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# MATE CHANGE ENHANCES DUETTING ACTIVITY IN THE SIAMANG GIBBON (HYLOBATES SYNDACTYLUS)

by

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(With 4 Figures)

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## Introduction

Siamang, like other hylobatids, live in tropical rain forest, in monogamous, territorial family groups (CHIVERS, 1971, 1972, 1973, 1974; CHIVERS et al., 1975; CHIVERS & RAEMAEKERS, 1980; CHIVERS & RAEMAEKERS, 1980; KAWABE, 1970; MCCLURE, 1964). Loud and spectacular calling bouts are mostly exhibited by mated pairs. Mates typically sing together with a partially sex-specific repertoire to produce a well patterned duet (CHIVERS, 1976, 1978; FOX, 1977; HAIMOFF, 1981, 1983, 1984; LAMPRECHT, 1970; MARLER & TENAZA, 1977; MARSHALL & MARSHALL, 1976). Duet songs have been suggested to fulfil a variety of functions. Functional interpretations, which most often have been suggested for duets of other mammals and birds, are that they serve predominantly as a territorial advertisement, but a possible cohesive function of these calls within the group has also been proposed (e.g. FARABAUGH, 1982; HOOKER & HOOKER, 1969). Probably, it is not one single function which can satisfactorily explain the duet song of the siamang.

Siamang duets show a high degree of complexity, that is richness in repertoire, in pair and individual specificity, and in interactive points

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within the duet (HAIMOFF, 1981; LAMPRECHT, 1970). As considered earlier by LAMPRECHT (1970), there is now some evidence that synchrony and coordination of the siamang duet song may only develop after some time of practice in newly mated captive (HAIMOFF, 1981; own unpublished data) and wild siamang pairs (CHIVERS, pers. comm.). Several authors have suggested that duetting in birds may function as advertisement of the presence and the status of a mated pair (FARABAUGH, 1982; WICKLER, 1980; WILEY & WILEY, 1977):

> "The additional time and uncertainty involved in mastering a duet repertoire during pair formation would in the end provide a signal, in the form of crystallized duets, that a stable breeding pair had established residence." (WILEY & WILEY, 1977, p. 33).

If duet development in newly mated pairs actually involves a certain time of practice, then the learning individual(s) should consequently try to concentrate the necessary time investment into a period as short as possible, because untypical duetting attempts of a not-yet-established pair could easily be detected and might attract competitors of either sex. In order to concentrate the learning time, a newly formed pair should therefore spend more time singing than an established one.

To test this prediction, the singing activity of a pair of captive siamang before and after a forced partner change was compared. Some more qualitative observations on a partner exchange in a second pair are also included here.

### Animals and methods

Data were collected at the Zoological Garden of Zürich and at the Zoo 'Seeteufel' in Studen. Two pairs of siamang were present at the Zürich Zoo at the beginning of this study:

Pair Na + Ga consisted of two adult, wild-born siamang. The male Na was born about in 1967, the female Ga about in 1963. The male had sired several infants with another female (Ra). Na and Ca had been together since 31 July 1980. Copulations were observed to occur frequently during this study. A premature infant was stillborn on 26 August 1981.

The second pair in Zürich, Bh + Ch, consisted of two younger animals which had been hand-raised together. The male Bh, a son of Na+Ra, was born on 23 July 1975. The female Ch was his full-sister and born on 25 December 1976. She used to remain silent during some parts of her brother's song bouts, and her bark series were not as regular as those of typical female song contributions. This can probably be attributed to her youth.

At the Studen Zoo, one single female, one adult pair and one family group were present at the beginning of this study:

The single female Vr was an adult animal, wild-born about in 1963. She gave birth to a son in 1979 and was kept alone after the death of her mate and her infant in the same year.

