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Taxon-Specific Pair Bonding in Gibbons (Hylobatidae)

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Abstract

This study provides the first statistically significant evidence that the mechanisms of how pair bonds are created or maintained differ between gibbon taxa. We examine the pair bond in captive pairs of three genera of gibbons (Hylobatidae): siamangs (*Symphalangus*, N = 17 pairs), crested gibbons (*Nomascus*, N = 7 pairs), and pileated gibbons (*Hylobates pileatus*, N = 9 pairs). In the first part of this study, we determine three generally-accepted indicators of pair-bond strength (mutual grooming, behavioral synchronization and partner distance). A pairwise comparison of our samples reveals a difference in relative partner distances between siamangs and pileated gibbons, suggesting that siamangs may have a stronger pair bond than pileated gibbons. No difference among the three taxa was found in other variables believed to indicate pair bond strength. In the second part we examine the amount of partner-directed grooming in each sex. In siamangs, males invest significantly more into pair bonds than females, whereas the opposite is true in crested and pileated gibbons. Our results for siamangs correspond to predictions derived from the ‘mate-defense hypothesis’ for the evolution of pair bonds, whereas our results for crested gibbons and pileated gibbons correspond to predictions derived from the ‘male-services hypothesis’.

Keywords: social structure, pair bond, *Symphalangus*, *Nomascus*, *Hylobates*, sex-specific investment, Hylobatidae

1. Introduction

Whereas the genera of great apes are known to differ strongly among each other in their social structure, the small apes or gibbons clearly are a more uniform group [1–3]. Distributed in Asian rain forests, its members typically live in socially monogamous, unimale unifemale, territorial groups [4, 5], although some flexibility in group composition and sexual behavior occurs [6–8]. Non-monogamous (extra-pair) matings and groups with multiple adult males and multiple adult females occasionally occur in gibbons [7, 9–15].

It has repeatedly been suggested, however, that gibbon taxa may differ in subtle details of their social organization [16]:

Wild family groups of Malayan siamangs (*Symphalangus syndactylus*) appear to be more tightly knit than those of white-handed gibbons (*Hylobates lar*), with siamang intra-group distances being shorter and intra-group communicatory signals being fewer or less conspicuous to observers, and paternal infant-carrying only occurring in siamangs [17–21]. A greater heterosexual cohesion in pair bonds of siamangs, as compared to white-handed gibbons, was also found in a field study in Sumatra [22], but differences in paternal investment appear to be less clear-cut. Paternal infant-carrying appears to be absent in some wild and many captive siamang groups and varies dramatically among males of the same population [10, 23–25], while it may occasionally occur in other gibbon taxa, at least in captive groups [23, 26].

Several reports suggest that the black-cheeked species of the crested gibbons (genus *Nomascus*) differ from other hylobatids in their social organization by more often forming bi-female groups [27–33]. This may not appear to apply to light-cheeked crested gibbon species [34, 35], but see [36].

Recent studies on gibbon calls documented that the various taxa strongly differ in how they present their long and loud morning song bouts [37–40]. In some taxa, mated pairs produce duet song bouts but usually no solo songs (genera *Hoolock*, *Nomascus* and *Symphalangus*), others produce sex-specific solo songs in addition to duets (*Hylobates agilis*, *H. lar*, *H. muelleri*, *H. pileatus*), and others yet produce sex-specific solo song bouts only (*H. klossii*, *H. moloch*). In all members of the genus *Nomascus* and most species of the genus *Hylobates*, for instance, most of the singing is produced by males, whereas in *H. moloch*, males sing rarely and most songs are produced by females. This pronounced diversity of sex-specific investment in resource defense provides indirect evidence for taxon-specific differences in social organization, and, possibly, in previously unrecognized factors of ecological adaptation or inter-specific competition.

Moreover, duets strongly differ in their complexity among taxa, with the most complex ones being uttered by siamangs (*S. syndactylus*) [41, 42]. These differences in song organization also strongly suggest differences in social organization. Because duet song bouts are believed to serve, among other things, to strengthen or advertise pair bonds, duetting and non-duetting gibbon species should differ either in their pair bond strength or in how the pair bond strength is achieved [43, 44].

Although the reports cited above suggest that some gibbon taxa may differ in social organization, very little quantitative evidence for such species-specific differences in the social structure are currently available. Previous comparisons have been limited to sample sizes of 2–3 pairs per genus [17, 19, 22, 23], thus precluding statistical testing. Palombit [3] correctly identified a great need for detailed data on more hylobatid pair bonds, so that we may identify consistent social patterns in light of intra-specific variation.

Early reviews on monogamy found shared behavioral traits in monogamous primates and suggested that the males generally initiate grooming and groom females more often than the reverse situation occurs [45]. In socially monogamous pairs, pair partners usually maintain close spatial association and often perform spectacular, well-coordinated, pair-specific display behavior. This does not necessarily imply, however, that the sexes share mutual socioreproductive interests [46]. Shared interests may not be required for the evolution of social monogamy, and pair formation does not require an absence of sexual conflict, or symmetric costs and benefits for males and females.

Several of the hypotheses explaining the evolution and maintenance of social monogamy in mammals make predictions regarding female and male contributions to the pair bond [47].

1. According to the 'resource-defense hypothesis', both a male and a female benefit from pair bonding to defend resources together [48]. In this case, a male and a female should be equally interested in maintaining proximity and affiliation with a pair mate and defending their territory.
2. According to the 'mate-defense hypothesis', a male should bond with a female when either the spatial distribution of females or the temporal distribution of fertile periods makes it difficult for males to defend access to more than one female at a time [49]. In this case, a male should be more interested in maintaining proximity and affiliation with the partner.
3. According to the 'male-services hypothesis', a female benefits from bonding with a male when the male provides important services such as territorial or anti-predator defense, infant care, or protection from infanticide by competing males [48, 50–52]. In this case, a female should be more interested in maintaining proximity and affiliation with the partner while the male should provide some significant services.

The goal of our study was to answer the following two questions: (1) Do gibbon taxa differ in the strength of their pair bonds? (2) Do gibbon taxa differ in the way pair bonds are created and maintained?

We present the first comparative and quantitative study on differences of the pair bond among multiple gibbon taxa. We have collected observational data on several captive groups of siamangs (genus *Symphalangus*), three species of the crested gibbons (genus *Nomascus*), and the pileated gibbon (*Hylobates pileatus*) as a representative of the dwarf gibbons (genus *Hylobates*). Our study will focus, therefore, on a comparison of these three genera. Photographs of three of the species we studied are shown in **Figure 1**. In addition, a compilation of previously-published data also permits us to make a limited comparison with other gibbons of the genus *Hylobates*.

In order to estimate pair bond strength, we quantified the following three generally-accepted indicators of pair bond strength (behavioral synchronization, relative distance between mates, and amount of partner directed grooming) following [44, 53].

In order to gain insight in the pair bonding mechanism, we examined which sex invests more in the pair bond by measuring the amount of grooming directed at the respective partner.

Although allogrooming *per se* may serve hygienic, social, communicatory, stress relief or thermal functions [54–59], these functions may be influenced by a species's social organization. For social systems with stable pair structures, allogrooming has been proposed to serve a pair-bonding function [45, 60, 61] and to reflect the investment into a pair bond [62, 63] and, therefore, the ultimate costs and benefits which partners can expect from a relationship [64]. Thus, sex-specific differences in partner-directed allogrooming indicate – on a proximate level – ultimate sex-specific strategies.

