



The relationship between duet songs and pair bonds in siamangs, *Hylobates syndactylus*

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One of the most commonly cited functional explanations for animal duet songs is strengthening of the pair bond. However, the evidence to support this view is, at best, limited. This study provides support by documenting a relationship between pair bonds and duet singing in siamangs. As a working hypothesis, we assume that if duetting were related to pair bonding, we might expect to see a relationship between duetting intensity and indicators of pair bond strength. Like most gibbon species, siamang pairs produce loud, long and well-coordinated duet songs. We recorded daily frequency and duration of duetting and three generally accepted indicators of pair bond strength (mutual grooming, behavioural synchronization and distance between mates) in 10 siamang groups in zoos. Duetting activity was positively correlated with grooming activity and behavioural synchronization, and negatively correlated with distance between mates. These results suggest that the production of coordinated duets by siamang pairs is related to pair bonding.

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Although maintenance or strengthening of the pair bond is one of the most frequently advocated functions of duet songs in animals (e.g. [Armstrong 1963](#); [Farabaugh 1982](#); [Brockelman & Srikosamatara 1984](#); [Levin 1996](#)), this function is particularly in want of evidence (e.g. [Arrowood 1988](#); [Levin 1996](#)) and 'has apparently not yet been demonstrated in any animal species that sings' ([Haimoff 1983](#), page iv).

Gibbons (Hylobatidae) are monogamous arboreal apes living in East Asian rainforests. Family groups, usually two to five animals, typically consist of an adult pair and their immature offspring ([Chivers 1977, 1989](#); [Leighton 1987](#)). All gibbon species produce loud and long vocal bouts. These songs are typically produced in the early morning and last about 15–30 min. In the majority of species, mates typically combine their species-specific and often sex-specific vocalizations to produce well-patterned duets. In several species, mated males additionally produce solo songs while in two species, *Hylobates klossii* and *H. moloch*, males and females produce only solo songs ([Geissmann 1993, 1995, 2000a](#); [Geissmann & Nijman 2000](#)).

Among gibbon species, the duet song of the siamang is particularly complex, as is evident from the richness of the partly sex-specific vocal repertoire, in the number of

different types of vocal interactions necessary to produce a typical great call sequence (i.e. the most spectacular and longest recurrent vocal pattern within gibbon songs), and in the strict rules that regulate the sequence of, and the intervals between, these vocal interactions ([Lamprecht 1970](#); [Haimoff 1981](#); [Geissmann 1999, 2000b](#)). The siamang duet 'is probably the most complicated opus sung by a land vertebrate other than man' ([Marshall & Sugardjito 1986](#), page 155).

As a working hypothesis, one can assume that, if duetting were related to pair bonding, duetting intensity would be related to indicators of pair bond strength. We assessed the correlation between two measures of duetting activity (i.e. song activity and number of songs per day) and three indicators of pair bond strength (mutual grooming, behavioural synchronization, distance between mates) in 10 siamang groups in zoos. If duetting indeed serves to form, to strengthen or to maintain the pair bond, we should expect to find positive correlations between duetting activity and both grooming and behavioural synchronization, and negative correlations between duetting activity and distance between mates.

METHODS

All the data were collected in a consistent form by M.O. between March 1990 and December 1992 at the following zoos: Branféré, France; Budapest, Hungary; Dresden,

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Duisburg, Frankfurt, Krefeld, Germany; and Studen, Switzerland. Ten siamang groups were observed (Br1, Br2, Bu, Dr1, Dr2, Du a and Du b, Fr, Kr1, Kr2, St), with group size ranging from two to four animals. Pairs had been living together for a median of 11.0 years (range 0.2–23.6 years) previous to our study.

Because of the profound behavioural changes occurring after the death of the infant in the group at the Duisburg zoo (Orgeldinger 1996), the observations made before and after the death of the infant had to be analysed separately (groups Du a and Du b, respectively). The childless pair was more active in play, bonding, agonistic and sexual behaviour and less active in territorial behaviour, than they had been when their infant was alive (Orgeldinger 1996). Among the variables collected for our study, the degree of synchronization in the 12 behavioural categories (as defined below) differed significantly before and after the death of the infant (Wilcoxon signed-ranks test: T (sum of negative ranks)=51, $N=10$, tied $P=0.017$).

At each zoo, observation time for each sampling method was distributed evenly across the animals' activity period between 0700 and 1800 hours (until 1700 hours in the winter). Only the behaviour of the adult pair was recorded.

We used focal animal sampling (Altmann 1974; Lehner 1979) to collect information on the frequency of grooming behaviour between mates. At the same time, we noted the occurrence and duration of duet songs. Focal animals were changed every 20 min. The total observation time per pair was 80 h, with the exception of groups Du a (60 h) and Du b (50 h). Grooming occurred in discrete sessions that could be counted. We allowed an interval of up to 10 s between bouts of grooming before we counted them as two sessions, rather than one.

