

Pair bonding in captive pileated gibbons

(Hylobates pileatus)

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Abstract

In this study, the pair bond in captive pileated gibbons (*Hylobates pileatus*, $n = 9$ pairs) is examined and compared with the unpublished data of two other genera of gibbons (Hylobatidae): siamangs (*Symphalangus*, $n = 18$ pairs) and crested gibbons (*Nomascus*, $n = 7$ pairs). In the first part of this study, three generally-accepted indicators of pair bond strength are analyzed (mutual grooming, behavioural synchronization and distance between mates). In the second part of the study, a comparison of indicators of how the pair bonds are maintained (sex-specific differences in mutual grooming) in the three gibbon genera is made. Siamangs and pileated gibbons appear to differ ($p > 0.05$) in the strength of their pair bonds. Siamangs and pileated gibbons do not exhibit similar relative partner distance, but do exhibit similar degrees of behavioural synchronization and similar amount of grooming. Siamangs and crested gibbons do not appear to differ ($p > 0.05$) consistently in the strength of their pair bonds as do crested and pileated gibbons. Siamangs and crested gibbons, pileated and crested gibbons exhibit similar degrees of behavioural synchronization ($< 35.02\%$), similar relative partner distance (average > 3 m) and similar amounts of grooming (< 4 grooming sessions/hour, $< 67\%$ time spent grooming and average duration of grooming sessions is < 102 s). The mechanisms how pair bonds are maintained, as indicated by the amount of partner directed grooming, differ between the gibbon taxa. Siamang males invest significantly more ($p < 0.05$) into the pair bond than females. For crested gibbons and gibbons of the *lar* group, the opposite is true. Differences appear to occur within the latter group. Grooming in pileated gibbons is mainly provided by females, whereas the grooming appears to be more balanced between male and female in white-handed gibbons. The findings of this study are furthermore strengthened by adding data on individual pairs from previous studies (thus bringing the sample size of this study to 69 pairs). The results demonstrate that the pair bond in gibbons is not a uniform entity. Furthermore, in the view of these results, the infanticide protection hypothesis for the evolution of pair bonds appears to be most unlikely for siamangs, because of the high male investment in the pair bond. The hypothesis cannot be rejected for crested gibbons, where females are the main groomers in most pairs. The situation in gibbons of the *lar* group appears to be less decisive. The ‘good-father’ hypothesis, which predicts high female investment into pair bonds with males providing paternal care for offspring, is not supported in the cross-genera comparison.

1. Introduction

Gibbons live in monogamous family groups consisting of an adult pair and its immature offspring (Benirschke, 1986). The genera of great apes are known to differ strongly among each other in their social structure (Geissmann et al., 2003). In contrast, gibbons (the small apes) are generally believed to be a remarkably uniform group with little differences among genera in social organisation (Palombit, 1999). An important characteristic in gibbons is the presence of a permanent pair bond. Reasons for a permanent pair bond are probably the long period (5–6 years) of dependence of the young on parental care and the territorial resources, like food and protection (Brockelman and Srikosamatara, 1984). Bond reinforcing behaviours occur after pair formation and include grooming, playing and maintaining proximity. In gibbons, duetting also seems to serve as an important bonding ritual and is not known to occur in unmated pairs.

Protection from male infanticide has been proposed as a potential benefit to females of bonds with males in a variety of primates, including gibbons (Palombit, 1999; Dunbar and Barrett, 2000). Male infanticide is a potential selective agent for the evolution of bonds between the sexes. It has been suggested to explain male-female relationships in several polygynous taxa, such as Malagasy lemurs, capuchin monkeys, mountain gorillas and savanna baboons.

Only a few studies describe the mechanisms of maintaining pair bonds in gibbons and differences between taxa have rarely been considered in these studies. It has been suggested that gibbon taxa may differ in details of their social organisation. Chivers (1972) and Palombit (1996) reported that wild family groups of siamangs (*Symphalangus syndactylus*) appeared 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. However, only five pairs (two pairs of white-handed gibbons and three pairs of siamangs) were observed by Palombit (1996) and three pairs (two pairs of siamangs and one pair of white-handed gibbons) were observed by Chivers (1972).

An ongoing long term research project is comparing pair bonding behaviour among different gibbon taxa (Geissmann et al., 2003). First results revealed that captive siamangs (genus *Symphalangus*, n = 18 pairs) and captive crested gibbons (genus *Nomascus*, n = 7 pairs) do not appear to differ consistently in the strength of their pair bonds: pairs in both genera exhibit similar degrees of behavioural synchronization, similar relative partner

distances and similar amounts of partner-directed grooming (both numbers of events and actual grooming time of male and female). However, the two genera differ fundamentally in their pair bonding mechanisms (Geissmann et al., 2003), as indicated by the amount of sex-specific partner-directed grooming. In siamangs, males invest significantly more into pair bonds than females, whereas the opposite is true in crested gibbons. These results demonstrate that the pair bond in gibbons is not a uniform entity and support recent vocal and molecular studies suggesting that gibbons are a much less homogenous group than generally assumed (Geissmann et al., 2003). Furthermore, in the view of these results, the infanticide-protection hypothesis for the evolution of pair bonds, which predicts that a female will invest substantially in a social relationship with a male willing to assume the costs of defending her offspring against attacking infanticidal males (Palombit, 1999), appears particularly unlikely to apply to siamangs.

No comparable quantitative data for the genus *Hylobates* are available so far. A comparison of published data on partner-grooming behaviour in the genus *Hylobates* produced no consistent results, possibly because of species-specific differences within the genus. Previous observations suggest that mated pileated gibbons invest comparatively little grooming in their pair bonds (Geissmann et al., 2003). But this is based on casual observations only.

The short study presented here will examine pair bonding among captive pileated gibbons (*Hylobates pileatus*). Its goal is to introduce the first quantitative data on a species of the genus *Hylobates* to the long-term project. In order to produce data that can be compared to the already available data on siamangs and crested gibbons, the same observation techniques as the earlier study were used (Geissmann et al., 2003).

This study tries to answer the following two main questions: (1) Do pileated gibbons differ from other gibbons in the strength of their pair bonds? (2) Do pileated gibbons differ from other gibbons in the way pair bonds are maintained?

To estimate the pair bond strength, generally-accepted indicators of pair bond strength were quantified; including (a) *behavioural synchronization*, (b) *relative distance between mates* and (c) *amount of partner directed grooming* (Geissmann and Orgeldinger, 2000). In order to gain insight in the pair bonding mechanism, it was examined which sex invests more in the pair bond by measuring the amount of partner-directed grooming for each mate.

The proposed functions of allogrooming (serving hygienic, social or communicatory functions) may be influenced by a species' social organisation. For social systems with stable

pair structures, allogrooming has been proposed to reflect the investment into a pair bond and, therefore, the ultimate costs and benefits which partners can expect from a relationship (Geissmann et al., 2003). Thus, ultimate sex-specific strategies can be indicated (on a proximate level) by sex-specific differences in partner-directed allogrooming.

In summary, to answer the two main questions about pair bond strength and pair bond maintenance, the following research questions will be answered: (a) What is the frequency and duration of *grooming behaviour* between pair mates and the difference between sex and genera? (b) What is the occurrence of *synchronized behaviour* between pair mates and the difference between gibbon genera? (c) What is the *relative distance* between pair mates and the difference between gibbon genera?

2. Materials and methods

Information about the gibbons which are observed and about their housing are presented in this part of the paper. A description about the behavioural observations, statistics and the compiled data from literature are also given.

2.1 Animals and housing

A minimum sample size of seven pairs was required for statistical comparison with data of other gibbon taxa. Observations are monitored directly by using protocol sheets. A partial data collection using video-recordings was recommended, because this method would produce valuable video documents of rare pileated gibbon behavioural elements.

In central Europe, family groups of pileated gibbons are kept in the zoos of Zürich, CH (2 groups), Mulhouse, F (1 group) and Twycross, UK (2 groups). Larger numbers of pairs are available in several Asian zoos, such as Dusit zoo in Bangkok and Khao Keow Open Zoo in Thailand. The largest numbers of pileated gibbons are probably kept at the Phnom Tamao Wildlife Rescue Centre south of Phnom Penh, Cambodia.

A total of seven adult gibbon pairs (more than 6 years old) were observed at the Phnom Tamao Wildlife Rescue Centre (PTWRC), Cambodia. Beside these seven gibbon pairs, there were also two gibbon pairs observed at Zürich Zoo, Switzerland. All of the observed gibbons came from the wild, except of one pair which was born in captivity. Table 1 presents an overview of the observed gibbon pairs.

Table 1: The observed gibbon pairs at PTWRC (Pairs 1 – 7) and Zürich Zoo (Pairs 8 – 9).

Pair	Man	Female	Comments
1	Mr. Battambang	Rita	≥ 3 years together, both > 9 years old (wild-born).
2	Bulack	Mrs. Battambang	≥ 3 years together, both > 9 years old (wild-born).
3	Noir	Jan	≥ 1 year together, both > 8 years old (wild-born).
4	Bong Toy	Srey Sart	≥ 4 years together, both between 13 and 14 years old (wild-born).
5	O'som	Spectacles	≥ 3 years together, both about 9 years old (wild-born).
6	Ci	Bones	≥ 3 years together, both about 9 years old (wild-born).
7	Beung (Mat)	Keng Kang (Seut)	≥ 6 years together, > 14 resp. 17 years old (wild-born).
8	Khmer	Willow	15 years together, 23 resp. 20 years old (captive-born).
9	Iaman	Iba	25 years together, ca. 48 resp. 33 years old (wild-born).