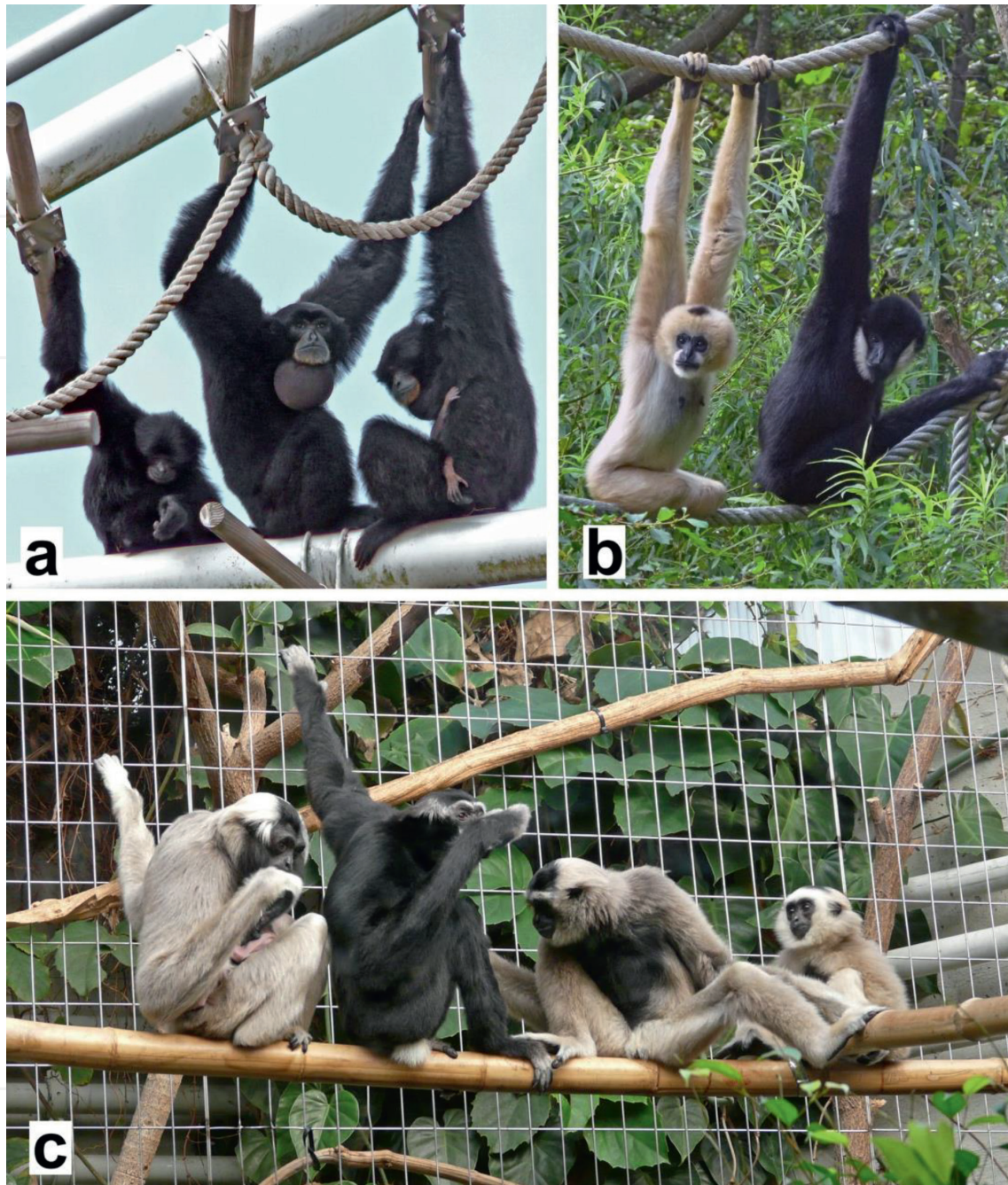


Figure 1.

Three of the gibbon species that were observed during this study. (a) Siamang (*Symphalangus syndactylus*), family group, showing from left to right: juvenile, adult male, and adult female carrying an infant. Siamangs are of mostly blackish fur coloration. Notice the half-inflated throat sacs, which play a role in siamang territorial vocalizations and can be inflated to about the size of the animals' head. (b) Northern White-cheeked Crested Gibbon (*Nomascus leucogenys*) pair, showing from left to right: adult female, and adult male. Adult male and female differ markedly in their fur coloration. Females are mostly yellowish, and males are blackish. (c) Pileated Gibbon (*Hylobates pileatus*) family group, showing from left to right: adult female carrying a neonate infant, adult male, subadult male, and juvenile male. Adult male and female of this species also differ markedly in their fur coloration. Females are pale grey or fawn-buff with black on crown, cheeks and chest, while males are blackish with white facial border, corona, digits, and genital tuft. Photographs by Thomas Geissmann.

2. Methods

Our data collection methods have previously been described [44, 53]. Siamang (*Symphalangus syndactylus*) data were collected in a consistent form by one of us

(M.O.) between April 1985 and March 1993. A total of 17 siamang groups were observed at the following zoos: Antwerp (An), Belgium, Branféré (Br1, Br2, Br3), France, Budapest (Bu), Hungary, Berlin Zoo (Be), Dortmund (Do), Dresden (Dr1, Dr2), Duisburg (Du), Frankfurt (Fr), Krefeld (Kr1, Kr2), Munich (Mn), Germany, Studen (St), Zurich (Zh), Switzerland and Washington (Wa), U.S.A., with group size ranging from two to six animals.

Crested gibbon data were collected in the same way by S.R.-W. between August and October 2001. A total of seven crested gibbon groups (*Nomascus*) were observed at the following zoos: Duisburg (Du), Eberswalde (Eb), Osnabrück (Os1, Os2), Germany, and Mulhouse (Mu1, Mu2, Mu3), France, with group sizes ranging from two to five animals. Three crested gibbon species are represented in our sample, including the Northern White-cheeked Crested Gibbon (*N. leucogenys*): Du, Mu1 and Os2; the Southern White-cheeked Crested Gibbon (*N. siki*): Mu2; and the Southern Yellow-cheeked Crested Gibbon (*N. gabriellae*): Eb, Mu3 and Os1. The gibbon classification used here follows [65].

Data for Pileated Gibbons (*Hylobates pileatus*) were collected in the same way by J.v.d.L. and K.N between February and May 2007. A total of nine groups were observed at the following zoos: Phnom Tamao, Cambodia (PT1–7), and Zurich, Switzerland (Zu1, Zu2), with group size ranging from two to five animals.

In order to assure comparability of data collected by the observers M.O., S.R., J.v.d.L. and K.N., dual observations were carried out on 31 July 2001 and on 13 February 2007, respectively, until consistent values of inter-observer concordance were obtained [66].

At each zoo, observation time for each sampling method was distributed evenly across the animals' activity period between 0700 and 1800 h (until 1700 h during the winter months, and between 0800 and 1800 h for crested gibbon groups Du, Eb, Mu, Os2).

We used focal animal sampling with the continuous recording rule [66–69] to collect information on the frequency and duration of grooming behavior between mates. Focal animals were changed every 20 min. Each of 11 siamang pairs was observed for 80 h, except for pairs Mu (50 h) and Du (90 h), and each crested and pileated gibbon pair for 35 h. Grooming occurred in discrete sessions that could be counted. We allowed an interval of up to 10 seconds between bouts of grooming before we counted them as two sessions, rather than one.