The pair Bb + Ra consisted of two adult, wild-born animals, which had been together since 21 July 1980. Copulations frequently occurred. The male Bb was born about in 1958 and supposed to be infertile. Song bouts of this male were analysed previously by

LAMPRECHT (1970), who reputed this animal to originate from Sumatra. The female Ra was born about in 1963 and was mentioned by SCHULTZ (1972) to originate also from Sumatra. Several offsprings derived from her former matings with Na (see above).

The family group consisted of an adult pair Ko + Cr, both wild-born about in 1963, and their offspring: the female Li was born on 22 July 1977, her brother Al on 11 October 1979.

The temporal changes in group composition are illustrated in Fig. 1. By exchanging two males, two new pairs were formed. Partner exchanges were not induced for the purpose of this study. On 14 July 1981, the male Na was transfered from Zürich to Studen and there brought together with the single female Vr. His former mate, the female Ga, was kept alone during one month after separation. On 12 August 1981, she and the male Bh were brought together while Bh's younger sister was thereafter kept with two juvenile males.

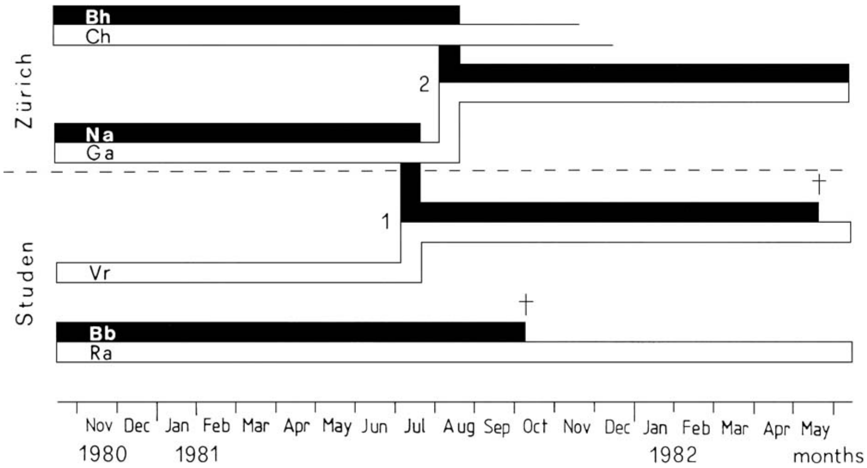

Fig. 1. Changes in group composition. Schematical presentation of the temporal process. (1) New pair formation Na + Vr, 14 July 1981. (2) New pair formation Bh + Ga, 12 August 1981.

It should he noted that all siamang groups could hear each other's song bouts in both zoos. In Zürich, both groups lived in adjacent cages, but without visual contact. In Studen, the pair Bb + Ra and the female Vr (later pair Na + Vr) also lived in adjacent cages, where they could clearly see each other. The cage of the family group (Ko + Cr) was situated more than 10 m apart. Visual contact to this group was somewhat hindered by trees and shrubbery.

The siamang groups in Zürich were observed at irregular intervals from 14 August 1980 to 28 April 1982, for several hours each day. The siamang groups in Studen were observed from dawn to dusk during three blocks of several days each, between 6 July 1981 and 24 November 1981. Later observations in both zoos were made only occasionally.

Starting-time and duration of all song bouts produced during an observation period were registered. Many of the song bouts were tape-recorded and their duration was later checked again by stop watch.

Nonparametric statistical tests were adapted from SIEGEL (1956) and used two-tailed.

## Results

On average, the single female Vr used to sing only 1.8 times a day during the eight days immediately before the arrival of the new male Na in Studen (R = 0-3, n = 14 songs in 8 days). During the same time span, immediately after the introduction of her new partner, her song frequency rose abruptly to 4.0 times per day (R = 2-5, n = 32 songs in 8 days) (Fig. 2a). The difference is statistically significant (Mann-Whitney U-test, $p < 0.001$).

