DUET SONGS OF THE SIAMANG, HYLOBATES SYNDACTYLUS: II. TESTING THE PAIR-BONDING HYPOTHESIS DURING A PARTNER EXCHANGE

by

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Summary

It has repeatedly been suggested for several duetting bird and primate species that duetting might act as a reinforcement of the pair bond. Until now, it has apparently not been demonstrated that the premises underlying the pair-bonding hypothesis are met by any duetting species. Siamangs (*Hylobates syndactylus*) are monogamous apes which produce long and complex duet songs. This study analyses the changes in duet structure in two pairs of siamangs during a forced partner exchange. The duet songs of the siamangs underwent many notable changes during partner exchange. Of 33 different variants of the great call sequence, 29% in one pair and 21% in the other were restricted to the first stage just after the partner exchange. Some of these changes were certainly due to individualistic traits of the new partner, and for some other changes, this possibility cannot be reliably excluded. At least two

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changes, however, can only be interpreted in terms of a learning effort by which one partner adapts its duetting behaviour to that of its new mate. The two newly formed pairs of this report appear to be the first documented cases to fulfil the requirements underlying Wickler's (1980) pair-bonding hypothesis: The animals under study were showing a stable song pattern with pair-specific traits. After the partner exchange, new pair-specific traits occurred, some of them obviously achieved through a partner-directed effort of one or both individual(s). Moreover, the pair-bonding hypothesis appears to be one of the few biological functions suggested so far which could explain a high degree of duet-complexity as adaptive. However, the loudness of the siamang song alone suggests that other functions are also involved. These are most probably related to territorial advertisement, pair bond advertisement and (possibly) mate attraction.

Keywords: Duet, song, siamang, *Hylobates syndactylus*, pair bond, gibbons.

1. Introduction

A number of animals are known to produce elaborate duet songs, most notably several species of monogamous birds and primates (*e.g.* Thorpe, 1972; Farabaugh, 1982; Haimoff, 1986; Geissmann, in press a). The functions most frequently suggested for duet songs include territorial advertisement and strengthening of pair bonds (Chivers, 1976; Farabaugh, 1982; Brockelman & Srikosamatara, 1984; Mitani, 1985). The latter function in particular is a matter of debate and "has not yet been demonstrated in any animal species that sings" (Haimoff, 1983, p. iv). According to Brockelman (1984, p. 286), "this function of duetting is poorly understood, for it is not clear how exactly duets would do this, or what kind of evidence would support the idea. In short, there is no explicit paradigm for analysing such communicative behaviour".

Wickler (1980) first suggested a plausible mechanism by which duet songs could have an effect on the cohesiveness of the pair bond: If duetting has to be learned at the beginning of each pair formation, this would reduce the probability of partner desertion, since learning investment would have to be provided anew with every new partner. In order to support Wickler's (1980) pair-bonding hypothesis, the following three conditions must be met: (1) Duet amelioration after pair formation has to be a necessary precondition to copulation. (2) Duets have to be pair-specific. (3) Pair-specificity must be based on a mate-specific duetting-relationship of at least one mate. It has apparently never been documented previously that these three conditions are met by a duetting species. In particular, the third condition has remained undocumented in previous studies.

The hypothetical fuction 'strengthening of the pair bond' resembles the function 'advertisement of the pair bond' (Geissmann, 1986; Cowlishaw, 1992). Both produce the prediction that newly mated pairs should learn to coordinate their duets prior to reproduction. Only the former hypothesis, however, predicts that duets should be pair-specific and that pair-specificity should result from a partner-directed learning effort. The strength of the pair bond, on the other hand, may be advertised without pair-specificity and, if pair-specificity occurs, it may simply reflect individual-specific characteristics.

Gibbons (Hylobatidae) are small apes living in East-Asian tropical rain forests. They exhibit a monogamous social structure and exclusive use of actively defended territories by small family groups (*e.g.* Chivers, 1984; Leighton, 1987).

All gibbon species produce long and loud song bouts which are typically produced in the early morning. In most species, mates combine their repertoire in relatively rigid, precisely timed and complex vocal interactions to produce well patterned duet songs (*e.g.* Marshall & Marshall, 1976; Haimoff, 1983, 1984; Geissmann, 1993, 1995).