We used scan sampling to record behavioral synchronization of activities between mates. We defined 11 behavioral categories: socio-positive behavior (including allogrooming, embracing) and infant care, play, agonistic, territorial, sexual, comfort-related, feeding and food-related behavior, observe, rest and sleep, excretion, and locomotion. Scans were made every 1 min (or every 2 min in siamang groups Dr1, Kr1, Kr2, St). Siamang pairs were scanned for synchronization of behavioral categories during blocks of 5 or 10 min, separated by intervals of 20 min. Crested and pileated gibbon pairs were scanned for synchronization in parallel to the focal animal observations of grooming behavior. Each of 13 siamangs pairs was observed for 20 h, except pairs Zu (15 h), Be and Fr (30 h), and Du (40 h). Each crested and pileated gibbon pair was observed for 35 h. The occurrence of synchronized behavior between pair-mates is expressed in % of the total number of scans for a given pair.

We also used scan sampling to record the distance between mates. Distances were recorded to an accuracy of 0.5 m. If the individuals were closer to each other than 0.5 m, we recorded distance according to the following definitions: 0.3 m: shortest distance without body contact, 0.2 m: body contact through extremities, 0 m: body contact through trunk. Siamang pairs were scanned during blocks of 10 min,

separated by intervals of at least 10 min. During each scan sampling block, distance was recorded every 10 s. Crested and pileated gibbon pairs were scanned for the distance between mates every 1 min, and scans were carried out in parallel to the focal animal observations of grooming behavior. Each of 17 siamangs pairs was observed for 10 h, except pairs BrA, Bu, DrA (20 h), Be, Du, KrA (30 h), and Fr (210 h). Each crested and pileated gibbon pair was observed for 35 h.

The size of the enclosure varied between zoos (some gibbon groups were held in cages, others on islands). In small cages, the cage walls set outer limits to the inter-individual distances. Because small cages may have forced our pairs into closer proximity than bigger enclosures, we did not directly use absolute inter-individual distances in our comparisons. Instead, we calculated the relative distance (%) between mates, i.e. the inter-individual distance relative to the maximal possible distance in the pair's given environment (cage or island). This method was described by [44]. In order to test whether cage size had an influence on pair bonding behavior, we used the maximal possible distance in the pair's given environment as an indicator of cage size. In siamangs, our largest sample, this value ranged from 5.7 m in the smallest cage to 43.5 m on the largest island. We arbitrarily defined cages with values of less than 10 m as "small enclosures", the others as "large enclosures".

In addition to determining relative distance, we used scan sampling to estimate the time pair partners spent in each of the following distance classes: 1: body contact or distance of less than 0.3 m, 2: 0.3–1 m, 3: >1 m–3 m, 4: >3 m.

For comparison of our data on partner-directed behavior with literature data, we used male and female proportions of these behavioral variables, where male and female proportions complement each other to 100%. Proportions should be independent of the observation method and permit comparison of data from different observers.

One-sample sign test tests were used to compare classes of sex-specific grooming proportions within genera. For comparison of data among three genera, we used Kruskal-Wallis tests with Dunn's *post hoc* tests [70]. In order to compare data between *H. pileatus* and *H. lar* (i.e. after inclusion of data compiled from the literature), we used the Mann-Whitney *U* tests [71]. All tests were two-tailed, and the null hypothesis was rejected at $P = 0.05$. Statistical were calculated using the software StatView 5.0.1 and SPSS 17.0 on a Macintosh G4 computer.

3. Results

3.1 Strength of pair bonds

3.1.1 Synchronization of behavioral variables

The average degree of behavioral synchronization across 11 behavioral variables is shown in **Figure 2**. Values range from 15.5% to 63.9% in siamangs, from 8.0% to 38.7% in crested gibbons, and from 19.2% and 42.7%. As shown in **Table 1**, however, the overall degree of behavioral synchronization does not differ significantly between the genera (Kruskal-Wallis test, $P = 0.186$).

3.1.2 Relative partner-distance

Average relative partner distances and time proportions spent in four distance classes for each study group are listed in **Table 2**. Considerable differences were found

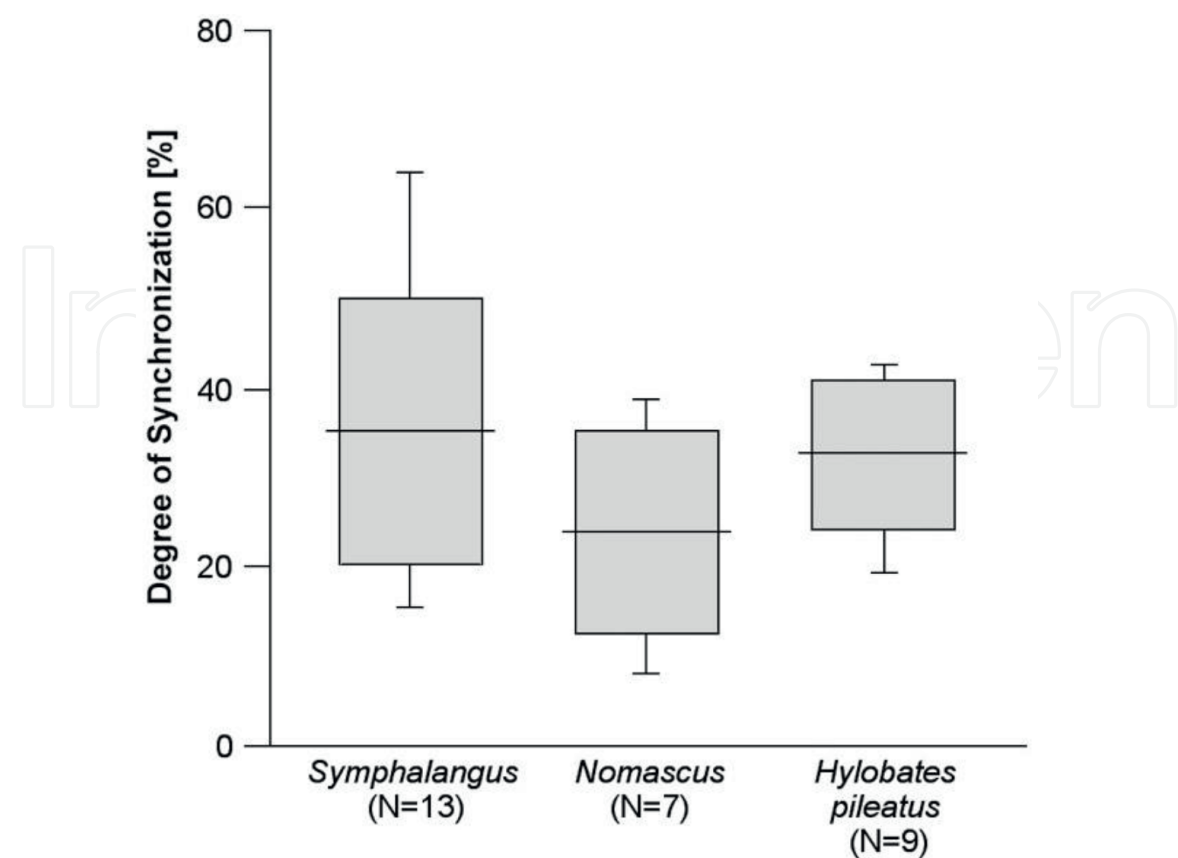


Figure 2. Comparison of the average degree of behavioral synchronization between siamangs (*Symphalangus*, $N = 13$ pairs), crested gibbons (*Nomascus*, $N = 7$ pairs), and pileated gibbons (*Hylobates pileatus*, $N = 9$ pairs). Box plots show mean values, standard deviations and minimum and maximum values. The difference between the genera is not statistically significant (Kruskal-Wallis test, $P > 0.05$, see text).