All gibbons were housed in cages except of pair 2 and 6 (Table 1) which were housed in enclosures. The smallest cages of the pairs at PTWRC were 297 m³ (pair 1, 3, 5) and the biggest was 454 m³ (pair 4). The enclosures of pair 2 and 6 were respectively 11520 m³ and 7560 m³. The cages of the two pairs at Zürich Zoo were 350 m³ (pair 8) and 468 m³ (pair 9). The pairs at PTWRC were all housed outdoors. At Zürich Zoo, the gibbons had an in- and outdoor cage.

Group composition was different among the observed gibbons. All gibbons at PTWRC were kept as pairs, whereas the Zürich pairs were kept in relatively large family groups. Pair 8 was kept with their three male infants of 5, 4 and 2 years old. Pair 9 was also kept with their three infants, two males of 6 and 3 years old and one female of 1 year old.

2.2 Behavioural observations

Data from pileated gibbons were collected in a consistent form by both of the observers between February 19th and March 15th 2007 in Cambodia and between May 11th and May 15th 2007 in Switzerland. Observation time for each sampling method was distributed evenly across the animals' activity period between 0630 h and 1800 h.

In order to assure comparability of data collected by the two observers, dual observations were carried out on February 13th 2007 until consistent values (agreement minimum 98%) of inter-observer reliability were obtained (Lehner, 1979).

The following observation methods were used, in order to make the results comparable to those collected by Geissmann et al. (2003) on siamangs and crested gibbons.

The study uses focal animal sampling (Altmann, 1974; Lehner, 1979; Martin and Bateson, 1993) to collect information on the frequency and duration of grooming behaviour between mates (research question a). The total observation time should be at least 35 hour per gibbon pair. Grooming occurs in discrete sessions that can be counted. An interval of up to 10 seconds between bouts of grooming is allowed before they are counted as two sessions, rather than one.

Scan sampling is used to record behavioural synchronization of activities between mates (research question b). Eleven behavioural categories (see table 2) are monitored. Scans are made every 1 min. Therefore, the total observation time is the same as for the focal animal sampling method. The gibbons in Cambodia are observed for 245 hours and due to scan sampling, 14700 observations are totally collected. The gibbons in Switzerland are observed

for 70 hours and due to scan sampling, 4200 observations are totally collected. The pileated gibbons in this research are totally observed for 315 hours. In total, 18900 observations are collected.

Table 2: Ethogram of *Hylobates pileatus* (continued on next page).

Abbreviation	Behaviour	Description
Socio-positive behaviour and infant care		
SAL	Allogrooming	Groom another gibbon →Activator
SMS	Mother being suckled	Infant drinking at mother
SSB	Sitting next to each other	Side-by-side contact
SCB	Belly carrying	Mother is carrying the young on her belly
SEB	Embrace	Embrace each other →Activator
Play		
PCH	Chasing	Chasing each other →Activator and Receiver
PAL	Alone	Turbulent behaviour without a goal, play alone
PGR	Grabbing	Grabbing each other →Activator and Receiver
Agonistic behaviour		
ABI	Biting	Biting each other →Activator and Receiver
ABE	Beating	Beating each other (fight) →Activator and Receiver
Territorial behaviour		
TSR	Singing as reaction	As a reaction to other singing gibbons
TSN	Singing	Singing (non-reaction)
TSB	Swing	Stereotypical swing or brachiation
Sexual behaviour		
SCO	Copulation	Sexual act
SRC	Refuse copulation	Refusing copulation
SCA	Copulation calls	Calls during copulation
SGI	Genital inspection	Genital inspection →Activator and Receiver
Comfort-related behaviour		
CAG	Auto-grooming	Grooming itself or washing itself
CLI	Lying	Lie
CSA	Sitting alone	Sitting alone
CSC	Scratching	Scratching itself
CBS	Body shake	Shaking the body
CYW	Yawning	Yawn
CST	Stretching	Stretch
Feeding and food-related behaviour		
FSH	Sharing food	Share food with another gibbon →Activator and Receiver
FEA	Eating	Eat food
FDR	Drinking	Drink water
FOR	Foraging	Looking for food (using the hands)
FMA	Manipulate	Using tools for getting food
FHU	Hunting	Hunting for insects and/or birds
Observe		
OLA	Looking around	Look around in the area or stare at something
Rest and sleep		
RSL	Sleeping	Sleep (sit position)
SAL	Allogrooming	Groom another gibbon →Receiver
SEB	Embrace	Embrace each other →Receiver
Excretion		
EUR	Urinating	Urinate
EDE	Defecating	Faeces
Locomotion		
LWA	Walking	Always a minimum of one foot on the ground
LRU	Running	For a moment there are no feet on the ground
LST	Standing	Stand without any other behaviour
LHA	Hanging	Hang without any other behaviour
LBR	Brachiating	Swing from tree to tree/ branch to branch
LCL	Climb	Climb

Table 2 (ctd.).

Abbreviation	Behaviour	Description
Locomotion		
LJU	Jumping	Jump
LFF	Free fall	Falling free
Others		
OTH	Other	All other behaviour than described above
OOS	Out of sight	The gibbon is out of sight

Scan sampling is also used to record the distance between mates (research question c). Distances are recorded to an accuracy of 0.5 m. If the individuals are closer to each other than 0.5 m, the following categories are used: 0.3 m: shortest distance without body contact, 0.2 m: body contact through extremities (hands and feet), 0 m: full body contact. Gibbon pairs are scanned for the distance between mates every 1 min and scans are carried out in parallel to the focal animal observations of grooming behaviour. Therefore, the total observation time is the same as for the focal animal sampling method (the pileated gibbons were observed for a total of 315 hours and 18900 observations are collected).

In addition to determining relative distance, scan sampling is used 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.

2.3 Data compiled from the literature

In addition to the data collected during this study and from Geissmann et al. (2003), data from relevant literature and unpublished studies on other gibbon groups were provided by Thomas Geissmann (personal communication) and also used in this study to compare pair bond maintenance between three genera (*Symphalangus*, *Nomascus* and *Hylobates*). Studies with the largest data set were used if several reports on the same pair were available. Table 3 shows an overview of the used data from previously-published literature.

Table 3. List of all the used data from relevant literature.

Source	Group ¹
(a) Siamangs (<i>Symphalangus</i>)	
* Orgeldinger (1999)	An, Be, Br1, Br2, Br3, Bu, Do, Dr1, Dr2, Du, Fr, Kr1, Kr2, Mu, St, Wa, Zh
* Chivers (1974)	TS1, RS2
* Fox (1977)	Mil
* Kawata (1980)	Tu
* Dielentheis & Zaiss (1987)	Be
* Philippart (1991)	MH21, MH23
* Bricknell (1992, p. 37)	Mel
* Palombit (1992)	CH-CJ, PP-PN, Pm-Pn
* Caeiro de Pereira Sousa (1998)	Lo1
* Eardley (2000)	ICGS
(b) Crested gibbons (<i>Nomascus</i>)	
Rosenkranz (2002)	Du (<i>N. leucogenys</i>), Eb (<i>N. gabriellae</i>), Mu1 (<i>N. leucogenys</i>), Mu2 (<i>N. siki</i>), Mu3 (<i>N. gabriellae</i>), Os1 (<i>N. gabriellae</i>), Os2 (<i>N. leucogenys</i>)
* Pollard (1983)	Tw1 (<i>N. concolor</i> & <i>N. leucogenys</i>), Tw2 (<i>N. leucogenys</i>)
* Embury (1983)	Pt (<i>N. leucogenys</i>)
* Bricknell (1992)	Mel (<i>N. leucogenys</i>)
* Schlegel (1995)	Mul1 (<i>N. gabriellae</i>), Mul2 (<i>N. leucogenys</i>), Mul3 (<i>N. siki</i>)
Hold (1998)	Adam (<i>N. leucogenys</i>), BB (<i>N. leucogenys</i>), Ho (<i>N. leucogenys</i>)
* Eardley (2000)	ICGS (<i>N. leucogenys</i>)
Lukas et al. (2002)	Lin (<i>N. leucogenys</i>)
(c) Lar gibbons (<i>Hylobates</i>)	
This study	PT1-7 (<i>H. pileatus</i>), Zh1-2 (<i>H. pileatus</i>)
* Eardley (2000)	ICGS (<i>H. pileatus</i>), ICGS (<i>H. agilis</i>), ICGS (<i>H. moloch</i>)
* Embury (1983)	Pe1 (<i>H. pileatus</i>)
Skyner (2002)	Bp (<i>H. pileatus</i>)
* Riess (1956)	BNY (<i>H. lar</i>)
* Steen (1969, p. 63)	PO (<i>H. lar</i>)
* Dielentheis & Zaiss (1987)	Be (<i>H. lar</i>), Be (<i>H. moloch</i>)
* Bricknell (1992, p. 38)	Mel (<i>H. lar</i>)
* Palombit (1992)	AS-AY (<i>H. lar</i>), GD-GM (<i>H. lar</i>)
* Reichard (1995)	Pair A (<i>H. lar</i>), Pair B (<i>H. lar</i>), Pair C (<i>H. lar</i>)
* Ebert (1999)	Pair T (<i>H. lar</i>)

¹ Abbreviations: See Appendix 3

* Stars identify sources which are found in Geissmann (in prep.). Other literature data were provided by Geissmann (pers. comm.).

2.4 Statistics

The occurrence of synchronized behaviour between pair mates is expressed in % of the total number of scans for a given pair.

For comparison of our data on partner-directed behaviour with literature data, male and female proportions of these behavioural variables were used, 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.

Chi-square tests were used to compare classes of sex-specific grooming proportions within genera. In order to compare data of grooming, partner-distance and synchronized behaviour among three genera (i.e. after inclusion of data compiled from the literature), the Kruskal-Wallis tests with Dunn's *post-hoc* tests (Lehner, 1979) is used. The Mann-Whitney *U* test (Lehner, 1979) is used to compare data among two genera, between *H. pileatus* and *H. lar* (i.e. after inclusion of data compiled from the literature). All tests were two-tailed and the null hypothesis was rejected at $p \leq 0.05$. Statistics were calculated using the software StatView 5.0.1 on a Macintosh G4 computer.