Compared with duets of other gibbon species, siamang (*Hylobates syndactylus*) duets exhibit a particularly complex vocal structure (*e.g.* Lamprecht, 1970; Haimoff, 1981, 1983; Geissmann, in press b). This complexity is manifest in the richness of the partly sex-specific repertoire, in the complicated rules which regulate how notes are combined to exactly timed phrases, and these, on their own, to longer sequences, in the number of points during which mates vocally interact in each great call sequence, and in the strict rules which regulate the sequence of, and the intervals between, these vocal interactions. According to Marshall & Sugardjito (1986, p. 155) "the [siamang] duet is probably the most complicated opus sung by a land vertebrate other than man".

A recent study concluded that duetting in gibbons is unrelated to pairbonding (Cowlishaw, 1992), because the Kloss gibbon (*H. klossii*) does not produce duets but apparently shows strong pair bonds like the duetting siamang (*H. syndactylus*). I doubt, however, that the function of duetting can be tested by comparing duetting activity between duetting and non-duetting species.

Interspecific comparisons can support arguments about ultimate causation by inference but cannot disprove them (Jarman, cited in Waser, 1985).

It has previously been reported that newly mated siamang pairs seemed to practise duetting (Haimoff, 1981; Geissmann, 1986; Palombit, 1992, p. 319, 1994). Song development was described in more detail only in one newly formed pair of siamangs (Maples *et al.*, 1989). These authors were able to demonstrate that the new pair initially produced a considerable amount of incomplete or atypical great call sequences; only after a few weeks did the pair mainly produce typical duets. It was not shown, however, whether the two animals have had any duetting experience prior to this pair formation. Therefore, the changes in duetting behaviour described by Maples *et al.* (1989) in a newly formed pair could possibly be explained as ontogenetic development of duetting behaviour, or they could occur only once when siamangs mate for the first time, but be absent in subsequent pair formations.

The third requirement of Wickler's (1980) pair-bonding hypothesis — *i.e.* a mate-specific duet-relationship — has not been demonstrated in any of the studies mentioned above. The duet song of siamangs exhibits pair-specific characteristics (Lamprecht, 1970; West, 1982; Maples *et al.*, 1989). Pair-specificity could, however, develop in two ways: (1) it could simply be the sum of individual characteristics of the mates, or (2) it could result from a mate-directed adaptation and learning effort of at least one pair partner and thus represent a mate-specific duet-relationship.

The comparison of pair-specific song characteristics of one siamang with different partners should make it possible to test the two alternative interpretations. The aims of the present study are twofold: 1. The duet songs of two captive pairs of siamangs during a forced partner exchange are analysed. Quantitative and qualitative changes in the structure and organisation of the duet songs in different stages of pair formation are documented. 2. These changes are assessed as to whether any of them can be regarded as evidence for a partner-directed learning effort and whether siamang duet songs meet the requirements of the pair-bonding hypothesis.

2. Animals, materials and methods

2.1. Animals, housing and changes in group composition

The study animals were kept in two zoos in Switzerland: the Zoological Garden of Zürich (2 groups) and the 'Zoo Seeteufel' in Studen near Biel (3 groups). These zoos will hereafter be

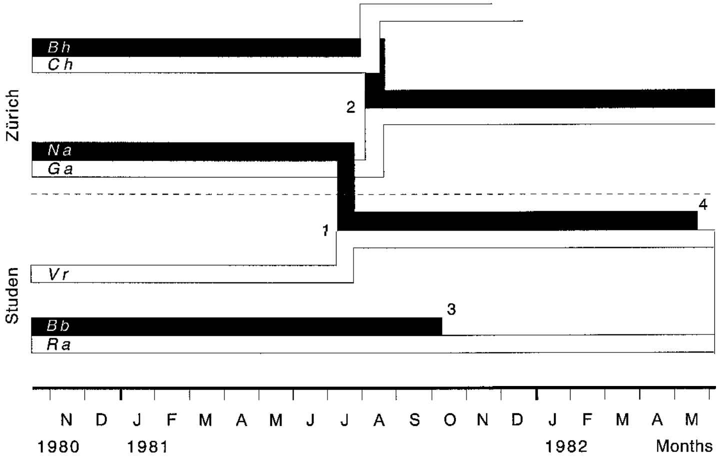

Fig. 1. Changes in group composition. Schematic presentation of the temporal process during this study. (1) = new pair formation *Na+Vr*, 14 July 1981; (2) = new pair formation *Bh+Ch*, 12 Aug. 1981; (3) = death of *Bb*, 8 Oct. 1981; (4) = death of *Na*, 19 May 1982.