	Taxon			Kruskal-Wallis test (<i>p</i>)
	<i>Symphalangus</i>	<i>Nomascus</i>	<i>Hylobates pileatus</i>	
Taxon mean	35.02 ± 15.39 (<i>N</i> = 14)	23.73 ± 11.30 (<i>N</i> = 7)	32.69 ± 7.95 (<i>N</i> = 9)	0.186

Table 1. Average degree of synchronization [% ± standard deviation] across 11 behavioral variables for siamangs (*Symphalangus syndactylus*), crested gibbons (*Nomascus* spp.), and pileated gibbons (*Hylobates pileatus*). Abbreviation: *p* = error probability.

among pairs. Time spent in distance class 1, for instance, varies from 0.3% to 49.7% in siamangs, from 5.6% to 32.3% in crested gibbons, and from 0.0% to 20.5% in pileated gibbons. Similarly, time spent in distance class 4 varies from 1.3% to 61.2% in siamangs, from 14.1% to 47.4% in crested gibbons, and from 31.6–84% in pileated gibbons. The time gibbon pairs spent in each of the four partner distance classes are shown in **Figure 3**. The three taxa do not differ significantly among each other in the time groups spent in any of the four partner distance classes (Kruskal-Wallis tests, $P > 0.05$), except for time spent in distance class 4 ($P = 0.014$). Dunn *post-hoc* tests revealed that pileated gibbon pairs spent more time in distance class 4 than siamangs ($P < 0.02$). Moreover, the difference in distance class 2 is close to significance ($P = 0.051$).

Group	Relative distance	Distance classes [%]			
	[%]	1	2	3	4
(a) Siamangs					
Antwerp	32.80	11.90	14.00	50.00	24.10
Berlin Zoo	29.80	13.70	10.00	40.80	35.50
Branféré 1	14.50	5.40	19.50	31.20	43.90
Branféré 2	12.10	10.30	29.70	23.90	36.10
Branféré 3	18.30	1.80	17.00	20.00	61.20
Budapest	29.30	10.70	21.10	34.10	34.10
Dortmund	10.10	29.50	34.80	16.60	19.10
Dresden 1	29.00	12.50	18.10	67.50	1.90
Dresden 2	24.00	12.90	31.10	54.70	1.30
Duisburg	29.10	12.30	12.20	48.70	26.80
Frankfurt	40.40	3.30	12.60	62.30	21.80
Krefeld 1	30.90	3.50	15.10	37.60	43.80
Krefeld 2	35.90	0.30	7.40	38.60	53.70
Munich	31.20	24.90	13.80	16.20	45.10
Studen	11.50	49.70	22.40	19.30	8.60
Washington	26.50	20.50	14.90	21.40	43.20
Zurich	36.10	1.30	17.80	62.30	18.60
Mean	25.97	13.21	18.32	37.95	30.52
(b) Crested gibbons					
Duisburg	33.68	5.70	39.19	41.04	14.07
Eberswalde	12.12	32.30	17.01	15.68	35.01
Mulhouse 1	30.40	7.65	19.52	25.40	47.42
Mulhouse 2	23.31	23.68	14.33	15.85	46.14
Mulhouse 3	21.12	30.73	14.79	17.03	37.45
Osnabrück 1	21.99	17.80	16.22	24.09	41.89
Osnabrück 2	21.63	5.64	30.05	27.01	37.30
Mean	23.47	17.64	21.59	23.73	37.04
(c) Pileated gibbons					
Phnom Tamao 1	28.77	7.30	14.20	28.20	50.30
Phnom Tamao 2	7.28	10.70	17.70	17.70	54.40
Phnom Tamao 3	41.99	0.00	3.90	11.30	84.80
Phnom Tamao 4	23.18	20.50	6.00	28.90	44.60
Phnom Tamao 5	24.58	11.30	16.70	23.60	48.40
Phnom Tamao 6	12.82	13.80	11.20	26.40	48.50
Phnom Tamao 7	23.13	5.50	9.70	53.20	31.60
Zurich 1	18.29	14.90	20.10	24.70	40.40
Zurich 2	34.83	0.90	7.40	17.20	47.50
Mean	23.47	9.43	11.88	25.69	50.06

Table 2.
Average relative partner distances and time proportions spent in four distance classes: (a) siamangs (Symphalangus syndactylus, N = 17 groups), (b) crested gibbons (Nomascus spp., N = 7 groups), (c) pileated gibbons (Hylobates pileatus, N = 9 groups).

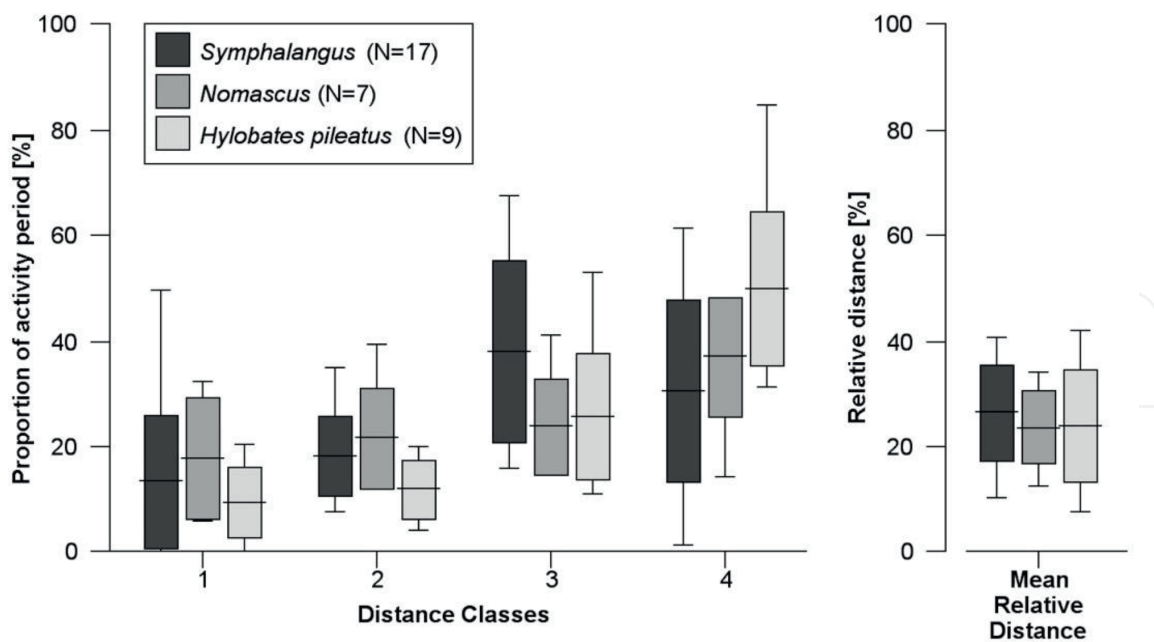


Figure 3.
 Time proportion spent in 4 distance classes (left) and of the mean relative partner distances (right) in siamangs (*Symphalangus*, N = 17 pairs), crested gibbons (*Nomascus*, N = 7 pairs), and pileated gibbons (*Hylobates pileatus*, N = 9 pairs). Box plots show mean values, standard deviations and minimum and maximum values. In a comparison between the genera (Kruskal-Wallis tests), only one of the five variables (distance class 4) are statistically significant ($P < 0.05$, see text).

The relative distance between pair partners is also shown in **Figure 3**. The three taxa do not differ in this variable (Kruskal-Wallis test, $P > 0.05$).