We used scan sampling to record behavioural synchronization of activities between mates. We defined 12 behavioural categories (infant care, play, sociopositive, agonistic, territorial, sexual, comfort-related, feeding and food-related behaviour, observe, rest and sleep, excretion and locomotion). Pairs were scanned for synchronization of these categories during blocks of 5 or 10 min, separated by intervals of 20 min. During each scan sampling block, scans were made every 1 min until May 1991, and every 2 min after that date (i.e. groups Dr1, Kr1, Kr2, St). The total observation time per pair was 20 h, with the exception of groups Du a (30 h), Du b (10 h) and Fr (30 h). The occurrence of synchronized behaviour between pairmates is expressed as a percentage of the total number of scans for a given pair.

We also used scan sampling to record the distance between mates. Groups 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 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. The total observation time per pair was 10 h.

The size of the enclosure varied between zoos (some siamang groups were held in cages, others on islands).

Because small cages may have forced pairs into closer proximity than bigger enclosures, we calculated the relative distance (%) between mates as the mean inter-individual distance in relation to the maximal possible distance in the pair's given environment (cage or island). The maximal possible distance (MPD) was 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 we determined the position of a siamang by the animal's centre of gravity, we subtracted 0.3 m in (1) and added 0.5 m in (2). These values are estimates based on our observations and should correspond to the highest possible height of a siamang's centre of gravity when the animal is below and above a support, respectively.

We calculated the number of songs per day by dividing the total time each group spent singing during the observation period by the number of days the group was observed (number of days=total observation time divided by the duration of the activity period) and by the average song duration. The average song duration was determined for each group independently.

Thus, for each pair we recorded: (1) mean number of song bouts per day; (2) song activity as a percentage of the observation period; (3) grooming between mates (sessions/h); (4) behavioural synchronization (%) between mates; and (5) relative distance (%) between mates, that is mean interindividual distance in relation to the maximal possible distance in the pair's given environment (cage or island).

These variables were separated into two groups: (1) duetting activity (variables 1 and 2) and (2) 'pair bond strength' (variables 3–5). Kendall rank order correlation coefficients (τ) were calculated only between variables representing different groups to avoid correlating dependent variables. Our statistical tests are two tailed.

RESULTS

Table 1 shows each group's scores in all the variables and Table 2 shows all statistically significant correlations. Each measurement of duetting activity was positively correlated with grooming and negatively with distance between mates. In addition song activity was also positively correlated with behavioural synchronization. The correlation between the number of songs per day and behavioural synchronization just failed to reach significance ($P=0.052$).

DISCUSSION

We found that duetting activity was higher in pairs that groomed more, behaved synchronously and kept closer together. In contrast, an earlier study comparing field data on several gibbon species failed to find any of these relationships and came to the conclusion that 'contrary

Table 1. Variables used in this study

Variable	Group										
	Br1	Br2	Bu	Dr1	Dr2	Du a	Du b	Fr	Kr1	Kr2	St
Group size	2	3	2	2	2	3	2	3	4	3	2
Duetting											
Mean no. of songs/day	2.56	2.73	1.13	2.41	2.28	1.64	1.04	1.58	0.78	0.45	4.86
Song activity (%)	7.4	7.5	3.3	5.0	5.1	4.0	2.5	3.6	2.2	1.0	12.6
Pair bond strength											
Grooming (sessions/h)	1.64	3.04	1.74	2.71	3.08	3.56	2.72	2.08	1.14	0	7.89
Behavioural synchronization between mates (%)	57.7	45.0	51.4	38.2	45.8	29.0	47.2	24.2	34.4	21.3	73.9
Distance between mates (%)	15.5	12.1	32.5	30.2	24.0	30.8	29.1	38.8	29.1	35.9	11.5

Song activity: time spent singing per observation time; behavioural synchronization between mates: occurrence of synchronized behaviour between mates per number of observation scans; distance between mates: mean interindividual distance in relation to the maximal possible distance in the pair’s given environment (cage or island).

Table 2. Kendall rank order correlations among the five variables used in this study

Pair bond strength	Duetting			
	Mean no. of songs/day		Song activity (%)	
	Kendall’s tau corrected for ties	P	Kendall’s tau corrected for ties	P
Grooming (sessions/h)	0.491	0.036	0.527	0.024
Behavioural synchronization between mates (%)	0.455	0.052	0.491	0.036
Distance between mates (%)	-0.587	0.012	-0.624	0.008

See Table 1 for explanation of variables.

to previous hypotheses, the production of coordinated duets by male and female pairs is found to be unrelated to pairbonding’ (Cowlshaw 1992, page 131). Clearly, these two sets of results are incompatible.

