's (1983b) recommendation that the *quality* of an interaction reflects its significance is relevant here. The open-mouth threats of gibbons AY and GM were accompanied by lunges, exaggerated head jerking, rigid body posture, and pilo-erection. Siamang threats lacked these behavioral and morphological correlates.

Grimace and lip-smacking displays were exchanged between adults extremely infrequently (and primarily performed by immatures). In contrast to threats, all of the few instances of these behaviors were performed by males: 1) siamang male CH directed lip-smacking at his mate

once immediately after he yawned; 2) siamang male PM gave one gri-
mace immediately after copulating with the female PN; 3) siamang male
PP lip-smacked at his mate PN once just prior to copulation and once
during a grooming session. In summary, except for the siamang pair
PP-PN, agonistic gestures were rare. The male PP was the recipient of
about half the threats and was the performer of half the appeasement ges-
tures.

Aggressive physical contact between paired adults was never observed.
Intense aggression was manifested twice in chases of the adult gibbon male
AS by his mate AY. The first chase occurred after this adult pair and as-
sociated immatures had left a tree within which the adult female had fed
briefly. She first chased the subadult female of the group and then turned
and chased the adult male several meters. The male dropped down lower
in the canopy, crouched as the female came near, screamed, then rolled
off the branch to hang by all four limbs below the adult female. The
second chase occurred after the adult female entered and began feeding
in a small *Mallotus sphaerocarpus* (Euphorbiaceae) tree, followed about a
minute later by the adult male and juvenile female. Within four minutes
of the adult male's entry into the tree, the female chased him out of it and
continued to feed for about five more minutes before she left. The adult
male did not enter the tree again. The second chase occurred during a
period of extremely low abundance of fruiting trees in the Ketambe rain
forest (Palombit, 1992).

Discussion

Sample size typically limits the conclusions of field studies of hylobatids:
logistical constraints conspire with the behavioral ecology and demogra-
phy of hylobatids to prevent the detailed study of more than one habituated
group in most field studies (Brockelman & Srikosamatara, 1984; Whitten,
1984). The sample size of five habituated pairs is an improvement over past
studies, but it is still small. The data regarding interspecific differences in
pair bonds must be interpreted accordingly as providing explanations and
hypotheses intended for future empirical tests.

Pair bonds in siamang and white-handed gibbon

Pair bond 'strength' (Kleiman, 1977) or male-female 'attachment' (Wickler, 1976) is a function not just of the *nature* of social interactions between the sexes, but of their *diversity* as well (Hinde, 1983b). This is exemplified by two measures — close proximity and (nongrooming) physical contact. Time devoted to these activities differs unambiguously and consistently in the two species, providing evidence for greater heterosexual affiliation in siamang. When considered in light of grooming, these patterns also suggest that a greater diversity of interactions contribute to pair bonds in siamang. Not only do siamang adults approach one another more frequently, but when white-handed gibbons *are* within one meter of one another, they spend proportionally more of that time engaged in grooming. Thus, approaches are causally closely linked to subsequent grooming in gibbons, but less so in siamang. That is, gibbon pair-mates appear to approach each other primarily in order groom (or, alternatively, allogrooming can be viewed as an interaction necessary to facilitate sustained nearness to a partner). A similar interpretation applies to touching: siamang spend much more time in relaxed (nongrooming) physical contact, but grooming (and, less often, copulating) are virtually the only contexts in which adult gibbons touch one another. Thus, approaches and touching are important affinitive processes operating independently of grooming to maintain pair bonds in siamang, whereas in gibbons they appear to be manifestations of a single pair-bonding process involving grooming.

Embraces may also contribute to a greater diversity of interactions maintaining the pair bond in siamang. Although infrequent in siamang, embraces are virtually nonexistent between adult gibbons. Previous hypotheses that embraces among white-handed gibbons function to inform adults of the maturational condition of offspring (Carpenter, 1940), or as a means for dominant individuals to reassure frightened subordinates (Ellefson, 1974), support observations at Ketambe that embraces in this species are exchanged primarily between adults and immatures. In contrast, most siamang embraces are between paired adults. It is possible that gibbon embraces are less likely to be observed since they last only a few seconds, but the strikingly longer duration of the siamang embraces itself suggests an interspecific difference in their relevance for maintaining pair bond affinity.