3.1.3 Allogrooming

The number of grooming sessions/hour (average of male and female) varies from 0.0 to 3.9 in siamangs (*Symphalangus*, N = 12 pairs), from 0.5 to 2.0 in crested gibbons (*Nomascus*, N = 7 pairs), and from 0.0 to 2.1 in pileated gibbons. The difference is not statistically significant (Kruskal-Wallis test, $P > 0.05$). The average duration of grooming sessions varies from 0 s to 76.0 s in siamangs, from 50.5 s to 132.1 s in crested gibbons, and from 0 s to 101.0 s in pileated gibbons. This difference is not statistically significant (Kruskal-Wallis test, $P > 0.05$). The proportion of time spent grooming varies from 0% to 66.9% in siamang pairs, from 9.3% to 28.7% in crested gibbon pairs, and from 0% to 57.7% in pileated gibbons. The difference is not statistically significant (Kruskal-Wallis test, $P > 0.05$). As a result, siamang pairs, crested gibbon pairs, and pileated gibbon pairs spend similar amounts of time grooming (**Figure 4**).

3.2 Mechanism of pair bonds

In order to study which sex invested more in maintaining the pair bond, we determined the %-proportion of partner-directed grooming for each adult. Because male and female proportions in a pair complement each other to 100%, the grooming proportion of one sex will suffice to provide the full information. The results are summarized in **Figure 5**.

In these analyses, one pair of siamangs (Kr2) and one pair of pileated gibbons (PT3) had to be excluded because pair partners were not observed to groom each

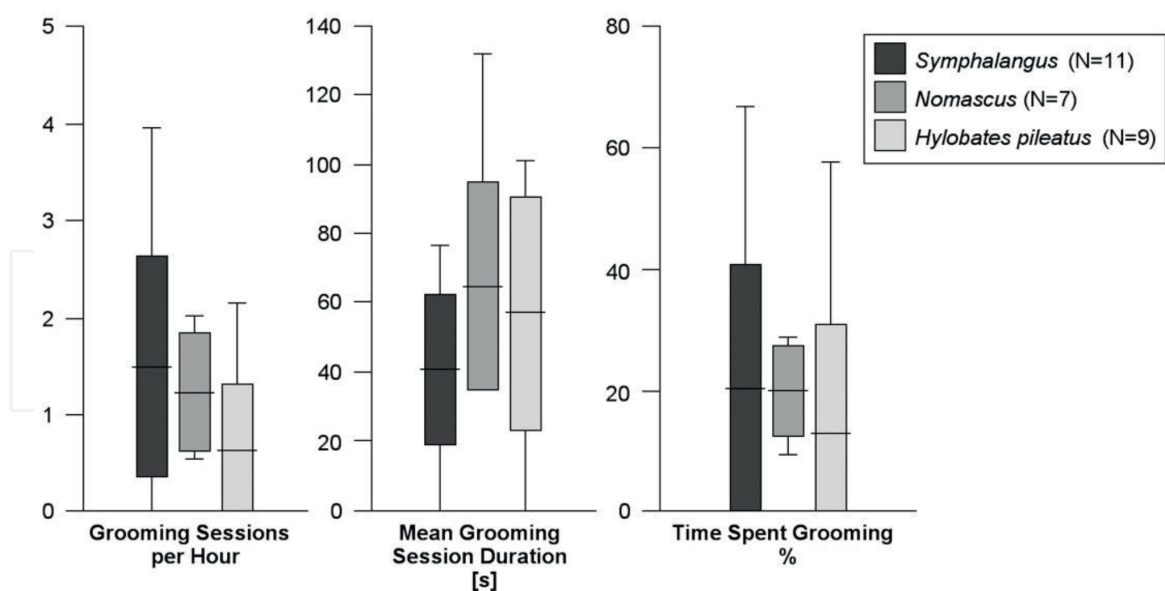


Figure 4. Average intra-pair grooming frequency per hour, mean duration of grooming sessions, and proportion of time spent grooming in siamangs (*Symphalangus*, N = 11 pairs), crested gibbons (*Nomascus*, N = 7 pairs), and pileated gibbons (*Hylobates pileatus*, N = 9 pairs). Box plots show mean values, standard deviations and minimum and maximum values. In a comparison between the genera (Kruskal-Wallis tests), none of the three variables are statistically significant ($P > 0.05$, see text).

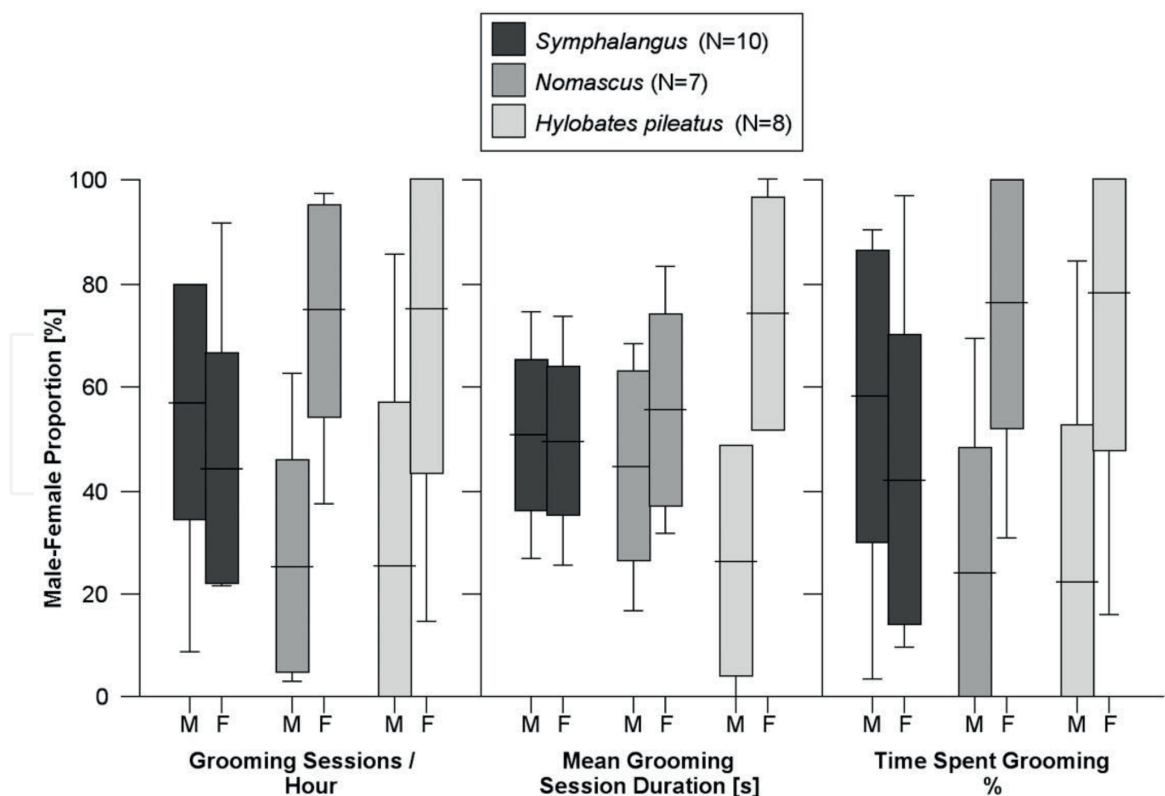


Figure 5. Average male-female proportions of intra-pair grooming frequency per hour, mean duration of grooming sessions, and time spent grooming in siamangs (*Symphalangus*, N = 10 pairs), crested gibbons (*Nomascus*, N = 7 pairs), and pileated gibbons (*Hylobates pileatus*, N = 8 pairs). Box plots show mean values, standard deviations and minimum and maximum values. In a comparison between the genera (Kruskal-Wallis tests), all three variables are statistically significant ($P < 0.05$, see text). Abbreviations: M = males, F = females.

other at all and male–female proportions of grooming variables could, therefore, not be calculated. Neither Kr2 nor PT3 were newly formed pairs, and the reason why no grooming occurred among pair partners is unknown.