referred to as Zürich and Studen, respectively. During the study, one male siamang (*Na*) was transferred from Zürich to Studen, and a further male (*Bh*) was switched from one female to another one at the Zürich Zoo. This resulted in the formation of two new pairs, one in Studen (*Na+Vr*) and one in Zürich (*Bh+Ga*).

A schematic presentation of the changes in group composition occurring during the study is shown in Fig. 1. The rearrangement of the siamang pairs was mainly caused in order to avoid inbreeding in the pair of siblings *Bh+Ch* in Zürich and to find a suitable mate for the adult solitary female *Vr* in Studen.

The age classes proposed by Geissmann (1993) for captive gibbons and siamangs were used: infants from 0 to 2 years of age; juveniles 2.1 to 4 years; subadults 4.1 to 6 years; adults more than 6 years.

At the beginning of this study, the two siamang groups at Zürich Zoo consisted of the pairs *Na+Ga* and *Bh+Ch*. The adult pair *Na+Ga* at the Zürich Zoo consisted of the male ***Narong*** (*Na*), wild-born about in 1967, several offspring, and the female ***Gaspa*** (*Ga*), wild-born about in 1963, no previous offspring. The pair was together since July 1980. *Na+Ga* were regularly seen copulating.

The younger pair *Bh+Ch* at the Zürich Zoo consisted of the subadult male ***Bohorok*** (*Bh*) and his juvenile sister ***Chandra*** (*Ch*), both captive-born offspring of *Na+Ra*, and both hand-reared at Zürich Zoo (their mother *Ra* was previously kept at the Zürich Zoo but was living in Studen during the present study, see below). *Bh* was 5 years and 5 months old at the beginning of this study, but his first song bouts recorded on tape (Nov. 1980), could not be distinguished from those of adult siamang males. His sister *Ch* was a 3 year 11 months old juvenile at the beginning of this study. Her song repertoire and the temporal structure of her song vocalisations were not yet fully developed. No copulations were observed in this pair.

In Zürich, the siamangs were kept in two adjacent indoor-cages (base area: 16 m^2 and 40 m^2, height: 4 m). In summer, both siamang groups were alternatively given access to a large outdoor cage (30 m^2 × 4.6 m). All cages were equipped with extensive bamboo scaffolding and ropes. The sleeping cages (2.4 m^2 × 2.5 m, and 4.8 m^2 × 1.6 m) were situated directly below the indoor cages. Both groups could hear (but not see) each other at any time.

On 14 July 1981 *Na* was transferred to Studen Zoo. In Zürich, his former partner *Ga* remained solitary until she was paired with *Bh* on 12 Aug. 1981.

In Studen, the original constellation consisted of one adult solitary female ***Vreneli*** (*Vr*), one pair (*Bb*+*Ra*) and one family group (*Ko*+*Cr*(+*Li*+*Al*)). *Vr* was wild-born about in 1963 and remained solitary after her offspring and her mate both died in 1979. On 14 July 1981, the adult male *Na* arrived from Zürich and was kept as a pair with *Vr*.

During summer, all three groups in Studen were kept in outdoor-cages (25 m^2 × 2.5 m) equipped with several horizontal metal bars, ropes, and a wooden sleeping box. Two of the cages stood close together at a sharp angle. The third cage (of the family group) was located in a distance of more than 10 m. The sight from cage 3 to the other two cages was somewhat reduced by shrubs and trees. During winter, the siamangs were housed in a separate building. Two of the winter cages (18 m^2 × 2 m, and 14 m^2 × 2 m, respectively) stood about 3.5 m apart; these two groups could see each other. The winter cage of the family group (6 m^2 × 3 m) could not be seen by the other two groups. As in Zürich, all groups could hear each other during the whole year.