The size of the enclosures/cages varies. Because small cages may force pairs into closer proximity than bigger enclosures, the relative distance (%) between mates is calculated as the mean inter-individual distance in relation to the maximal possible distance in the pair's given environment (cage or enclosure). This method was described by Geissmann and Orgeldinger (2000), see figure 1. The maximal possible distance (MPD) is determined as: $MPD = \sqrt{(MD^2 + MH^2)}$, where MD=maximal enclosure floor diagonal available to the animal -0.3 m and MH=maximal enclosure height available to the animal, identified as either (1) the maximal support height the animal could use for brachiating -0.3 m, or (2) the maximal support height on which the animal could sit +0.5 m. Because the position of a gibbon is determined by the animal's centre of gravity, 0.3 m are subtracted in (1) and 0.5 m are added in (2). These values are estimates and should correspond to the highest possible height of a gibbon's centre of gravity when the animal is below and above a support, respectively (Geissmann et al., 2003).

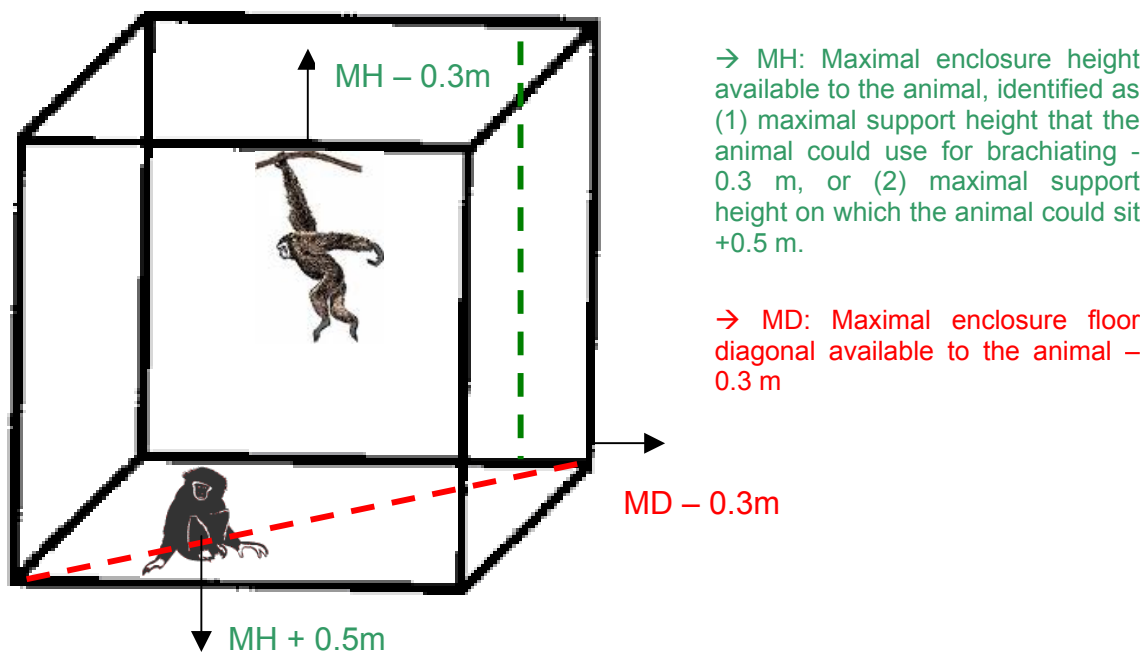


Fig. 1: Maximal Possible Distance (MPD) = $\sqrt{(MD^2 + MH^2)}$

Box plots will be used when results are presented in graphs. Box plots show mean values, standard deviations and minimum and maximum values. The variables from the graphs will be ordered according to decreasing average coordination found in siamang (*Symphalangus*) pairs.

3. Results

The results are split up in two sections. The first section is about the pair bond strength with the three indicators. The second part is about the pair bond mechanism.

3.1 Strength of pair bonds

Synchronization of behavioural variables

The degree of synchronization observed in siamang, crested gibbon and pileated gibbon pairs in each of the eleven behavioural variables are shown in Fig. 2. As can be seen, siamang (*Symphalangus*) pairs show the highest values of behavioural synchronization in five of the variables (territorial behaviour, agonistic behaviour, feeding and food-related behaviour, observe, rest and sleep). Pileated gibbon (*Hylobates pileatus*) pairs show the highest synchronization in six variables (sexual behaviour, sociopositive behaviour and infant care, play, locomotion, comfort-related behaviour, excretion). Among crested gibbon (*Nomascus*) pairs, two variables (agonistic behaviour, excretion) were not synchronized at all.

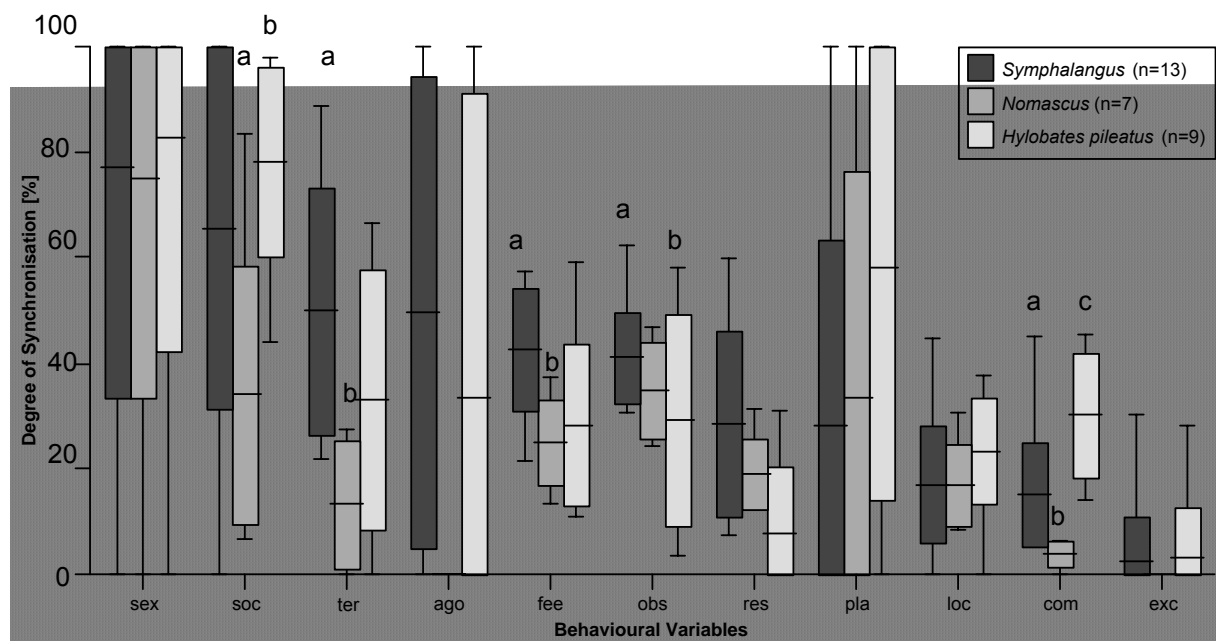


Fig. 2. Degree of synchronization [%] in eleven behavioural variables for siamangs (*Symphalangus*, n = 13 pairs; Orgeldinger, 1999 in: Geissmann et al., 2003), crested gibbons (*Nomascus*, n = 7 pairs; Rosenkranz, 2002) and pileated gibbons (*Hylobates pileatus*, n = 9 pairs; this study). Abbreviations: sex = sexual behaviour, soc = sociopositive behaviour and infant care, ago = agonistic behaviour, ter = territorial behaviour, fee = feeding and food-related behaviour, obs = observe, pla = play, res = rest and sleep, loc = locomotion, com = comfort-related behaviour, exc = excretion. Different letters within a behavioural variable indicate a significant difference ($p \leq 0.05$).

Significant differences between the three genera for five of the eleven variables are shown in a statistical comparison of behavioural synchronization. The five variables with significant differences are: sociopositive and infant care behaviour ($p < 0.05$), territorial behaviour ($p < 0.05$), feeding and food-related behaviour ($p < 0.05$), rest and sleep behaviour ($p < 0.05$) and comfort-related behaviour ($p < 0.0001$) (Appendix 1). Siamang (*Symphalangus*) pairs show the highest values in the overall taxon mean (Appendix 1). To find out between which genera the significant differences are, the Dunn's *post-hoc* tests are done for the five variables (Appendix 1). In most cases siamangs (*Symphalangus*) show higher synchronization than pileated gibbons (*Hylobates pileatus*) and crested gibbons (*Nomascus*) (territorial behaviour, feeding and food-related behaviour, rest and sleep, comfort-related behaviour). In the other cases, pileated gibbons (*Hylobates pileatus*) show higher synchronization than crested gibbons (*Nomascus*) (sociopositive behaviour and infant care, comfort-related behaviour).

The overall average degree of behavioural synchronization is variable among pairs (Fig. 3). Values range from 15.5% (Zh) to 63.9% (St) in siamangs (*Symphalangus*), from 8.0% (Du) to 38.7% (Eb) in crested gibbons (*Nomascus*) and from 19.2% (PT 2) and 42.7% (PT 7) in pileated gibbons (*Hylobates pileatus*). The overall degree of behavioural synchronization does not differ ($p = 0.186$) between the genera (Appendix 1).