Male proportions in the number of grooming sessions per hour varied from 8.5% to 78.3% in siamangs, from 2.9% to 62.5% in crested gibbons, and from 0.0% to 85.4% in pileated gibbons. The difference between the genera is statistically significant (Kruskal-Wallis test, $P = 0.032$). The Dunn *post-hoc* test revealed no significant pair-wise differences, but as a trend, male proportions were higher in siamangs than in pileated gibbons ($P < 0.1$). Male proportions in grooming session duration varied from 26.7% to 74.6% in siamangs, from 16.6% to 68.2% in crested gibbons, and, and from 0.0% to 48.0% in pileated gibbons. The difference between the genera is statistically significant (Kruskal-Wallis test, $P = 0.043$), and the Dunn *post-hoc* test revealed that male proportions were higher in siamangs than in pileated gibbons ($P < 0.05$). Male proportions in the time spent grooming varied from 3.3% to 90.4% in siamangs, from 0.9% to 69.1% in crested gibbons, and from 0.0% to 84.3% in pileated gibbons. The difference between the genera is statistically significant (Kruskal-Wallis test, $P = 0.035$), and the Dunn *post-hoc* test revealed that male proportions were higher in siamangs than in pileated gibbons ($P < 0.05$). As a result, siamang males groom partners in longer sessions and spend more time grooming them than pileated gibbon males. Only as a trend, siamang males also tend to groom their partners during more grooming sessions than pileated gibbons.

In addition to the grooming data collected by focal animal sampling, we also collected data on male–female grooming proportions for three additional siamang groups (An, Be, Zu) during the scan sampling observations. Male grooming proportions in these groups amounted to 95.4%, 85.7% and 100%, respectively.

Finally, we compiled data from the pertinent literature on other gibbon groups. If several reports were available on the same group, we used the study with the larger data base. These data are summarized in **Table 3** and also includes members of the dwarf gibbons (*Hylobates*) and hoolock gibbons (*Hoolock*) other than the species observed by us. The sample size for the hoolocks (**Table 3d**), however, comprises only three groups and is too small for statistical analysis. Pairs that did not exhibit partner-directed grooming are also excluded from the analysis. Our resulting sample comprises 76 pairs. For summary statistics, we split male grooming contribution evenly into three classes: (1) 0–33%, (2) >33–66%, (3) >66%. Pairs should be evenly distributed across these classes if male and female contributions were balanced. As shown in **Table 3**, this is not the case in siamangs ($N = 28$). Most pairs fall into class 3, suggesting that siamang males, as a rule, provide most of the intra-pair grooming. In crested gibbons ($N = 22$) and dwarf gibbons ($N = 26$), the situation is exactly reversed. Most pairs fall into class 1, indicating that females provide most of the intra-pair grooming in *Nomascus* and *Hylobates*. The difference from the expected value of 50% is statistically significant for the genera *Nomascus* and *Symphalangus* (One-sample sign test, $P = 0.002$, and $P = 0.013$), but not for *Hylobates* (One-sample sign test, $P > 0.05$). As indicated by the species labels in **Figure 6c**, the distribution appears to differ among species of the genus *Hylobates*. Whereas partner-directed grooming is mainly provided by females in *H. pileatus* ($N = 11$), the distribution appears to be more randomly distributed in *H. lar* ($N = 11$). Although the difference between the two species is statistically significant (Mann–Whitney U test, $P = 0.032$), the samples are relatively small and the result should be regarded with caution. If only *H. pileatus* is considered, the difference from the expected value of 50% is still not significant (One-sample sign test, $P > 0.05$), but the sample is very small in this case ($N = 11$).

Group	Cap- tive/ wild	Data type	Classes of male grooming proportion [%]			Source
			1	2	3	
(a) Siamangs (<i>Symphalangus</i>)						
An	c	f			95.4	ts
Be	c	f			85.7	ts
Br1	c	f	8.5			ts
Br2	c	f			78.3	ts
Br3	c	f			74.1	ts
Bu	c	f	29.5			ts
Do	c	f		60.1		ts
Dr1	c	f			69.7	ts
Dr2	c	f		51.5		ts
Du	c	f		49.2		ts
Fr	c	f	—	—	—	ts
Kr1	c	f			76.7	ts
Kr2	c	f			72.0	ts
Mu	c	f	8.5			ts
St	c	f			78.3	ts
Wa	c	f			74.1	ts
Zh	c	f			100.0	ts
TS1	w	t		60.5		[19]
RS2	w	t			73.7	[19]
Milwaukee	c	f	26.0			[72]
Tulsa	c	f?			88.8	[73]
Berlin	c	f	—	—	—	[74]
Cheyenne, MH 21	c	t			86.3	[75]
Cheyenne, MH 23	c	t	7.0			[75]
Melbourne	c	?		60.8		[76]
Ketambe, CH-CJ	w	f		ca 48.0		[10]
Ketambe, PP-PN	w	f			ca 84.0	[10]
Ketambe, Pm-Pn	w	f		ca 60.0		[10]
Lourosa, pair 1	c	t			88.9	[77]
ICGS	c	t		56.9		[26]
Siamangs, total number of pairs			5	8	15	
(b) Crested gibbons (<i>Nomascus</i>)						
Du (<i>Nle</i>)	c	f	4.4			ts

(b) Crested gibbons (<i>Nomascus</i>)						
Eb (<i>Nga</i>)	c	f	24.7			ts
Mu1 (<i>Nle</i>)	c	f		62.5		ts
Mu2 (<i>Nsi</i>)	c	f	20.6			ts
Mu3 (<i>Nga</i>)	c	f	22.1			ts
Os1 (<i>Nga</i>)	c	f		38.3		ts
Os2 (<i>Nle</i>)	c	f	2.9			ts
Twycross (<i>Nco</i> + <i>Nle</i> mixed pair)	c	t	17.7			[78]
Twycross (<i>Nle</i>)	c	t	18.0			[78]
Perth, old pair (<i>Nle</i>)	c	t		36.4		[79]
Perth, new pair (<i>Nle</i>)	c	t		50.0		[79]
Perth, family gr. (<i>Nle</i>)	c	t		37.9		[79]
Melbourne (<i>Nle</i>)	c	f	19.5			[76]
Besançon (<i>Nga</i>)	c	t	6.0			[80]
Mulhouse, group 1 (<i>Nga</i>)	c	t	0			[81]
Mulhouse, group 2 (<i>Nle</i>)	c	t	—	—	—	[81]
Mulhouse, group 3 (<i>Nsi</i>)	c	t	0			[81]
Amsterdam (<i>Nle</i>)	c	t	16.0			[82]
Beekse Bergen (<i>Nle</i>)	c	t	22.2			[82]
Hannover (<i>Nle</i>)	c	t		57.5		[82]
ICGS (<i>Nle</i>)	c	t			100	[26]
Lincoln Park (<i>Nle</i>)	c	f	0			[83]
San Antonio (<i>Nle</i>)	c	?	1.6			[84, 85]
<i>Nomascus gabriellae</i> , total number of pairs			4	1	0	
<i>Nomascus leucogenys</i> , total number of pairs			8	5	1	
Crested gibbons, total number of pairs			15	6	1	
(c) Dwarf gibbons (<i>Hylobates</i>)						
Phnom Tamao 1 (<i>Hpi</i>)	c	f		55.7		ts
Phnom Tamao 2 (<i>Hpi</i>)	c	f	0			ts
Phnom Tamao 3 (<i>Hpi</i>)	c	f	—	—	—	ts
Phnom Tamao 4 (<i>Hpi</i>)	c	f	8.1			ts
Phnom Tamao 5 (<i>Hpi</i>)	c	f	0			ts
Phnom Tamao 6 (<i>Hpi</i>)	c	f			85.4	ts
Phnom Tamao 7 (<i>Hpi</i>)	c	f	12.5			ts
Zurich 1 (<i>Hpi</i>)	c	f		38.2		ts
Zurich 2 (<i>Hpi</i>)	c	f	0			ts