2.2. *Materials and methods*

The tape-recorded song bouts are listed in Table 1. The song bouts from the stage before the partner exchange (B) were collected between 13 Nov. 1980 and 23 May 1981. *Na* was introduced to a new partner on 14 July 1981, and *Ga* was introduced to a new partner on 12 Aug. 1981. The song bouts after the exchanges (A) were collected between 15 July 1981

TABLE 1. *Song bouts analysed in order to study the occurrence of variants of the great call sequence in various stages of a partner exchange and pair formation*

Pair	Partner exchange stage[1]	Time period	Number of days since partner exchange[2]	Number of song bouts analysed
Na+*Ga*	B	13 Dec. 1980-23 May 1981		7
Na+*Vr*	A1	15 July 1981-21 July 1981	1-7	19
Na+*Vr*	A2	03 Sept. 1981-04 Sept. 1981	51-52	3
Na+*Vr*	A3	21 Nov. 1981-24 Nov. 1981	130-133	8
Bh+*Ga*	A1	12 Aug. 1981-02 Sept. 1981	0-21	9
Bh+*Ga*	A2	10 Sept. 1981-06 Oct. 1981	29-51	6
Bh+*Ga*	A3	28 Dec. 1981-01 April 1982	138-232	8

[1] B = stage before the partner exchange; A1-A3 = stages after the partner exchange.

[2] At the beginning and end of each stage (new pair formations: *Na*+*Vr* 14 July 1981; new *Bh*+*Ch* 12 Aug. 1981).

and 21 Nov. 1981 in Studen and between 12 Aug. 1981 and 1 April 1982 in Zürich. Both 'A'-samples were divided into three blocks of a duration of several days each (A1, A2 and A3), each covering a different period of time.

Tape-recordings were made with a UHER 4200 Report Stereo S and a UHER 4200 Report Stereo IC reel tape recorder (with tape speed set at 9.5 cm/s), equipped with a AKG directional microphone. Sonagrams were generated with Canary 1.2.4 software on an Apple personal computer (PowerMacintosh 7600/120). Recording parameters: 11 kHz sampling rate, 16 bit sampling. Analysis parameters: FFT, Hamming analysis window; analysis resolution: 43.7 Hz filter bandwidth, 1024 points frame length; grid resolution: 23.1 ms time, 75% overlap, 5.4 Hz frequency, 2048 points FFT size.

Non-parametric statistical tests were adapted from Siegel (1956). All tests are two-tailed, with a significance level of 0.05.

2.3. *Description of the siamang song*

The acoustic terms and definitions used in this paper, as well as the note repertoire and the sequential structure of siamang song bouts are described in detail in Geissmann (in press b) and will only be summarised here briefly. Four distinct classes of vocalisations have been described: booms, barks, ululating screams, and bitonal screams. Various types of booms and barks may be recognised. The ranges of the fundamental frequency and of the duration of each note class and type are listed in Table 2.

In the song bouts of adult siamangs, all types of vocalisations may be uttered by either sex, with the following exceptions: Long barks are typically produced by females only, bitonal screams by males only. Ascending booms and ululating screams are produced by males and also by some, but not all, females. In most males, two variants of ululating screams (US-I and US-II) may be separated based on their sonagraphical structure.

The composition of a typical siamang song bout is organised according to relatively strict rules. At the highest level of subdivision, the song bout consists of 4 different types of sequences (Geissmann, in press b) which follow each other as shown in Fig. 2. Two of these, the grunting sequence and the introductory sequence, occur only once at the beginning of a song bout. Afterwards, the song bout consists of two sequences which are repeated in alternation until the end of the song bout: the interlude sequence and the great call sequence. The present study is focused on the great call sequence, because it makes up the main part of the siamang song bout and because its organisation is more stable.