Cowlshaw’s comparisons include data from *H. klossii* (which does not produce duets) and one or several duetting species, and so his analysis confounds within- and between-species variation. Because the duetting and non-duetting gibbon species apparently shared a similar pair bond strength, this seemed to indicate that duetting activity may not be related to the pair bond. However, it is debatable whether the function of duetting can be tested by comparing duetting activity between duetting and nonduetting species (Geissmann 1999). Presence of a pair bond in the absence of duetting in *H. klossii* need not imply ‘that duetting is not necessary for pairbonding’ in gibbons (Cowlshaw 1992, page 145), but merely that it is not necessary for pair bonding in *H. klossii*. Information on the function of duetting in one species is not necessarily valid for every species.

It has often been suggested that duetting may serve several functions in gibbons and that the importance of each function may differ between gibbon species (see Geissmann 1999, 2000a). Species-specific differences in song (structure, the amount of solo singing of either sex, the amount of duetting, and the complexity of vocal coordination) all suggest that the functions of singing differ in weight across gibbon species. If

duetting fulfils a particular function in some gibbon species, but not in others, then a correlation between duetting and that particular function may disappear in a cross-species comparison. As a result, a cross-species comparison may not produce correlations for existing functions of duetting, even if the comparison were restricted to duetting species only. To eliminate the effects of species-specific differences, duetting activity and the pair bond should be compared among pairs of the same species.

In addition, Cowlshaw’s comparisons were based on very small data sets (two populations for behavioural synchronization, two family groups for interindividual distance and six populations for grooming; only this last sample permitted a correlational analysis) and his data came from studies by different researchers. All data in our study were collected in a consistent form by one observer, and so they provide a more satisfactory basis for the analysis of the covariation between duetting activity and strength of the pair bond.

The evidence now available supports the hypothesis that duetting in siamangs is related to pair bonding. It remains to be shown how far this applies to other gibbon species that produce less complex duets, such as gibbons of the *lar* and *concolor* groups (Geissmann 1993, 1995). Similarly, our results do not question earlier studies on bird duets which failed to find a relationship between duetting and pair bonding (see Introduction).

A disadvantage of our study is the use of captive animals. Our observations should, therefore, be repeated on wild siamangs. In addition, although mutual grooming, behavioural synchronization and distance between mates are often said to be indicators of pair bond strength, it is difficult to measure the actual strength of a social bond independently (Lamprecht 1984), and the relative usefulness of the indicators remains undetermined.

Our findings are fully compatible with those of an earlier study (Geissmann 1999) which tested several predictions derived from the so-called pair bonding hypothesis. If duetting has to be learned each time a pair forms, this would reduce the probability of a partner deserting, since the learning investment would have to be repeated with every new partner (Wickler 1980). Changes in duet structure of two pairs of siamangs during a forced partner exchange showed that the predictions are met, suggesting that the pair bonding hypothesis is supported by the available evidence on siamang duets (Geissmann 1999).

We did not address all possible functions of siamang songs in our study. The loudness of the siamang song suggests that functions other than strengthening or maintaining the pair bond are also involved. These other functions are most probably related to territorial advertisement and defence, pair bond advertisement, mate guarding and defence and/or mate attraction.

The hypothesis that duetting may advertise pair bond strength, in particular (Haimoff 1984; Geissmann 1986, 1999; Cowlshaw 1992), does not compromise but supplements the pair bonding hypothesis (Geissmann 1999, this study). To avoid letting competitors know that a pair is newly mated, such pairs should try to concentrate their learning time into as short a period as possible, which probably explains why newly mated siamang pairs spend more time singing than established pairs (Geissmann 1986). If newly mated pairs singing atypical duet songs attract more competitors than established pairs with well-coordinated songs, this should also reduce the probability of mate desertion in established pairs, because deserting animals would initially produce imperfect duets with their next partner.

While our study indicates that there is a correlation between high duetting and behavioural indicators of a strong pair bond, correlation does not prove causation. There is, however, a type of analysis (cross-lagged panel analysis) that addresses this issue, at least in principle. If large samples of variables A and B are determined on two different occasions 1 and 2, inference about a causal relationship between A and B is possible if correlations are crossed and lagged over time. If A causes B, then the correlation between A on the first occasion (A1) and B on the second (B2) should be reliably greater than the A2–B1 correlation. If the opposite held, then B would be inferred to cause A. If the cross-lagged correlations do not differ significantly, no causal relationship can be inferred. Deary (1995, page 242ff) presented an example of a study using cross-lagged panel data. In practice, this would require substantially more data, normally distributed data, and a repetition of the data collection on the same animals at a certain interval.

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