Use of sleep trees may have at least two implications for pair bonds. First, sleep sites are often important venues for social behavior (Mason, 1968; Kinzey *et al.*, 1977; Kinzey & Wright, 1982; Nakagawa, 1992). Since both gibbons and siamang enter sleep trees 1-3 h before sunset and depart the next day 0.25-1.5 h after sunrise (Palombit, 1992), adult gibbons that habitually sleep in separate trees sacrifice opportunities for affinitive interaction over several daylight hours each day. Conversely, communal use of sleep trees in siamang permits more social interaction and proximity during daylight hours and, conceivably, into the night (*e.g.* Anderson, 1984; Ansorge *et al.*, 1992). Second, a cyclical increase in social intolerance in the late afternoon may underlie the daily transition from coordinated foraging of multiple animals to individual use of dispersed sleep trees (Kummer, 1970). These causal mechanisms may contribute to the development of differences in cohesion between adults.

Maintenance of pair bonds

Intrasexual (and, in some cases, intersexual) aggression is a well-established mechanism generating one male-one female associations by limiting an individual's opportunities for interactions with other adults (Leighton, 1987; Mitani, 1989; Snowdon, 1990). Cohesive and persistent pair bonds (as in obligate monogamy), however, are likely to additionally involve attraction — either unilateral or mutual — between pair-mates (Eisenberg *et al.*, 1972; Wickler, 1976; Kleiman, 1981). At first glance, unilateral attraction is suggested in both siamang and white-handed gibbons by the greater responsibility of males for approach/withdrawal interactions surrounding close proximity and grooming sessions. The distribution of allogrooming between mates, however, suggests a species difference. Female gibbons rarely initiate grooming sessions and provide far less grooming to males than they receive from them. In two siamang pairs, however, grooming was more reciprocal. This result suggests a pronounced 'asymmetry of interest' in investment in the pair bond: the sexes contribute differentially in gibbons (females less than males), but more equally in siamang (the conspicuous sex difference in grooming in the third siamang pair, PP-PN, is discussed below).

A greater male contribution to grooming in white-handed gibbons is not solely a matter of male initiative. Rather, female gibbons appear to actively

solicit this enhanced investment by presenting for grooming significantly more often than female siamang do and more than conspecific males do. Moreover, male gibbons fail to elicit grooming from their mates at higher rates than female gibbons (or siamang of both sexes). Siamang males and females, in fact, do not differ from one another in the effectiveness of presents in garnering grooming investment. This result further illustrates how the magnitude of the sex difference in investment patterns varies between the two species. Female gibbons not only offer less and solicit more investment from their mates, but they also reject male solicitations for reciprocation from them more often than siamang adults do. Greater sexual equality of grooming in siamang is not simply the result of sexually monomorphic rates of presenting in this species: an adult siamang more often offers grooming without any previous 'request' from its mate.

Although existing data are not directly comparable to this study, other descriptions of grooming in wild siamang and white-handed gibbon suggest the possibility of intraspecific variation. The male siamang of Chivers's (1974) study group appeared to groom his mate slightly more than she groomed him, although the statistical magnitude of this difference is not clear. Ellefson (1974) did not quantify grooming, but qualitatively appraised grooming reciprocity between the sexes as variable.

Evolution of pair bonds

Several hypotheses for the evolution of monogamous pair bonds in primates emphasize the possible benefits females derive from close affiliation with males, *e.g.* predator surveillance, territorial defense, direct paternal care (Dunbar, 1988), and, in the most recent elaboration of this principle specifically for hylobatids, protection from conspecific infanticidal males (van Schaik & Dunbar, 1990). This hypothesis predicts that females invest in these advantageous pair bonds as much as males do, *e.g.* in maintenance of proximity (Birkhead & Møller, 1992). Female white-handed gibbons at Ketambe do not do so. Compared to males, they not only contribute less to proximity maintenance, initiation of grooming sessions, and reciprocation of grooming, they also frequently reject male solicitations for such investment. Moreover, although paired gibbons (and siamang) rarely interact agonistically, *all* threats and attacks are performed by females and directed at males, whereas the converse is true for conciliatory-appeasement

gestures. Taken together, these patterns suggest that female white-handed gibbons are slightly dominant to males, though not to the same degree as in some Malagasy prosimians (e.g. Richards, 1985) (the importance of considering intraspecific variation, however, is highlighted by Ellefson's (1974) qualitative description of male dominance in one gibbon pair).

Thus, the pair bond of the white-handed gibbon seems less an arrangement in which a female benefits substantially from associating with a male than one in which she tolerates his presence. The 'useless male' (Hrdy, 1981; van Hooff & van Schaik, 1992) or 'unavoidable partner' (Mock & Fujioka, 1990) phenomena may not strictly characterize these pair bonds since males cooperate with females in territorial defense and are not exclusively responsible for intra-pair social attraction. Nevertheless, the extent to which males enhance female reproductive success is by no means obvious.