(c) Dwarf gibbons (<i>Hylobates</i>)						
ICGS (<i>Hpi</i>)	c	t		69.6		[26]
Perth, group 6 (<i>Hpi</i>)	c	f?	0			[86]
Blackpool (<i>Hpi</i>)	c	f	0			[87]
<i>Hylobates pileatus</i> , total number of pairs			7	2	2	
Bronx, New York (<i>Hla</i>)	c	t		71.3		[88]
Portland, Oregon (<i>Hla</i>)	c	f		45.0		[89]
Berlin (<i>Hla</i>)	c	f	25.0			[74]
Besançon (<i>Hla</i>)	c	t		53.6		[80]
Melbourne (<i>Hla</i>)	c	f	10.8			[76]
Ketambe, AS-AY (<i>Hla</i>)	w	f		ca 81.0		[10]
Ketambe, GD-GM (<i>Hla</i>)	w	f		93.0		[10]
Khao Yai, Pair A (<i>Hla</i>)	w	t		64.3		[13]
Khao Yai, Pair B (<i>Hla</i>)	w	t		37.5		[13]
Khao Yai, Pair C (<i>Hla</i>)	w	t		71.4		[13]
Khao Yai, Pair T (<i>Hla</i>)	w	t	20.0			[90]
<i>Hylobates lar</i> , total number of pairs			3	4	4	
Berlin (<i>Hmo</i>)	c	f	—	—	—	[74]
ICGS (<i>Hmo</i>)	c	t	0			[26]
Munich (<i>Hmo</i>)	c	f		50.7		Average of [91–93]
Perth (<i>Hmo</i>)	c	t		50.0		[79]
<i>Hylobates moloch</i> , total number of pairs			1	2	0	
ICGS (<i>Hag</i>)	c	t	0			[26]
Dwarf gibbons, total number of pairs			12	8	6	
(d) Hoolock gibbons (<i>Hoolock</i>)						
Gibbon Wildlife Sanctuary, Assam, 1 (<i>Hho</i>)	w	f	25.0			[94]
Gibbon Wildlife Sanctuary, Assam, 2 (<i>Hho</i>)	w	f		50.0		[94]
Gibbon Wildlife Sanctuary, Assam, 3 (<i>Hho</i>)	w	f		41.5		[94]
Hoolock gibbons, total number of pairs			1	2	0	

Table 3. Male contributions (%) to intra-pair grooming in gibbons. Classes of male grooming proportion are defined as (1) 0–33%, (2) >33–66% and (3) >66%. Abbreviations: Hoolock: *Hho* = *H. hoolock*; *Hylobates*: *Hag* = *H. agilis*, *Hla* = *H. lar*, *Hmo* = *H. moloch*, *Hpi* = *H. pileatus*. *Nomascus*: *Nco* = *N. concolor*, *Nga* = *N. gabriellae*, *Nle* = *N. leucogenys*, *Nsi* = *N. siki*. Captive/wild: c = captive, w = wild. Data type: f = frequency, t = time. Grooming: – = no partner-directed grooming observed. Source: ts = this study.

(Mann–Whitney U test, 20 captive pairs vs. 6 wild pairs, $U = 24.0$, $P = 0.027$). It should be noted, however, that all available data for wild dwarf gibbons stem from only one species (*H. lar*), whereas several other species are represented in the captive sample of the same genus. If the comparison is restricted to *Hylobates lar*, the difference is not statistically significant (Mann–Whitney U test, 5 captive pairs vs. 6 wild pairs, $U = 8.0$, $P > 0.05$). Therefore, the variability of male grooming proportion among dwarf gibbons may be influenced by, and differ among, the species.

The frequency distribution of male grooming proportion is shown in **Figure 6**. These data differ significantly among the genera (Kruskal-Wallis test, $df = 2$, $P < 0.0001$). As revealed by the Dunn *post-hoc* tests, the male proportion in partner grooming is significantly higher in *Symphalangus* than in both *Nomascus* ($P < 0.001$) and *Hylobates* ($P < 0.005$), whereas no differences were found between *Hylobates* and *Nomascus* ($P > 0.05$).

4. Discussion

Monogamy is common among birds [95], but established in only about 3–9% of all mammals and about 15–29% of all primate species [45, 48, 96]. Among hominoid apes, only gibbons typically live in social monogamy (in the sense of [46]).

Various hypotheses explaining the proximate and ultimate mechanisms, which led to the evolution of social monogamy among gibbons are under debate [48, 97–99]. In these discussions, monogamy among gibbons is usually treated as, and implicitly assumed to be, a comparable, uniform entity. Cowlshaw [100], for instance, assumes that the pair bond is created by the different resource interests of the partners. The female is interested in the territory and the food resources in it, whereas the male is interested in the female partner.

Although several reports suggested that gibbon taxa might exhibit subtle distinctions in their group coherence or group composition (see Introduction), quantitative data for representative numbers of pairs have been lacking. It is generally assumed that pair bonds in all gibbon taxa are built up and maintained in the same way, and that males are mainly responsible for maintaining the pair bonds [3, 52].

As will be discussed below, this study provides evidence to the contrary. We compared indicators of pair bond strength and sex-specific pair bond investment between 7 pairs of crested gibbons, 9 pairs of pileated gibbons, and 11–17 pairs of siamangs (depending on the variable in question).

4.1 Pair bond strength

We determined three variables to compare pair bond strength between siamangs and crested gibbons (synchronization of behavioral variables, relative partner-distance, and allogrooming).

1. Synchronization of behavioral variables: The overall degree of behavioral synchronization does not differ significantly among the genera, suggesting that they do not differ in the strength of the pair bond as expressed by behavioral synchronization.
2. Relative partner-distance: The three gibbon taxa did not differ in the time spent in any of the four partner distance classes, except that siamang pairs spent less

time in the largest distance class 4 (>3 m) than pileated gibbon (*H. pileatus*) pairs, suggesting that pair bond strength in siamangs may be more pronounced than in pileated gibbons. Similarly, Palombit [22] found that siamang pairs spent significantly more time in close proximity to one another than white-handed gibbons (*H. lar*). However, we found no significant differences in the other distance classes or in the mean relative distance between pair partners.

3. **Allogrooming:** The three gibbon taxa did not differ in the number of grooming sessions/hour (average male and female), the proportion of time spent grooming, and the average duration of grooming sessions. As a result, siamang pairs, crested gibbon pairs and pileated gibbon pairs are involved in similar numbers of grooming sessions and spend similar amounts of time grooming.