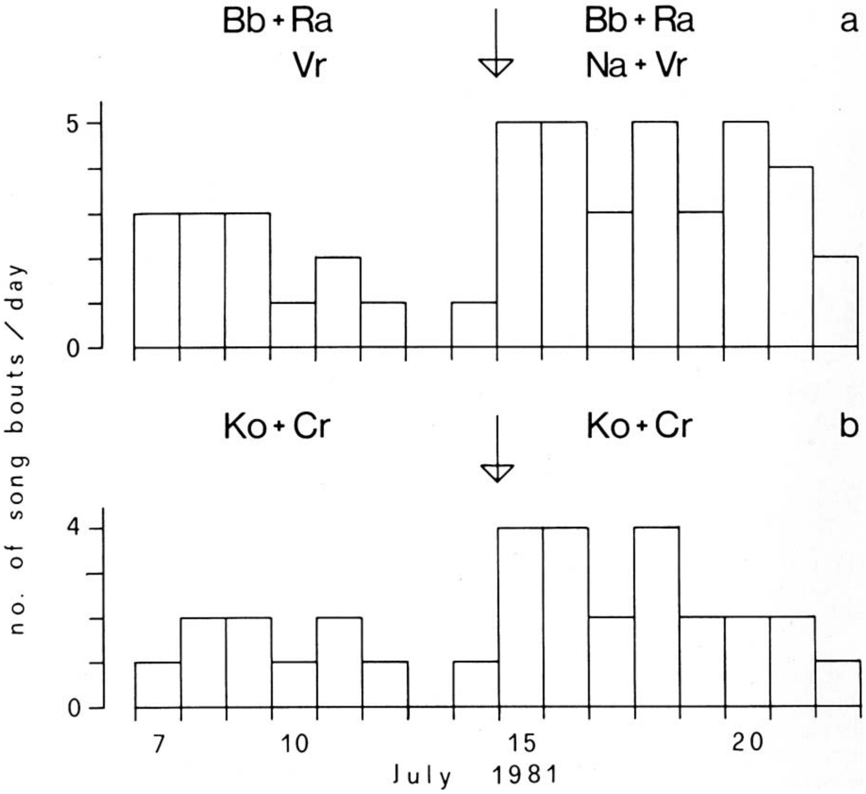

Fig. 2. Number of song bouts per day during the eight days immediately before and after the arrival of Na (arrow) in Studen. a. Pair Bb + Ra and female Vr, later pair Na+Vr (Mann-Whitney U-test, $p<0.001$). b. Family group Ko+Cr (Mann-Whitney U-test, $p<0.05$).

The adjacent pair Bb + Ra started and ended its song bouts always and exclusively in synchrony with Vr. Therefore, the results above are valid for this pair as well.

The family group Ko + Cr, which was located further away, would on average sing 1.4 times per day (R = 0-2, n = 11 songs) during the eight days prior to the arrival of Na (Fig. 2b). In this group too, a remarkable increase in song bouts followed the formation of the new pair Na + Vr (mean = 2.6, R = 1-4, n = 21 songs in 8 days). Again, the difference is statistically significant (Mann-Whitney U-test, $p < 0.05$).

In a pair of white-handed gibbons (*Hylobates lar*), living in a cage immediately adjacent to that of the family group, no increase in the frequency of song bouts per day could be detected. They produced an average of 1.9 song bouts before (R = 0-4, n = 15 songs in 8 days), and of 1.7 song bouts after the arrival of Na (R = 0-5, n = 12 songs in 7 days).

After the exchange of the male Bh in Zürich (Bh+Ch –> Bh+Ga), a similar increase of song bouts per day could be observed at least as a trend (see Fig. 3). Bh used to sing on average 2.0 times per day (R = 1-3) in each of the months June (n = 3 days), July (n = 3 days) and the first half of August (n = 2 days). After the partner exchange, his song bout frequency rose immediately to 4.0 times per day (second half of August, n = 2 days), only to drop again to 2.3 in September (n = 3 days). This sample is however too small to allow a conclusive statement.