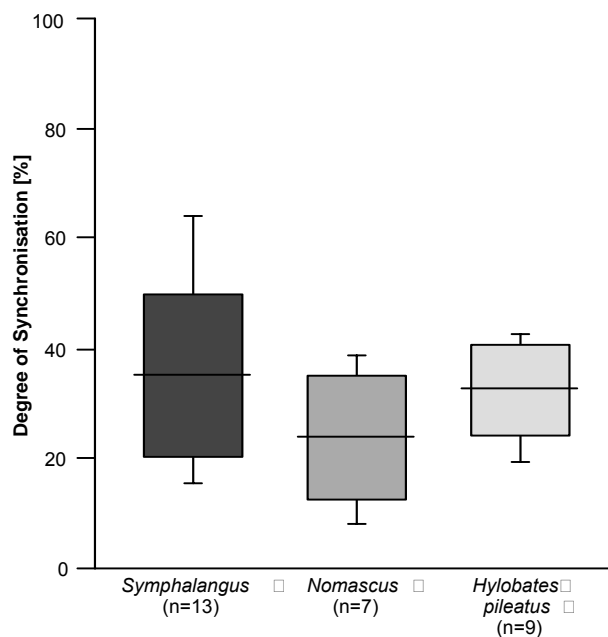


Fig. 3. Comparison of the average degree of behavioural synchronization between siamangs (*Symphalangus*, $n = 13$ pairs; Orgeldinger, 1999 in: Geissmann et al., 2003), crested gibbons (*Nomascus*, $n = 7$ pairs; Rosenkranz, 2002) and pileated gibbons (*Hylobates pileatus*, $n = 9$ pairs; this study). The difference is not statistically significant ($p > 0.05$).

Relative partner-distance

The average relative partner distances and the time proportions spent in the four 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 each study group are listed in Appendix 2. Considerable differences were found among pairs. Time spent in distance class 1, for instance, varies from 0.3% (K2) to 49.7% (St) in siamangs, from 5.6% (Os1) to 32.3% (Eb) in crested gibbons and from 0.0% (PT3) to 20.5% (PT4) in pileated gibbons (Appendix 2). Similarly, time spent in distance class 4 varies from 1.3% (Dr2) to 61.2% (Br3) in siamangs, from 14.1% (Du) to 47.4% (Mu1) in crested gibbons and from 31.6% (PT7) to 84% (PT3) in pileated gibbons (Appendix 2).

The time gibbon pairs spent in each of four partner distance classes is shown in Fig. 4. The three taxa do not differ ($p > 0.05$) in the time groups spent in any of the four partner distance classes, except for time spent in distance class 4 ($p < 0.05$). In that case, pileated gibbon (*Hylobates pileatus*) pairs spent more ($p < 0.02$) time in distance class 4 than siamang (*Symphalangus*) pairs. Moreover, the difference in distance class 2 is close to significance ($p > 0.05$).

The three taxa do not differ ($p > 0.05$) in the relative distance between pair partners which is also shown in Fig. 4.

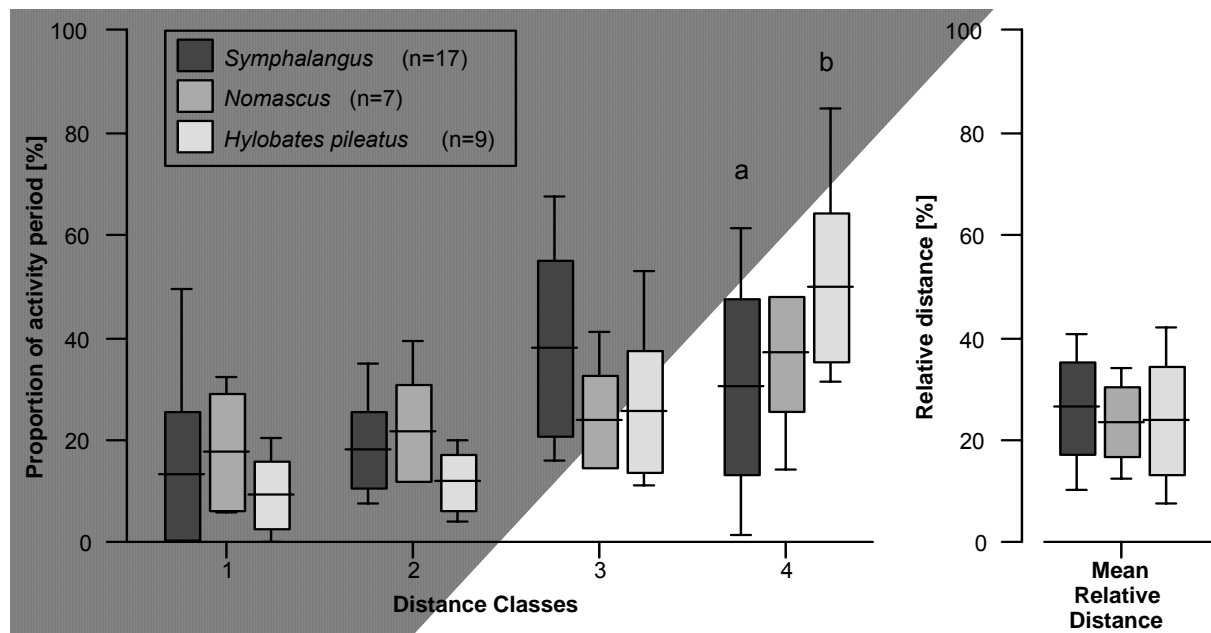


Fig. 4. Time proportion spent in 4 distance classes (1: body contact or distance of less than 0.3 m, 2: 0.3-1 m, 3: >1 m-3 m, 4: >3 m) (left) and of the mean relative partner distances (right) in siamangs (*Symphalangus*, $n = 17$ pairs; Orgeldinger, 1999 in: Geissmann et al., 2003), crested gibbons (*Nomascus*, $n = 7$ pairs; Rosenkranz, 2002) and pileated gibbons (*Hylobates pileatus*, $n = 9$ pairs; this study). Different letters within a distance class indicate a significant difference ($p \leq 0.05$).

Allogrooming

The number of grooming sessions/hour (average of male and female) varies from 0.0 (Kr2) to 3.9 (St) in siamangs (*Symphalangus*, $n = 12$ pairs), from 0.5 (Os2) to 2.0 (Mu1) in crested gibbons (*Nomascus*, $n = 7$ pairs) and from 0.0 (PT3) to 2.1 (PT4) in pileated gibbons. The number of grooming sessions/hour does not differ ($p > 0.05$) among the three genera (Fig. 5).

The proportion of time spent grooming varies from 0% (Kr2) to 66.9% (Mu) in siamang pairs, from 9.3% (Eb) to 28.7% (Mu1) in crested gibbon pairs and from 0% (PT3) to 57.7% (PT4) in pileated gibbons, but does not differ ($p > 0.05$) among the three genera (Fig. 5).

The average duration of grooming sessions varies from 0 s (Kr2) to 76.0 s (Mu) in siamangs, from 50.5 s (Eb) to 132.1 s (Os2) in crested gibbons and from 0 s (PT3) to 101.0 s (PT5) in pileated gibbons. The average duration of grooming sessions does not differ ($p > 0.05$) among the three genera. As a result, siamang pairs, crested gibbon pairs and pileated gibbon pairs spend similar amounts of time grooming (Fig. 5).

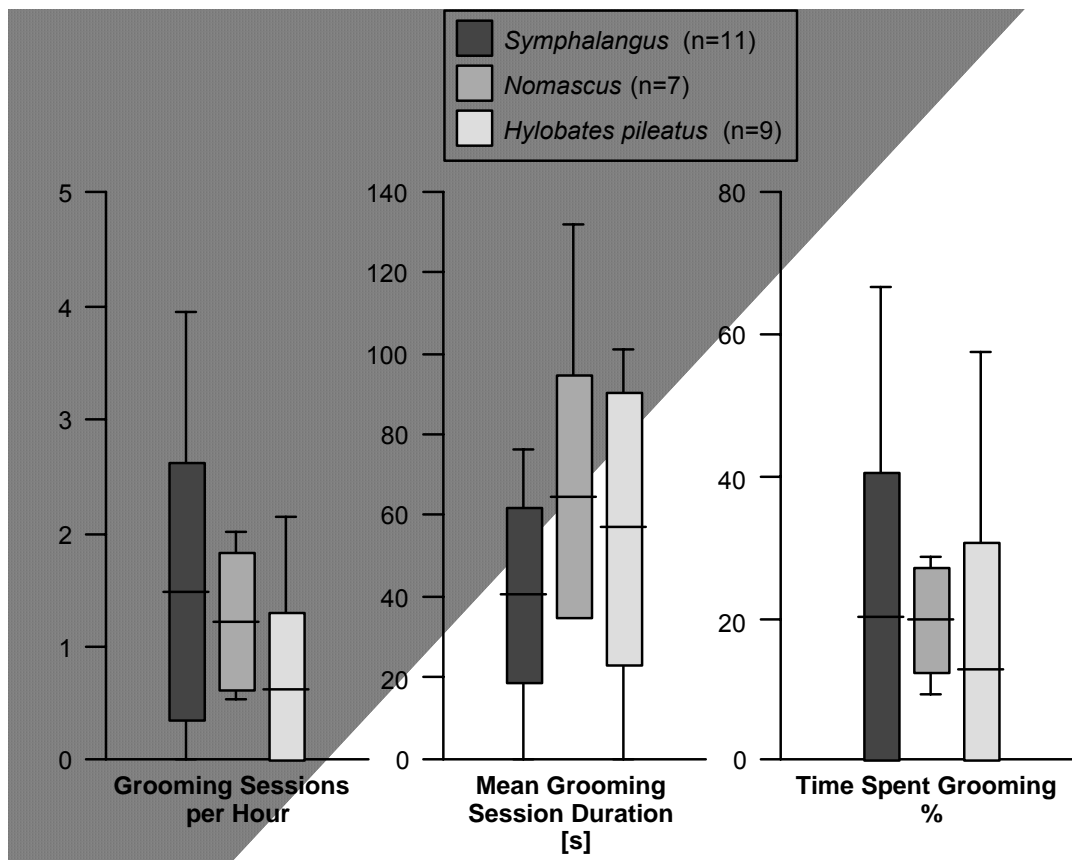


Fig. 5. Average intra-pair grooming frequency per hour, mean duration of grooming sessions and proportion of time spent grooming in siamangs (*Symphalangus*, $n = 11$ pairs; Orgeldinger, 1999 in: Geissmann et al., 2003), crested gibbons (*Nomascus*, $n = 7$ pairs; Rosenkranz, 2002) and pileated gibbons (*Hylobates pileatus*, $n = 9$ pairs; this study).