The evolutionary origin of pair bonds in white-handed gibbons and siamang may have had less to do with the fitness advantages accrued by females associating with single males than with "mate guarding" by males, since this tactic often discourages extra-pair copulations and may be manifested as male-initiated proximity (Trivers, 1972; Clutton-Brock, 1989; Birkhead & Møller, 1992). Observations of mate-switching in hylobatids (Palombit, 1994a), of extra-pair copulations (Palombit, 1994b; Reichard, 1995), and of male responsibility for proximity in both species suggest that mate guarding has potential advantages for males.

Although this selective force may have operated in both species, the evolution of differences in pair bonds may have resulted from contrasting selective forces surrounding feeding ecology and paternal care. Phenological patterns suggest that the food resources utilized by white-handed gibbons entail greater intragroup feeding competition than those used by siamang. The siamang's primary foods — fig fruit (Ficus spp., Moracae) and immature foliage from lianas — occur in large and temporally consistent patches; white-handed gibbons rely disproportionately more on non-fig fruits and insects, which, though of greater individual value, are also less abundant in space as well as seasonally scarce (Palombit, 1992; see also Leighton & Leighton, 1983; van Schaik, 1986). Divergent ecological costs of close association may contribute to the evolution of less cohesive pair bonds in gibbons relative to siamang.

In siamang, lower feeding competition combined with the consequent greater proximity of mates may pre-adapt males for extensive care of young by permitting higher rates of affiliative interaction between adults and young (*e.g.* Kleiman & Malcolm, 1981) and by increasing certainty of paternity (*e.g.* van Rhijn, 1991). Adult male siamang are known to carry infants in their second year of life (Chivers, 1974; Alberts, 1987; Dielentheis *et al.*, 1991), in contrast to male gibbons, which do not provide any substantial direct care in the wild (Carpenter, 1940; Ellefson, 1974) and only exceptionally in captivity (*e.g.* Berkson, 1966). Parenting by male siamang may then 'feedback' and select for enhanced female investment in and protection of pair bonds with these care-giving males (*e.g.* Price, 1992). The result may be more reciprocal maintenance of stronger pair bonds in siamang than in gibbons.

It is this positive correlation between male-female cohesion and male care of infants — which variably characterizes nonhuman primates in general (Hamilton, 1984) — that may be relevant in evaluating the social relationship of the siamang pair PP-PN. This pair bond resembled conspecifics in showing a high level of attachment (*e.g.* in close proximity, physical contact, sleep tree use), but was more similar to gibbons in the disproportionately lower contribution of the female to intra-pair grooming. This result may reflect natural intraspecific variation in the behaviors generating pair bonds, which may contradict a possible species difference and must therefore be accounted for more fully if stable species differences are to be identified. On the other hand, a comparison of the two pair bonds of this female — when evaluated in light of the male PP's previous parental behavior — suggest that the nature of her relationship with PP is consistent with the theoretical framework presented above. Two patterns are important.

First, the female PN invested significantly less in the pair bond with her former mate PP (than with her subsequent mate PM), as reflected in less reciprocation of grooming, a much higher rate of threats, and higher Hinde indices for both grooming sessions and close proximity. Given that PP and PN spent more time sitting together than any other subject pair, the difference in the Hinde index for close proximity for PP-PN and PM-PN (43 *vs* 14) suggests a strikingly low female contribution to proximity maintenance with PP. Some differences between the two pair bonds

could conceivably result from the more recent pairing of PN with PM. On the other hand, the possibility that the PP-PN pair bond was also new (when the study began) cannot be rejected, and the relative contributions of the sexes in maintaining the pair bond may be independent of its age (even though rate of social interaction is often higher in newly formed pairs) (Evans & Poole, 1984; Savage *et al.*, 1988). Thus, the difference in PN's pair-bonding behavior may implicate lower tolerance of the male PP, which may have promoted his eventual abandonment of the female (and territory) in the absence of any local mating opportunity to exploit (Palombit, 1994a). Termination of this pair bond via the *departure* of the male is noteworthy since active substitution of an adult's partner (as opposed to passive loss of a mate from death) suggests intrinsic behavioral processes promoting the dissolution of the pair bond. Adult female hylobatids may often exert sufficient control over the pair bond to incite replacement of incompatible mates in this way (Palombit, 1994a).

Second, the female's reduced investment in this pair bond was correlated with the failure of the male PP to provide parental care during the infant's second year of life. Only 14 bouts of infant-carrying were observed during focal sessions and these were brief (Mean $\pm$ SD $= 120 \pm 181$ s). This is considerably less carrying than reported for a wild male siamang (Chivers, 1974) and in some captive males (Alberts, 1987; Dielentheis *et al.*, 1991), although captivity may depress male infant-carrying (*e.g.* Fox, 1972; Dal Pra & Geissmann, 1994) by depriving females of opportunities to escape from infants they leave with males (Chivers, 1974). Although the female PN frequently 'deposited' her infant with the male PP (and then withdrew from both), regular infant-carrying by the male failed to develop.