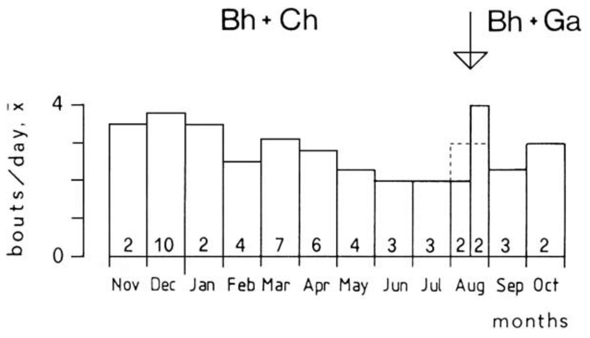

Fig. 3. Number of song bouts per day of the male Bh in Zürich from December 1980 to October 1981. The figure at the bottom of each column indicates the number of analysed days. The arrow shows the time of the partner exchange Bh + Ch –> Bh + Ga. The data for August are plotted in two separate columns representing two days before and two days after the partner exchange, respectively. In addition, the hatched column shows the number of bouts per day for the whole month and contains four analysed days.

On two consecutive days (2 and 3 September 1981), one and a half month after the arrival of Na in Studen, an average of only 1.5 song bouts per day was produced by the two pairs Na + Vr and Bb + Ra, and of 1.0 song bout per day by the family group Ko + Cr.

Nevertheless, the number of song bouts per day does not say anything about how much time is actually spent singing. The observed increase in song bouts after a pair formation might have been compensated by shortening the duration of song bouts.

The songs of the pair Bb + Ra and the female Vr, *before* the arrival of Na, had an average duration of 21.0 min (R = 9-30 min, n = 14), and *thereafter* of 17.5 min (R = 10.5-25 min, n = 32). The song bouts after the formation of the new pair lasted on average 3.5 min less long, but in fact, this difference cannot be statistically confirmed (Mann-Whitney U-test, $p > 0.l$).

In contrast to this, the total time these animals spent singing averaged at 36.7 min per day (n = 14 songs in 8 days) before the arrival of Na, and 69.9 min after this event (n = 32 songs in 8 days). The daily time investment in singing activity rose by a factor of 1.9 after the new pair had been united; it thus amounted to nearly twice as much as before. This difference is statistically significant (Mann-Whitney U-test, $p < 0.05$). It can be asserted ($p = 0.05$), even if two additional songs are included in the comparison which I had artificially triggered in the week before the arrival of Na by playback of tape-recorded song excerpts.

A comparison of the distribution of the song bouts over the day reveals an augmentation of the period of time used for singing activity after the formation of the new pair (Fig. 4). This extension mainly arose by including the late afternoon hours from 15.30 h to 18.00 h into the period of singing activity. In contrast to it, the early morning hours pre

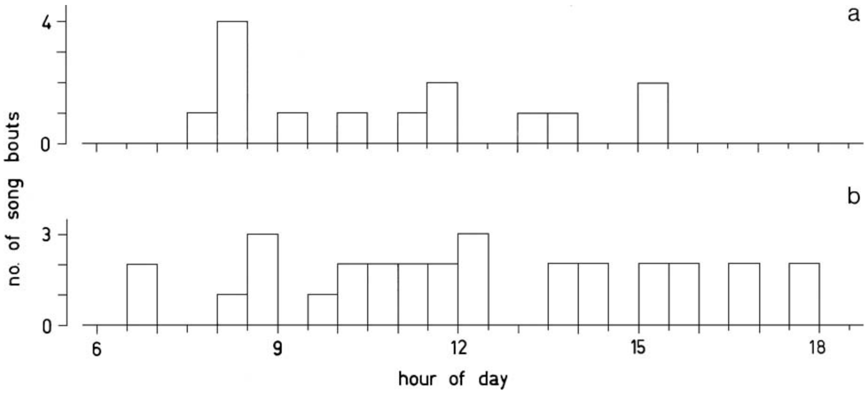

Fig. 4. Number of all song bouts and their distribution (starting time) over the daily activity period of the pair Bb + Ra and the female Vr (later pair Na+Vr) in Studen: a. during the eight days immediately before the arrival of Na (n = 14 song bouts) and b. during the eight days immediately thereafter (n = 32 song bouts).

ceding the usual peak of singing activity – that means, the hours before 08.00 h – are hardly used for additional songs.