3.2 Mechanism of pair bonds

The percentage of the contribution of each partner is determined, to study which sex invested more in maintaining or building the pair bond. Only results of male grooming proportion are given (except in Fig. 6), because male and female proportions in a pair complement each other to 100%. Hereby, the grooming proportion of one sex will suffice to provide all information. The results are shown in Fig. 6 which is related to the results shown in Fig. 5.

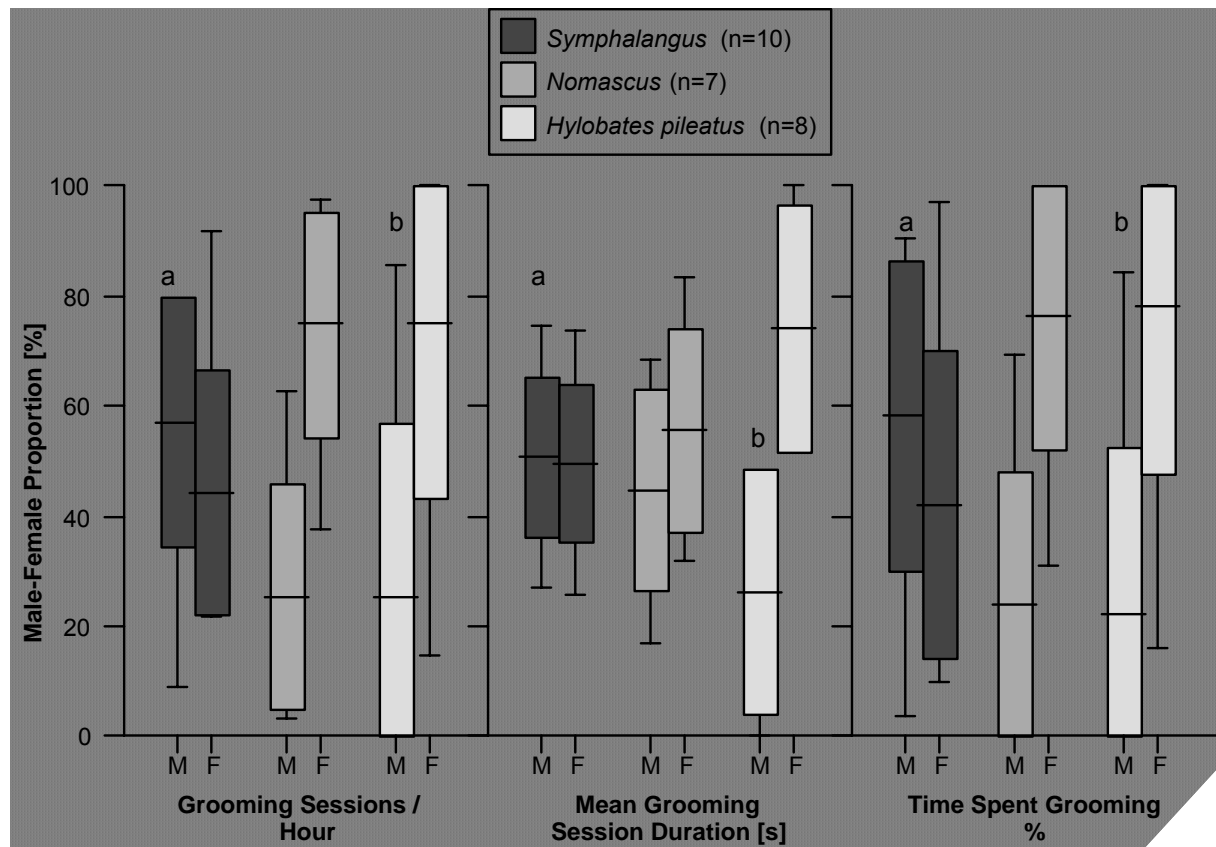


Fig. 6. Average male-female proportions of intra-pair grooming frequency per hour, mean duration of grooming sessions and time spent grooming in siamangs (*Symphalangus*, $n = 10$ pairs; Orgeldinger, 1999 in: Geissmann et al., 2003), crested gibbons (*Nomascus*, $n = 7$ pairs; Rosenkranz, 2002) and pileated gibbons (*Hylobates pileatus*, $n = 8$ pairs; this study). Abbreviations: M = males, F = females. Different letters between the genera indicate a significant difference ($p \leq 0.05$).

One pair of pileated gibbons (PT3) and one pair of siamangs (Kr2) were excluded from these analyses, because these pairs were not observed to groom each other at all and male-female proportions of grooming variables could not be calculated.

The male-female proportion of intra-pair grooming frequency per hour in siamangs is higher in males than in females ($n = 7$) but in crested and pileated gibbons higher in females ($n = 6$ and $n = 8$, respectively) than in males. The male-female proportion of mean duration of

grooming sessions are higher in male siamangs ($n = 7$) than in females, but higher in female crested ($n = 3$) and pileated ($n = 8$) gibbons than in males. The male-female proportion of time spent grooming in siamang is higher in males ($n = 5$) than in females, but in crested and pileated gibbons higher in females ($n = 6$ and $n = 4$, respectively) than in males.

Male proportions in the number of grooming sessions per hour varied from 8.5% (Br1) to 78.3% (Br2) in siamangs, from 2.9% (Os2) to 62.5% (Mu1) in crested gibbons and from 0.0% (PT2, PT5 and Zh2) to 85.4% (PT6) in pileated gibbons and differs ($p < 0.05$) among the three genera. However, Dunn's *post-hoc* tests did not reveal a difference ($p > 0.05$), but there was almost a difference between pileated and siamang gibbons, where siamang males have a higher ($0.1 > p > 0.5$) number of grooming sessions per hour than pileated gibbon males.

Male proportions in grooming session duration varied from 26.7% (Br1) to 74.6% (Mu) in siamangs, from 16.6% (Du) to 68.2% (Os2) in crested gibbons and from 0.0% (PT2, PT5, and Zh2) to 48.0% (PT6) in pileated gibbons and differs ($p < 0.05$) among the three genera. The difference is between pileated gibbons and siamangs, where siamang males have a higher ($p < 0.05$) grooming session duration than pileated gibbon males.

Male proportions in the time spent grooming varied from 3.3% (Br1) to 90.4% (Mu) in siamangs, from 0.9% (Du) to 69.1% (Mu1) in crested gibbons and from 0.0% (PT2, PT5 and Zh2) to 84.3% (PT6) in pileated gibbons and differs ($p < 0.05$) among the three genera. The difference is between pileated gibbons and siamang, where siamang males spent more ($p < 0.05$) time in grooming than pileated gibbon males.

As a result, siamang males groom partners more often than crested gibbon males, but time spent grooming and male proportions in duration of grooming sessions do not appear to differ between siamangs and crested gibbons. Male proportions in grooming session duration and time spent grooming are higher in siamangs than in pileated gibbons, whereas the number of grooming sessions per hour did not differ.

Data was also collected, in addition to the grooming data collected by focal animal sampling, on male-female grooming proportions for three additional siamang groups (An, Be, Zh, Table 3; Orgeldinger, 1999 in: Geissmann et al., 2003). These data were collected during the scan sampling observations. Male grooming proportions in these groups were 95.4%, 85.7% and 100%.

A total of 69 pairs (including data from relevant literature, Table 3) were used in the sample of this study after excluding two pairs that did not groom each other at all. Male

grooming contribution was split evenly into three classes: (1) 0-33%, (2) >33-66%, (3) >66% in order to calculate summary statistics. If male and female contributions are balanced, the pairs should be evenly distributed across the three classes. As shown in Table 4 and Appendix 3, this is not the case in siamangs ($n = 28$). Most pairs ($n = 15$) fall into class three. These results suggest that male siamangs provide most of the intra-pair grooming. It is also not the case in crested gibbon ($n = 18$) were most pairs ($n = 13$) fall into class one. This suggests that females provide most of the intra-pair grooming. This also appears for lar gibbons ($n = 23$). Were most of the lar pairs fall into class 1 ($n = 12$).

Table 4. Overall group mean in male contributions (%) to intra-pair grooming in gibbons.

Classes of male grooming proportion	Group		
	Siamangs (<i>Symphalangus</i>)	Crested gibbons (<i>Nomascus</i>)	Lar gibbons (<i>Hylobates</i>)
(1) 0-33%	5	13	12
(2) >33-66%	8	4	5
(3) >66%	15	1	6

The difference from the expected value of 50% for each sex differs between the genera *Nomascus* and *Symphalangus* ($p < 0.01$ and $p < 0.05$), but not for *Hylobates* ($p > 0.05$). As indicated by the species labels in Fig. 7c, 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 is more balanced in *H. lar* ($n = 10$). Although the difference between the two species is statistically significant ($p < 0.05$), 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 ($p > 0.05$), but the sample is very small in this case ($n = 11$).