Thus, if the siamang female PN's lower contribution to her pair bond with PP was causally related to his low investment in her infant, then this relationship may reflect the kind of fundamental asymmetry of interest that has operated over evolutionary time on white-handed gibbons. That is, higher levels of direct, depreciable paternal care engender greater female investment in the pair bond. In siamang, the fact that some males will provide substantial care of infants under certain (currently unclear) circumstances means that co-variation in pair bond strength and paternal investment can conceivably be observed over ecological time: a trivial male contribution to his mate's reproductive effort may lead to reduced

female interest in the pair bond and even its eventual disintegration Since the parental behavior of male white-handed gibbons apparently does not vary similarly, its absence does not affect the stability of an individual pair bond so profoundly. Nevertheless, this interspecific difference in male parenting may reflect contrasting selective pressures acting ultimately on the contributions of the sexes to maintaining pair bonds in the two species.

Conclusions

The siamang and white-handed gibbon both fall toward the 'obligate' end of Kleiman's (1981) continuum of social systems relative to other monogamous mammals characterized by low rates of social interaction, spatial proximity, and physical contact. Nevertheless, the two species separate out on this continuum along the pair bond dimension, as Chivers (1972, 1976) proposed. Analogous divergence of species at the other 'facultative' end of Kleiman's continuum has also been suggested by quantitative variation in pair bonds in three monogamous antelopes — the dik-dik (*Madoqua kirkii*), klipspringer (*Oreotragus oreotragus*), and blue duiker (*Cephalophus monticola*) (Kranz, 1991).

Since Kleiman's (1981) continuum proposes systematic covariaton of numerous inter-related biological processes, divergent pair bonds in siamang and gibbon suggest that social relationships between adults and immatures — as well as among immatures — also differ in these species. Siamang social structure may fall far enough to the obligate end of this continuum to represent 'incipient extended families' pre-adapted for (but not necessarily evolving towards) systems in which older immature or adult offspring remain in the group to help care for younger individuals (*e.g.* wild dogs (Frame *et al.*, 1979) or some callitrichids (Terborgh & Goldizen, 1985)). Although infant-carrying is not regularly performed by subadult siamang, it has been recorded occasionally in captivity (Fox, 1977; Dielentheis *et al.*, 1991) and in the wild (Chivers & Raemaekers, 1980).

Study of relationships of adults and immatures will also clarify the adaptive significance of pair bonds. For example, Hrdy (1986) describes alternate ways of viewing how paternal care, mating system, certainty of paternity, and pair bond cohesion co-evolve. An important goal of future studies — especially of siamang — is to improve understanding of natu-

ral variation in direct and indirect male parental investment, its effect on female reproduction, and its behavioral and ecological causes.

Results of other studies suggest that variation in pair bonds in the Hylobatidae extends beyond that proposed for the siamang and white-handed gibbon. For example, grooming between pair-mates appears to be virtually nonexistent in *H. agilis* (Gittins & Raemaekers, 1980) and *H. klossii* (Whitten, 1980), in contrast to the substantial grooming investments of siamang and white-handed gibbons at Ketambe and in Malaya (Chivers, 1974; Ellefson, 1974). Given that *Hylobates* is distributed over a diverse array of southeast Asian habitats (Brockelman & Srikosamatara, 1984), and that even subtle ecological differences may promote variation in social relationships (Wickler, 1976; Hinde, 1983a; Wrangham, 1980), wider social variation within the genus would not be entirely unexpected.

These differences endorse the view that the monogamous lesser apes are characterized by subtle but biologically significant differences in social systems without dramatic departures from a 'family' group structure. At the very least, these data support strongly Brockelman & Srikosamatara's (1984) call for an end to the practice of using the white-handed gibbon as the "standard model" of hylobatid behavior. The labels typically employed to designate hylobatid societies — 'monogamous' and 'territorial' — may provide a useful context for analyzing social behavior, but they underestimate social variation (just as the terms 'polygynous' and 'nonterritorial' fall short of describing macaque and baboon societies).

Clearly, more groups must be studied in the field to verify differences in heterosexual relations in siamang and white-handed gibbon, particularly in light of intraspecific variation. This study indicates the potential importance of such individual variation, but it also suggests the existence of stable, biologically meaningful species differences in the nucleus of hylobatid social systems: the male-female pair bond.

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