The great call sequence of siamang pairs is a complex, ordered chain of interactions between the mates. Its typical organisation is shown in Fig. 3. The sequence has a duration of

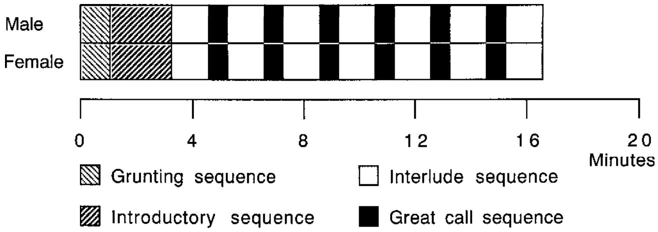

Fig. 2. Stylised diagram illustrating the sequential nature of the duet song bout produced by adult siamang pairs (after Haimoff, 1984; Geissmann, in press b).

TABLE 2. *Duration and frequency measures for note classes and types used in siamang song bouts (after Geissmann, in press b)*

Class Type	Adult song repertoire[1]	*N*[2]	Duration (s)		Fundamental frequency (kHz)					
					Minimum		Maximum		Modulation range	
			Median	Range	Median	Range	Median	Range	Median	Range
Booms										
Grunts	m, f	14	0.15	0.10-0.19	0.167	0.127-0.216	0.282	0.231-0.317	0.109	0.047-0.190
Short booms	m, f	26	0.18	0.05-0.31	0.286	0.215-0.346	0.369	0.304-0.410	0.079	0.060-0.132
Long booms	m, f	12	0.50	0.28-0.69	0.225	0.203-0.270	0.314	0.279-0.491	0.084	0.053-0.222
Ascending booms	m, (f)	14	0.55	0.46-0.89	0.224	0.194-0.239	0.335	0.276-0.377	0.111	0.064-0.153
Barks										
Short fast barks (SFB)	m, f	14	0.14	0.11-0.15	0.375	0.333-0.463	0.808	0.742-0.869	0.405	0.361-0.488
Short slow barks (SSB)	m, f	19	0.13	0.10-0.16	0.385	0.311-0.438	0.720	0.670-0.831	0.346	0.289-0.467
Long barks (LB)	f	12	0.25	0.17-0.33	0.573	0.493-1.135	0.798	0.691-1.472	0.214	0.120-0.371
Ululating scream (US)										
US I	m	12	0.61	0.38-0.72	0.648	0.508-0.808	0.913	0.773-0.978	0.221	0.113-0.470
US II	m, (f)	14	0.74	0.32-1.25	0.642	0.340-0.816	0.878	0.807-0.956	0.226	0.093-0.500
Bitonal scream (BS)										
BS, first phase	m	13	1.05	0.67-1.40	0.463	0.357-0.486	0.598	0.486-0.824	0.128	0.076-0.349
BS, second phase	m	13	0.48	0.30-0.68	0.477	0.415-0.780	0.892	0.766-1.008	0.377	0.120-0.510

1) Abbreviations: m = male, f = female, (f) = produced by some females only.

2) *N* = number of calls = number of individuals (*i.e.* one call was analysed per individual), except for ‘grunts’: 14 grunts of 11 individuals, and ‘short booms all’: 26 calls of 15 individuals.