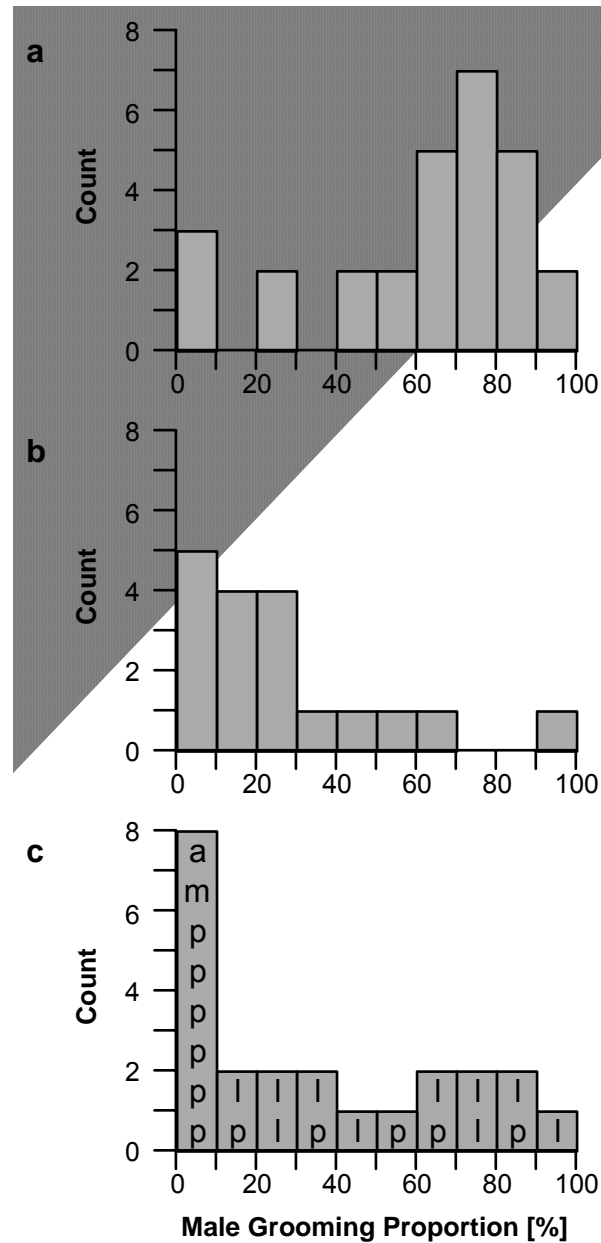


Fig. 7. Male contributions to intra-pair grooming in gibbons. (a) Siamangs (*Symphalangus*, n = 28 pairs); (b) crested gibbons (*Nomascus*, n = 18 pairs); (c) lar-group of gibbons (*Hylobates*, n = 23 pairs). Abbreviations in (c) identify the following species: a – *H. agilis*, l – *H. lar*, m – *H. moloch*, and p – *H. pileatus*.

Frequency distribution of male grooming proportion is shown in Fig. 7. These data differs among genera ($df = 2, p < 0.05$). The difference is between crested gibbons and siamangs, where crested gibbon males have a higher ($p < 0.05$) grooming proportions than siamang males. There was also a difference between gibbons of the *lar*-group and siamangs, where siamang males have a higher ($p < 0.01$) grooming proportions than gibbon males of the *lar*-group.

4. Discussion

Approximately 3% of non-primate mammalian species are monogamous (Kleiman, 1977) in contrast to 15% of all primate species (Reichard, 1995). The gibbons (*Hylobates*, Hylobatidae) of South-east Asia are the most often cited example of obligate monogamy in nonhuman primates (Palombit, 1996).

The gibbons (genus *Hylobates*) have played a prominent role in the construction of a hypothesis for the occurrence of two adult, pair-bonded, or ‘monogamous’ social organization (Palombit, 1999; Wittenberger and Tilson, 1980). In early studies (Brockelman and Srikosamatara, 1984; Ellefson, 1974) the hylobatids were seen as the paragons of fidelity, the model family unit and the standard bearers of the ‘monogamous’ primates (Fuentes, 1999). It is generally assumed that pair bonds in all gibbon taxa are built up and maintained in the same way (Geissmann et al., 2003), in other words a uniform entity.

Various hypotheses explaining the proximate and ultimate mechanism, like infanticide protection, mate guarding and male parental care (Fuentes, 2002), which have led to the evolution of monogamy among gibbons are under debate (Geissmann et al., 2003). Gibbons in the wild have shown to perform extra-pair copulations. These extra-pair copulations can make up as much as 12% of the observed copulations and occur during the female’s receptive period (Reichard, 1995). This behaviour is in contrast with the expected behaviour for monogamous individuals.

Given what is known about the primate species that occur in one male/one female group, it is safe to say that there is no uniform social organization called ‘monogamy’ (Fuentes, 2000). Thus, the mating relationship between male and female gibbons may not be as strict and exclusive as thought and the overall social dynamics of the hylobatids may involve much more than the simple “family unit” (Palombit, 1996). This hypothesis is supported by the results of this study. Generally-accepted indicators of pair bond strength and pair bond maintenance differ among *Nomascus*, *Symphalangus* and *Hylobates* gibbons.

4.1 Strength of pair bonds

Pair bond strength (Kleiman, 1977) or male-female ‘attachment’ (Wickler, 1976) is not just depend on the nature of social interactions between the sexes but also of the diversity of the social interaction between sexes (Palombit, 1996). This is exemplified by three generally accepted indicators: synchronization of behavioural variables, relative partner-distance and

allogrooming. In this study, pair bond strength among siamangs, crested and pileated gibbons were determined.

Synchronization of behavioural variables

Significant differences among siamangs, crested and pileated gibbons were found in five of the eleven variables. In most cases, siamangs exhibited higher synchronization than pileated and crested gibbons. In the other cases, pileated gibbons exhibited higher synchronization than crested gibbons. Previous studies (Rosenkranz, 2002; Geissmann and Orgeldinger, 2000) found that crested gibbon pairs exhibit a higher degree of synchronization than siamang pairs. However, the overall degree of synchronization do not differ among the three genera, suggesting that they do not differ in the strength of the pair bond, related to synchronization, as determined by this variable.

Relative partner-distance

The three taxa did not differ in the time spent in any of the four partner distance classes, except for the time spent in distance class 4 (>3 m): Pileated gibbon pairs spent more time in distance class 4 than siamang gibbons. Geissmann and Orgeldinger (2000) found that gibbon pairs that performed synchronized duets spent more time grooming each other, performing the same activities and being in close proximity to each other than did pairs whose duets were less synchronized. Palombit (1996) found that siamang pairs spent significantly more time in close proximity to one another than white-handed gibbons do. This earlier findings are only moderately paralleled by the results of this study: siamang pairs spent significantly less time in distance class 4 than pileated gibbons, suggesting that pair bond strength in siamangs may be more pronounced than in pileated gibbons. In distance class 4 siamangs show closer proximity than pileated and crested gibbons. However, the mean relative distance between pair partners did not differ among the three genera.

Allogrooming

The three taxa did not differ in the number of grooming sessions/hour (average of male and female), the proportion of time spent grooming and average duration of grooming sessions. As a result, siamang pairs, crested gibbon pairs, and pileated gibbon pairs spent

similar amounts of time grooming. Palombit (1996) compared pair bonds between siamang (*Symphalangus*) and white-handed gibbon (*Hylobates lar*) and found no species-specific differences in the time adults spent grooming or in the duration of grooming sessions. This result resembles those of this study, suggesting that the taxa do not differ in the amount of intra-pair allogrooming.

4.2 *Pair bond maintenance*

In order to gain insight in the pair bonding mechanism, it was examined which sex invests more in the pair bond. This was done by measuring the amount of partner-directed grooming for each mate. To simplify, only the male proportion was taken into account, because the proportion of the male and the female supplement each other to 100%. This study showed that in pileated and crested gibbon pairs partner-directed grooming is mostly provided by females whereas in siamang pairs the males are the main groomers. It seems a rule in siamang pairs that males participate more in grooming than the females (Chivers, 1972; Leighton, 1987; Palombit, 1996). Furthermore, male proportion in grooming session duration and time spent grooming are higher in siamangs than in pileated gibbons, whereas 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. The pair wise comparison shows statistically significant differences for siamangs/crested, but not for siamangs/pileated or pileated/crested. These results suggest that each genus differs in the mechanism of how pair bonds are maintained. Especially siamangs differ compared to pileated and crested gibbons; as grooming is male-driven in siamangs and female-driven in crested and pileated gibbons. Based on these results, the pair bond in gibbons does not appear to be a uniform entity.

Grooming

Social grooming (allogrooming) has been observed to occur in many primate species. Although the functions of grooming are not well understood, it is generally accepted that there is a relationship between grooming and something like a social bond (Fischer and Geissmann, 1990). Among the social functions commonly attributed to allogrooming behaviour in primates, some kind of tension- or aggression-reducing effect has frequently been proposed.

However, it is not clear to what degree grooming actually reduces existing tensions and to what degree it is merely a reflection of already low tension (Fischer and Geissmann, 1990). Grooming is important from the viewpoint of group integration; not only does it depend, seemingly, upon a previous state of positive conditioning in the participating animals, but the behaviour further enhances and strengthens the social relationship (Fischer and Geissmann, 1990). Allogrooming may have much more complex, and probably multiple social functions. Several authors have suggested that allogrooming in gibbons acts as a pair bonding device (Ellefson, 1974).