## Discussion

After a partner exchange, an increase in the number of call bouts per day was observed in Studen and – at least as a trend – after a second exchange in Zürich as well. On the other hand, the average song duration in Studen diminished only slightly, so that in fact an increase in the singing time resulted. The slightly shorter average duration of the song bouts after the partner exchange is probably due to the fact that songs tended to be shorter, the more songs preceded them on the same day ($r_s = -0.585$, $p < 0.001$) and the later they start during the day ($r_s = -0.695$, $p < 0.001$, $n = 46$ songs in 16 days). If, therefore, more song bouts are uttered per day after the partner exchange, the percentage of song bouts with a preceding song will automatically increase. Consequently, the average duration of song bouts can he expected to decrease.

This does not, however, imply that the siamang, after a new pair formation, tended to shorten their song bouts, but merely, that they would insert then the additionally uttered song bouts into that part of their activity period, during which no songs had occurred previously. As the song bouts prior to the partner exchange already occupied the beginning of the activity period, a supplementary singing activity was bound to be inserted almost entirely into the later parts of the activity period. In fact, by increasing the number of songs per day, the singing activity was mainly extended to the later hours of the day, whereas a preponement of singing activity occurred at best to a very small degree (Fig. 4).

Several factors may possibly influence the *duration* of the time span of increased singing, and it may vary with individual pairs. No attempt was made in this study to determine that duration. At the end of the observation period, the song bout level per day seems still somewhat increased in pair Na + Vr (see Fig. 2a). It seems, however, that by one and a half month after the partner exchange in Studen the number of song bouts per day had dropped again to the lower level of the days before the exchange.

One could argue that in Studen the increase of singing activity after the arrival of Na might be attributed to an individual trait of this arriving male, which is, that Na had been a very active singer already before his transfer to Studen. He might then have elicited the songs of the resident siamang groups in Studen by his own songs. Song bouts of siamang (and other gibbons) can be provoked by playback or by mimicking their phrases (CHIVERS & MACKINNON, 1977; FOX, 1972; HARAWAY et al., 1981; HESS-HAESER, 1971; LA MALFA, 1969; MILLER, 1971; and pers. observ.), and MCCLURE (1964) observed that wild siamang would sing more frequently when more family groups were present in the area.

But this argument cannot or not completely explain the observations presented here. The average song bout frequency of Na in Zürich was 2.5 times per day during the months of February and March as well as during the months of April and May 1981 (n = 28 song bouts on 11 days, and n = 15 song bouts on 6 days, respectively). Moreover, all song bouts were started by Bh, his neighbour at that time; no song bout started by Na was observed in Zürich. Besides that, Bh's song bout frequency even dropped in the following months (2.0 times per day in June and July 1981, n = 12 songs in 6 days), and as a consequence Na's song bout frequency must also have been lower at that time immediately prior to his transfer to Studen. The increased song bout frequency of the new pair Na + Vr in Studen after the arrival of Na (mean = 4.0 songs per day) cannot be explained by the individual singing tendency of the new male; it seems rather to have arisen as a direct consequence of either the partner exchange itself or the male's transfer to a new place (but see below). On the other hand, the increased singing activity of the two neighbouring groups (Bb + Ra and Ko + Cr) may indeed have been stimulated by the increased singing activity of Na + Vr and/or the mere presence of this newly formed pair.