In summary, pileated gibbons appear to spend more time apart by the largest distance class than siamangs. Based on this variable alone, their pair bond may be weaker than that of siamangs. No consistent differences in pair bond strength were found between siamangs and crested gibbons or between crested gibbons and pileated gibbons.

4.2 Pair bond maintenance

We examined which sex invests more in the pair bond by measuring the amount of grooming directed at the respective partner. For simplicity, we indicate the male proportion only; the female partner's proportion is its complement to 100%.

Our results show that in pileated and crested gibbon pairs partner-directed grooming is mostly provided by females, whereas males are the main groomers in siamang pairs. This result is further supported by additional data we collected from the literature. In most siamang pairs, males are the main groomers. Furthermore, male proportion in grooming session duration and time spent grooming are higher in siamangs than in pileated gibbons, whereas the male proportions in the numbers of grooming sessions per hour do not differ between siamangs and pileated gibbons. Siamang males groom their partners more often than crested gibbon males do, but time spent grooming and male proportion in duration of grooming do not differ between siamangs and crested gibbons. Our pairwise comparison revealed statistically significant differences for *Symphalangus/Nomascus*, but not for *Symphalangus/Hylobates* or *Hylobates/Nomascus*.

These results suggest that each genus differs in the mechanism of how pair bonds are created or maintained. Especially siamangs differ compared to pileated and crested gibbons: male-driven in the former, female-driven in the latter two. Obviously, the pair bond in gibbons does not appear to be a uniform entity. Data compiled in **Table 3** also suggest that field and zoo observations are consistent (except that only one wild pair exhibits a "Class 1" male grooming proportion of 0–33%).

Our results support vocal and molecular studies suggesting that gibbons are a much less homogenous group than generally assumed [39, 101, 102]. It is becoming more and more obvious that including one gibbon taxon into comparative studies in order to represent "the gibbon" is not useful practice anymore.

In our overall sample of dwarf gibbon pairs (*Hylobates*, N = 26) as well as in the subset of *H. pileatus*-pairs (N = 11), females provided more partner-grooming than males in most pairs. In *H. lar*-pairs (N = 11), on the other hand, the amount of grooming provided by males and females was very variable (**Table 3**) and the reason for this variability in this sample is not clear.

Kleiman [45] proposed that males should be the more active groomers in monogamous primates because their dominance situation is reversed as compared to primates with polygynous social organizations. Simple dominance relationships, however, do not seem the only variables influencing partner-directed allogrooming in gibbons.

If partner-directed allogrooming reflects the investment into a pair bond [62, 63], then our results document that the readiness to invest differs among pairs. In most (but not necessarily all) pairs, both partners appeared to be interested in maintaining the pair bond, and both partners provided at least some allogrooming. In addition to individual differences, the interest in a pair partner may vary with time. Probably, the benefit of a pair bond is related to the reproductive potential of a partner. Observations on wild *H. lar* and *H. moloch* suggest that the reproductive status of females may play an important role [13, 103, 104]. Males may have a higher interest to invest into the pair bond with females when they are receptive, in order to guard them more efficiently, copulate more frequently and improve the probability of their paternity. If partner-directed grooming is part of a mate-guarding strategy with fluctuating relevance to the groomer, it becomes clear why data of relatively large numbers of pairs need to be compared in order to discover species-specific differences.

How do our findings compare to the predictions of the three hypotheses for the evolution of pair bonds presented in the Introduction?

1. The 'male-services hypothesis' predicts that a female will invest substantially in a social relationship with a male willing to assume the costs of territorial or antipredator defense, infant care or protection from infanticidal males. This should result in females investing more than males in maintaining the pair bond. This prediction is met by our samples of crested gibbons (N = 22 pairs, **Table 3**), pileated gibbons (N = 11 pairs) and the combined sample of all dwarf gibbons (N = 26 pairs). In all three samples, females were the main groomers in most pairs.
2. The 'mate-defense hypothesis' predicts that bonding with a female is beneficial for a male when either the spatial distribution of females or the temporal distribution of fertile periods makes it difficult for the males to defend access to more than one female at a time. This should result in males investing more than females in maintaining the pair bond. This prediction is met by our sample of siamangs (N = 28 pairs), where males were the main groomers in most pairs.
3. The 'resource-defense hypothesis' predicts that both a male and a female benefit from pair bonding to defend resources together. This should result in a male and a female being equally interested in maintaining proximity and affiliation with a pair mate and defending their territory. None of the gibbon samples of this study appears to meet this prediction.

Only very limited information on the direction of partner-grooming is available for the fourth of the gibbon genera, the hoolocks (genus *Hoolock*). Ahsan [105], who studied three groups of the western hoolock gibbon (*H. hoolock*) at two sites in Bangladesh, reported that grooming was most frequent between adult pairs and that it was "mostly performed by the adult male". Unfortunately, the author did not publish the quantitative data in support of his statement. Sankaran [94] observed three

groups of the same species in the Gibbon Wildlife Sanctuary in Assam. However, none of his males provided more than 50% of the partner-grooming (**Table 3**). Apparently, the results of the two studies differ, but the overall sample size is too small to assess the directionality of partner grooming in hoolock gibbons with any reliability.

It has also been reported that allogrooming between pair mates is virtually non-existent in wild *Hylobates agilis* [21] and *H. klossii* [106], in contrast to the situation in wild *H. lar* and siamangs [10, 13, 19, 103]. This suggests that the range of variation in gibbon pair bonds may be larger than what we covered in our study. Several species of dwarf gibbons (*Hylobates*) are hardly represented or not represented at all in our data, including *H. agilis* and *H. klossii*.

Within crested gibbons (*Nomascus*), most of our data are from one species, *N. leucogenys* (N = 14 pairs), whereas few pairs of other light-cheeked species and only one male of a black-cheeked species (*N. concolor* in a mixed pair) are available.

5. Conclusions

1. A comparison of pair bond strength in three gibbon taxa – siamangs (*Symphalangus*), crested gibbons (*Nomascus*) and pileated gibbons (*Hylobates pileatus*) revealed a difference in relative partner distances between siamangs and pileated gibbons, suggesting that siamangs may have a stronger pair bond than pileated gibbons. No difference between the three taxa was found in other variables believed to indicate pair bond strength: degree of behavioral synchronization and amounts of grooming (both numbers of events and actual grooming time).
2. This study provides the first statistically significant evidence that the mechanisms of how pair bonds are created or maintained, differ between gibbon taxa. As indicated by the amount of partner-directed grooming, siamang males invest significantly more into the pair bond than females, whereas the opposite is true in crested gibbons, pileated gibbons, and an enlarged sample of dwarf gibbons (genus *Hylobates*). Additional species-specific differences may, however, occur within the latter group, with partner-grooming investment being highly variable in *H. lar*.
3. Our results for crested gibbons, pileated gibbons, and a combined sample of dwarf gibbons correspond to predictions derived from the ‘male-services hypothesis’ for the evolution of pair bonds. According to this hypothesis, a female will invest substantially in a social relationship with a male willing to assume the costs of territorial or antipredator defense, infant care or protection from infanticidal males.
4. In contrast, our results for siamangs correspond to predictions derived from the ‘mate-defense hypothesis’. According to this hypothesis, bonding with a female is beneficial for a male when either the spatial distribution of females or the temporal distribution of fertile periods makes it difficult for the males to defend access to more than one female at a time.
5. Species-specific analyses are recommended for additional species of the genera *Hylobates*, *Nomascus* (especially the black-cheeked taxa) and *Hoolock*.

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Conflict of interest

There is no financial/personal interest, or contractual employment involving matters in this article or belief that could affect the authors' objectivity.

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