An example of grooming in some primate species is a display of dominance; the dominant animal receives more grooming than that it gives (honolulu zoo.org) This suggests that males are more active groomers in monogamous primates because females are dominant over males as compared to primates with polygynous social organisations (Kleiman, 1977). For gibbons there are relatively few clear, consistent differences in the social roles between males and females (Leighton, 1987). However, simple dominance relationships do not seem the only variable influencing partner-directed grooming in gibbons (Geissmann et al., 2003). If partner-directed grooming reflects the investment into a pair bond, the results of this study suggest that the willingness to invest in the pair bond differ among pairs. In almost all observed pairs, both partners are interested in maintaining the pair bond, because both partners show at least some allogrooming. The reason why grooming did not occur among pair partners in two pairs (one siamang pair and one pileated gibbon pair) is unknown, because neither PT3 nor Kr2 were newly formed pairs.

The benefit of a pair bond may be related to the reproductive potential of a partner. This – in addition to individual differences – is probably the reason why the interest in a pair partner may vary with time. Partners in long established pairs normally interact in a relaxed, tolerant and well-coordinated manner. In contrast to many species of primates, the female gibbons are often ‘co-dominant’ with males (*lar*, *agilis* and *syndactylus*; Leighton, 1987). In one of the two *lar* groups observed by Ellefson (1974), the male was dominant to the female, whereas in the other pair, dominance varied unpredictably until, in late pregnancy and early postpartum, the female became dominant to the male in feeding contexts. In two other species (*pileatus*: Srikosamatar, 1980; *muelleri*: Leighton, 1987), the female of one studied group was more aggressive than the male, groomed him much less frequently than he groomed her and, for *muelleri* at least, successfully displaced him at preferred feeding sites. This suggests that the reproductive status of females plays an important role in the benefit of a pair bond.

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 (Geissmann et al., 2003). It becomes clear why data of relatively large numbers of pairs or relatively more hours per pair need to be compared in order to discover species-specific differences when partner-directed grooming is part of a mate guarding strategy with fluctuating relevance to the groomer.

Infanticide-hypothesis

The infanticide hypothesis rests on the assumption that infanticide is an important evolutionary force in primates and that it occurs in many or most taxa. It is assumed that females cannot defend their infants from infanticidal adult males and therefore need to form an alliance with adult males to protect their offspring. A pair bond in this case should include some form of exclusive mating between the pair or relatively high degree of paternity certainty on the part of the male (Fuentes, 2002). The infanticide hypothesis states that a female will invest substantially in a social relationship with a male willing to assume the costs of defending her offspring against attacking infanticidal males (Palombit, 1999); while the male is given a high degree of paternity certainty. This may be reflected by females contributing as much as, if not more than, their male partners to maintaining the bond between them (Palombit, 1999). This assumption is not supported by the behavioural data collected by Palombit (1999). Based on that study (three pairs of siamangs and two pairs of white-handed gibbons), gibbon males appeared to invest more than, or as much as, their female partners into grooming. This contrasts with the situation in chacma baboons and gorillas, where infanticide occurs relatively frequently and where most of allogrooming is done by females (Palombit, 1999). The conclusion of Palombit (1999) is “among hylobatids, particularly white-handed gibbons, the contribution of the sexes to maintaining pair bonds are contrary to those predicted by infanticide-protection hypothesis.”

Based on the dataset presented in this paper (table 5), the results for siamangs do not support the infanticide hypothesis because of the high male investment in the pair bond ($n = 28$ pairs). In contrast, using the same variable, the hypothesis is supported by the results found for crested gibbons, where females are the main groomers in most pairs ($n = 18$ pairs). The situation in gibbons of the *lar* group ($n = 23$ pairs) appears to be less decisive. Partner-directed grooming is mainly provided by females in pileated gibbons ($n = 11$), whereas in

white-handed gibbons (n = 10) the distribution is more balanced. It should be noted, that this result should be regarded with caution because the samples are relatively small.

“Good father” hypothesis

According to the “good father” hypothesis, female investment in pair bonds should vary accordingly if males vary in their propensity to provide care for offspring (Palombit, 1999). When males provide care for the offspring, females will invest more into the pair bond, than when males do not provide care for the offspring. Because siamang males appear to be active fathers (which is observed both in the wild and in captivity), it is expected to find a high proportion of females in grooming investment. A low female investment in both *lar* and crested groups is expected, because males of these groups do not appear to provide care for the offspring. Siamangs are probably the only gibbon males that help carry infants and they appear to be more active than the females in both socializing and eventually evicting offspring (Leighton, 1987). Nothing is known in crested gibbons and gibbons from the *lar* group which provide direct paternal care on a regular basis. As documented in this study, the opposite appears to be true. Can we rule out the “good father” hypothesis based on this cross-taxon comparison?

Similar cross-taxon testing previously led to the rejection of the hypothesis that duetting may serve to strengthen pair bonds in gibbons, whereas the same hypothesis was later supported when tested within one species (*S. syndactylus*) (Geissmann et al., 1999; Geissmann and Orgeldinger, 2000). The assumption that the function is the same in all taxa by testing functional hypothesis by a cross-taxon comparison does not appear to be justified for all functional aspects of gibbon singing (nor is it justified for gibbon pair bonds) (Geissmann et al., 2003). If pair bonds are maintained in different ways in different gibbon taxa, as suggested by the results of this study, then the “good father” hypothesis may well apply to one species and not to another. This means that it should be tested for each genus or even each taxon separately. For example, it has been reported that allogrooming between pair mates is virtually nonexistent in wild *H. agilis* and *H. klossii* (Leighton, 1987), in contrast to the situation in wild *H. lar* and siamangs (Ellefson, 1974; Reichard, 1995). This suggests that the range of variation in pair bonds even within the genus *Hylobates* may extend beyond what would be expected of a genus-specific variable.

5. Conclusions

The two main questions of this study are: (1) Do pileated gibbons differ from other gibbons in the strength of their pair bonds? (2) Do pileated gibbons differ from other gibbons in the way pair bonds are maintained?

In order to answer the first main question, about pair bond strength, three research questions had to be answered. The three research questions were: (a) What is the frequency and duration of *grooming behaviour* between pair mates and the difference between sex and genera? (b) What is the occurrence of *synchronized behaviour* between pair mates and the difference between gibbon genera? (c) What is the *relative distance* between pair mates and the difference between gibbon genera?

The following conclusions can be drawn after this study.

5.1 *Pair bond strength*

Siamangs (*Symphalangus*) and pileated gibbons (*Hylobates pileatus*) do appear to differ in the strength of their pair bonds. Siamangs and pileated gibbons do not exhibit similar relative partner distance. Siamangs and pileated gibbons do exhibit similar degrees of behavioural synchronization and similar amounts of grooming (both numbers of events and actual grooming time). Siamangs and crested gibbons (*Nomascus*) do not appear to differ consistently in their pair bonds as do crested and pileated gibbons. Siamangs and crested gibbons exhibit similar degrees of behavioural synchronization, similar relative partner distance and similar amounts of grooming (both numbers of events and actual grooming time), which pileated and crested gibbons also do.

5.2 *Pair bond maintenance*

(1) The mechanisms how pair bonds are maintained, as indicated by the amount of partner-directed grooming, differ between gibbon taxa. Siamang males invest significantly more into the pair bond than females. For crested gibbons and gibbons of the *lar* group, the opposite is true. Differences appear to occur within the latter group. Grooming in *H. pileatus* is mainly provided by females, whereas the grooming appears to be more balanced between male and female in *H. lar*.

(2) The pair bond in gibbons is not a uniform entity.

(3) The infanticide-protection hypothesis for the evolution of pair bonds appears to be most unlikely for siamangs, because of high male investment in the pair bond. The hypothesis cannot be rejected for crested gibbons, where females are the main groomers in most pairs. The situation in gibbons of the *lar* group appears to be less decisive. Partner-directed grooming is mainly provided by females in pileated gibbons, whereas in white-handed gibbons the distribution is more balanced.

(4) The ‘good-father’ hypothesis, which predicts high female investment into pair bonds with males providing paternal care for offspring, is not supported in the cross-genera comparison. Additional species-specific analyses are recommended.

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Appendix 1: Synchronization

Average degree of synchronization [%] in eleven behavioural variables for siamangs (*Symphalangus*), crested gibbons (*Nomascus*) and pileated gibbons (*Hylobates pileatus*).

Behavioural variable	Taxon			Kruskal-Wallis test (<i>p</i>)	Dunn's <i>post-hoc</i> test	
	<i>Symphalangus</i>	<i>Nomascus</i>	<i>Hylobates pileatus</i>		Taxa compared ¹	<i>p</i>
Sexual behaviour	77.12 (n = 9)	75.00 (n = 6)	82.67 (n = 6)	0.990	–	–
Sociopositive behaviour and infant care	65.57 (n = 13)	33.97 (n = 7)	78.18 (n = 9)	* 0.027	H>N	<0.05
Territorial behaviour	49.80 (n = 13)	13.10 (n = 6)	32.85 (n = 9)	* 0.011	S>N	<0.01
Agonistic behaviour	49.58 (n = 10)	0.00 (n = 3)	33.33 (n = 3)	0.098	–	–
Feeding and food-related behaviour	42.41 (n = 13)	24.79 (n = 7)	28.19 (n = 9)	* 0.011	S>N S>H	<0.05 <0.05
Observe	40.94 (n = 13)	34.76 (n = 7)	29.23 (n = 9)	0.251	–	–
Rest and sleep	27.99 (n = 13)	18.76 (n = 7)	7.59 (n = 9)	* 0.011	S>H	<0.01
Play	27.92 (n = 13)	33.31 (n = 7)	58.14 (n = 9)	0.308	–	–
Locomotion	16.82 (n = 13)	16.66 (n = 7)	23.22 (n = 9)	0.111	–	–
Comfort-related behaviour	14.97 (n = 13)	3.76 (n = 7)	30.01 (n = 9)	*<0.0001	H>N S>N	<0.001 <0.05
Excretion	2.31 (n = 13)	0.00 (n = 7)	3.17 (n = 9)	0.698	–	–
Taxon mean	35.02 (n = 14)	23.73 (n = 7)	32.69 (n = 9)	0.186	–	–

¹ Abbreviations: H = *Hylobates pileatus*, N = *Nomascus*, S = *Symphalangus*

* Stars identify significant differences between the genera (Kruskal-Wallis tests). Dunn's *post-hoc* tests shows between which genera significant differences are.