HESS-HAESER (1971:13) reported that an already established pair of siamang sang more frequently immediately after its transfer to another zoo than some time after its arrival. In an unfamiliar environment, the animals are exposed to a set of new stimuli which might in themselves activate duetting. In addition, one might assume that more vocal advertisement is necessary in a new territory than in an already established one. The same circumstances may also have affected the singing activity of Na after his transfer from Zürich to Studen. In the second partner exchange in Zürich, however, none of the new mates was in an unfamiliar place, and no new other siamang was present at the zoo. If the increase of singing activity following this partner exchange was real, as could be suggested from Fig. 3, it can be inferred that the cause for the increased singing activity in Zürich, and probably in Studen as well, has at least partially to be considered as a direct consequence of the confrontation of new partners.

The increased singing activity after the formation of a new pair can best be interpreted as a result of a selective pressure favouring a shortening of the period during which one or both pair partners have to learn to duet with each other.

Nevertheless, the high degree of complexity exhibited by the siamang duet song (see above) cannot easily be explained as being adaptive by any of the biological functions of duetting suggested so far (i.e. functions which could not be fulfilled by solo singing or by simpler duet patterns as well), except one:

The hypothesis that duetting might act as a reinforcement of the pair bond has led to a promising explanatory model. DAWKINS (1976) and MAYNARD SMITH (1977) argued that an individual could prevent its partner from deserting by demanding a certain amount of investment from every new sexual partner prior to mating. If, as suggested by WICKLER (1980), duetting has to be learned at the beginning of pair-formation, the probability of a partner change is reduced as every individual would have to invest anew with every new partner. But in this case, at least the demanding partner should not tend to shorten the period of time investment. If the siamang duet song acts both as a pair bonding device and as advertisement of the presence and the status of a mated pair, then the amount of time investment in duet learning would be under divergent evolutionary constraints.

This paper presents evidence supporting the latter of the two functions here considered. On the other hand, the premises underlying the pair bonding hypothesis were outlined by WICKLER (1980). It still remains, however, to be directly demonstrated if these premises are actually fulfilled. This could be done by comparing the duet structure of newly formed and established pairs. Such an analysis is currently being carried out by the author.

**Summary**

Siamang gibbons produce long and complex duet songs. The hypothesis that duetting may act as advertisement of the presence and the status of a mated pair has repeatedly been suggested for duetting birds. If a pair bonding effect of the duet is actually attained through a partner-directed learning effort resulting in a pair-specific duet, the learning investment should be concentrated into a time period as short as possible in order to avoid competitors. Therefore, after the formation of a new pair, an increase of singing activity should be expected. In order to test this prediction, the singing activity of a pair of captive siamang before and after a partner exchange was compared. In the newly formed pair, an increase in singing activity was observed. Additional observations on a second new pair show a similar trend. In this case, both new mates remained in their familiar place so that their singing activity was unlikely to he affected by the process of establishing a new territory.

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## Zusammenfassung

Siamangs *(Hylobates syndaclylus)* äussern lange und komplexe Duett-Gesänge. Es wurde schon mehrfach die Hypothese vorgeschlagen, dass bei duettierenden Vögeln die Präsenz oder der Grad einer Paarhindung durch das Duett angezeigt würde. Wenn neu gebildete Paare tatsächlich lernen müssen, in paar-spezifischer Weise miteinander zu duettieren, dann sollten sie diese Lerninvestition auf eine möglichst kurze Zeitperiode konzentrieren, um keine Konkurrenten mit einem unperfekten Duett anzulocken. Dann aber sollte man nach der Bildung eines neuen Paares einen Anstieg der Gesangsaktivität erwarten. Um diese Voraussage zu testen, wurde die Gesangsaktivität eines Siamangpaares in Gefangenschaft vor und nach einem künstlich herbeigeführten Partneraustausch verglichen. Das neugebildete Paar zeigte tatsächlich einen Anstieg seiner Gesangsaktivität. Zusätzliche Beobachtungen an einem zweiten neuen Paar zeigten einen ähnlichen Trend. In diesem Fall verblieben beide neuen Partner an ihrem vertrauten Ort, so dass ihre erhöhte Gesangsaktivität nicht darauf zurückzuführen sein kann, dass ein neues Territorium hätte etabliert werden müssen.