Appendix 2: Partner distances

Average relative partner distances and time proportions spent in four 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): (a) siamangs (n = 18 groups), (b) crested gibbons (n = 7 groups) and (c) pileated gibbons (n = 9 groups).

Group	Relative distance [%]	Distance classes [%]			
		1	2	3	4
(a) Siamangs (<i>Symphalangus</i>)					
Antwerpen	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
Zürich	36.10	1.30	17.80	62.30	18.60
Mean	25.97	13.21	18.32	37.95	30.52
(b) Crested gibbons (<i>Nomascus</i>)					
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

Appendix 2 (ctd.)

(c) Pileated gibbons (<i>Hylobates pileatus</i>)					
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
Zürich 1	18.29	14.90	20.10	24.70	40.40
Zürich 2	34.83	0.90	7.40	17.20	47.50
Mean	23.47	9.43	11.88	25.69	50.06

Appendix 3: Male contribution to intra-pair grooming

Male contributions (%) to intra-pair grooming in gibbons. Abbreviations: c = captive, w = wild, – = no partner-directed grooming observed. Stars identify sources which are found in Geissmann (2003). Other literature data were provided by Geissmann (pers. comm.).

Group	Cap- tive / wild	Data type	Classes of male grooming proportion:			Source
			(1) 0-33%, (2) >33-66%, (3) >66%	1	2	
(a) Siamangs (<i>Synphalangus</i>)						
Antwerpen (An)	c	Frequency			95.4	* Orgeldinger (1999)
Berlin Zoo (Be)	c	Frequency			85.7	* Orgeldinger (1999)
Branféré pair 1 (Br1)	c	Frequency	8.5			* Orgeldinger (1999)
Branféré pair 2 (Br2)	c	Frequency			78.3	* Orgeldinger (1999)
Branféré pair 3 (Br3)	c	Frequency			74.1	* Orgeldinger (1999)
Budapest (Bu)	c	Frequency	29.5			* Orgeldinger (1999)
Dortmund (Do)	c	Frequency		60.1		* Orgeldinger (1999)
Dresden pair 1 (Dr1)	c	Frequency			69.7	* Orgeldinger (1999)
Dresden pair 2 (Dr2)	c	Frequency		51.5		* Orgeldinger (1999)
Duisburg (Du)	c	Frequency		49.2		* Orgeldinger (1999)
Frankfurt (Fr)	c	Frequency	–	–	–	* Orgeldinger (1999)
Krefeld pair 1(Kr1)	c	Frequency			76.7	* Orgeldinger (1999)
Krefeld pair 2 (Kr2)	c	Frequency			72.0	* Orgeldinger (1999)
Munich (Mu)	c	Frequency	8.5			* Orgeldinger (1999)
Studen (St)	c	Frequency			78.3	* Orgeldinger (1999)
Washington (Wa)	c	Frequency			74.1	* Orgeldinger (1999)
Zürich (Zh)	c	Frequency			100.0	* Orgeldinger (1999)
TS1	w	Time		60.5		* Chivers (1974, p. 213)
RS2	w	Time			73.7	* Chivers (1974, p. 212f)
Milwaukee	c	Frequency	26.0			* Fox (1977)
Tulsa	c	Frequency?			88.8	* Kawata (1980)
Berlin	c	Frequency	–	–	–	* Dielentheis and Zaiss (1987)
Cheyenne, MH 21	c	Time			86.3	* Philippart (1991, p. 24)
Cheyenne, MH 23	c	Time	7.0			* Philippart (1991, p. 24)
Melbourne	c			60.8		* Bricknell (1992, p. 37)
Ketambe, CH-CJ	w	Frequency		ca 48.0		* Palombit (1992, p. 256-258)
Ketambe, PP-PN	w	Frequency			ca 84.0	* Palombit (1992, p. 256-258)
Ketambe, Pm-Pn	w	Frequency		ca 60.0		* Palombit (1992, p. 256-258)
Lourosa, pair 1	c	Time			88.9	* Caeiro de Pereira Sousa (1998)
ICGS	c	Time		56.9		* Eardley (2000)
Number of pairs			5	8	15	

Appendix 3 (ctd.)

(b) Crested gibbons (<i>Nomascus</i>)					
Duisburg (Du) (<i>N. leucogenys</i>)	c	Frequency	4.4		Rosenkranz (2002)
Eberswalde (Eb) (<i>N. gabriellae</i>)	c	Frequency	24.7		Rosenkranz (2002)
Mulhouse pair 1 (Mu1) (<i>N. leucogenys</i>)	c	Frequency		62.5	Rosenkranz (2002)
Mulhouse pair 2 (Mu2) (<i>N. siki</i>)	c	Frequency	20.6		Rosenkranz (2002)
Mulhouse pair 3 (Mu3) (<i>N. gabriellae</i>)	c	Frequency	22.1		Rosenkranz (2002)
Osnabrück pair 1 (Os1) (<i>N. gabriellae</i>)	c	Frequency		38.3	Rosenkranz (2002)
Osnabrück pair 2 (Os2) (<i>N. leucogenys</i>)	c	Frequency	2.9		Rosenkranz (2002)
Twycross (<i>N. concolor</i> , <i>N. leucogenys</i>)	c	Time	17.7		* Pollard (1983, p. 32)
Twycross (<i>N. leucogenys</i>)	c	Time	18.0		* Pollard (1983, p. 32)
Perth, group 5 (<i>N. leucogenys</i>)	c	Frequency?		45.8	* Embury (1983, Table 7)
Melbourne (<i>N. leucogenys</i>)	c	Frequency	19.5		* Bricknell (1992, p. 37f)
Mulhouse, group 1 (<i>N. gabriellae</i>)	c	Time	0		* Schlegel (1995, p. 19)
Mulhouse, group 2 (<i>N. leucogenys</i>)	c	Time	–	–	* Schlegel (1995, p. 20)
Mulhouse, group 3 (<i>N. siki</i>)	c	Time	0		* Schlegel (1995, p. 21)
Amsterdam (<i>N. leucogenys</i>)	c	Time	16.0		Hold (1998, Anh. 3)
Beekse Bergen (<i>N. leucogenys</i>)	c	Time	22.2		Hold (1998, Anh. 3)
Hannover (<i>N. leucogenys</i>)	c	Time		57.5	Hold (1998, Anh. 3)
ICGS (<i>N. leucogenys</i>)	c	Time		100	* Eardley (2000)
Lincoln Park (<i>N. leucogenys</i>)	c	Frequency	0		Lukas et al. (2002, p. 423)
Number of pairs			13	4	1

Appendix 3 (ctd.)

(c) Lar gibbons (<i>Hylobates</i>)			
Phnom Tamao 1 (PT1) (<i>H.pileatus</i>) c	Frequency	55.7	This study
Phnom Tamao 2 (PT2) (<i>H.pileatus</i>) c	Frequency	0	This study
Phnom Tamao 3 (PT3) (<i>H.pileatus</i>) c	Frequency	– – –	This study
Phnom Tamao 4 (PT4) (<i>H.pileatus</i>) c	Frequency	8.1	This study
Phnom Tamao 5 (PT5) (<i>H.pileatus</i>) c	Frequency	0	This study
Phnom Tamao 6 (PT6) (<i>H.pileatus</i>) c	Frequency		85.4 This study
Phnom Tamao 7 (PT7) (<i>H.pileatus</i>) c	Frequency	12.5	This study
Zürich 1 (Zh1) (<i>H. pileatus</i>) c	Frequency	38.2	This study
Zürich 2 (Zh2) (<i>H. pileatus</i>) c	Frequency	0	This study
ICGS (<i>H. pileatus</i>) c	Time		69.6 * Eardley (2000)
Perth (Pe1) (<i>H. pileatus</i>) c	Frequency?	0	* Embury (1983, Table 7)
Blackpool (Bp) (<i>H. pileatus</i>) c	Frequency	0	Skyner (2002)
Bronx, New York (BNY) (<i>H. lar</i>) c	Time		71.3 * Riess (1956)
Portland, Oregon (PO) (<i>H. lar</i>) c	Frequency	45.0	* Steen (1969, p. 63)
Berlin (Be) (<i>H. lar</i>) c	Frequency	25.0	* Dielentheis and Zaiss (1987)
Melbourne (Mel) (<i>H. lar</i>) c	Frequency	10.8	* Bricknell (1992, p. 38)
Ketambe (AS-AY) (<i>H. lar</i>) w	Frequency		ca 81.0 * Palombit (1992, p. 256-258)
Ketambe (GD-GM) (<i>H. lar</i>) w	Frequency		93.0 * Palombit (1992, p. 256-258)
Khao Yai (Pair A) (<i>H. lar</i>) w	Time	64.3	* Reichard (1995, p. 74)
Khao Yai (Pair B) (<i>H. lar</i>) w	Time	37.5	* Reichard (1995, p. 74)
Khao Yai (Pair C) (<i>H. lar</i>) w	Time		71.4 * Reichard (1995, p. 74)
Khao Yai (Pair T) (<i>H. lar</i>) w	Time	20.0	* Ebert (1999, p. 65)
ICGS (<i>H. agilis</i>) c	Time	0	* Eardley (2000)
Berlin (Be) (<i>H. moloch</i>) c	Frequency	– – –	* Dielentheis and Zaiss (1987)
ICGS (<i>H. moloch</i>) c	Time	0	* Eardley (2000)
Number of pairs		12	5 6