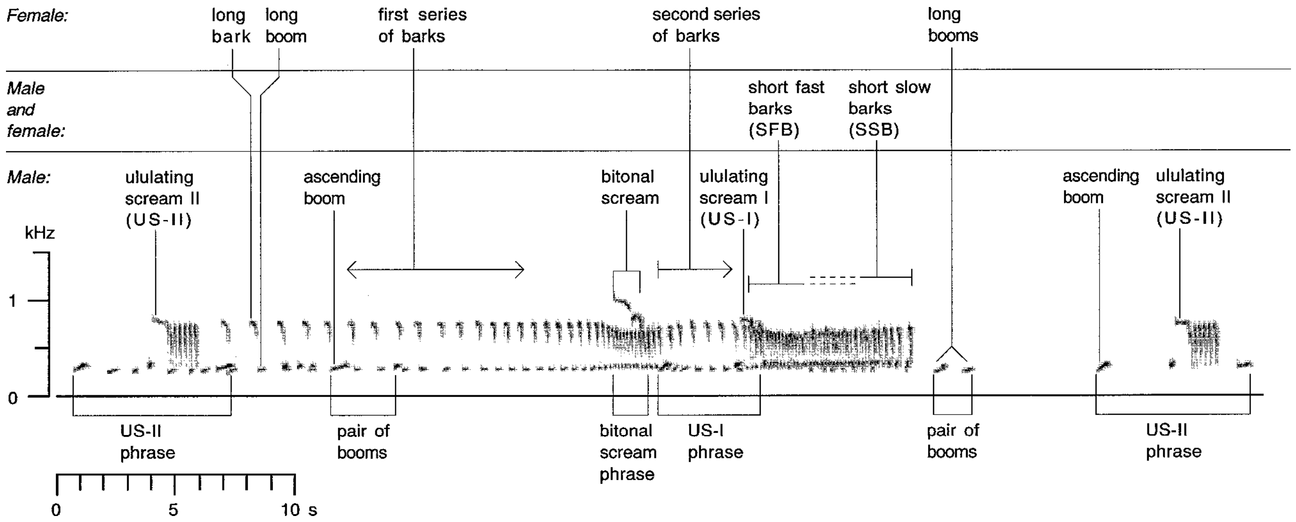

Fig. 3. Organisation of a typical great call sequence of pair *Na*+*Ga*. Selected notes or groups of notes are individually indicated.

about 20-50 s and includes two series of accelerated barks produced by the female, each beginning with long barks. Together, the two series are the female's 'great call' phrase. At certain points in each great call sequence, the male inserts particular combinations of vocalisations. The first long barks of the female usually coincide with an initial ululating scream (US-II) by the male. Particularly conspicuous is the male's bitonal scream, uttered at the climax of the female's first series of barks, and his ululating scream (US-I) uttered at the climax of the second series. This is followed by a burst of short fast barks (SFB phrase) uttered together by both mates while they exhibit a fast, vigorous brachiation display. The great call sequence usually ends with a further ululating scream phrase (US-II) by the male. Variations of the typical pattern occur mainly at the beginning of a song bout, but once the great call sequence is fully developed, it remains essentially constant until the end of the song bout.

The classification of siamang vocalisations used here follows Geissmann (in press b) and differs from the earlier classification of Haimoff (1981) in several respects; only the major changes are summarised here. Geissmann (in press b) described the grunting sequence (not recognised by Haimoff, 1981) and changed the name of the organising sequence to interlude sequence in order to avoid implying a particular function and in analogy to the sequence terminology used for songs of *Hylobates lar* by Raemakers *et al.* (1984). The ululating screams (US-II) at the beginning and at the end of the great call sequence were regarded as part of the interlude sequence by Haimoff (1981). Because of the consistency of their occurrence and because of their stable time interval to the other parts of the great call sequence they were counted to the more stereotyped great call sequence rather than to the more variably organised interlude squence (Geissmann, in press b).

Because the great call sequence reaches its typical form only after a certain developmental phase of the song bout (see above), only those sequences which were produced *after* the initial build-up part of a song bout were analysed. In established siamang pairs, the great call sequence usually reached its stabilised, typical form once the male had produced its first bitonal scream. All great call sequences produced *before* the male's first bitonal scream were, therefore, excluded from this analysis.

2.4. *Variants of the great call sequence*

In order to describe the variability of great call sequences, 33 variants were defined (Table 3), including the typical form of the great call sequence (T, described above), and different deviations of this sequence (V1-V32). Only the most conspicuous variants were included in the analysis; their number could easily be enlarged. If a particular great call sequence deviated from the typical form in more than one criterion, it was counted as one occurrence of each of the respective variants. In addition to the 33 variants, three quantitative song parameters (as defined in Table 3) were also included in the analysis.

A '*series of barks*' is defined here as a series of more than 7 long barks uttered by the female in rhythmical or accelerated sequence. A female's '*reaction*' to a male vocalisation is defined as an acceleration, a slowing down or a restart of an ongoing series of barks.

The absolute number of each variant was determined for each song bout. The relative frequency of each variant was calculated by dividing the absolute number of each variant by the number of attempted great calls (song parameter N). The ratio of the absolute frequency of a variant (V_i) and the number of great call sequences which did not correspond to this variant ('not-V_i' = N minus V_i) were also determined and statistically compared among

TABLE 3. *Descriptions of variants of the great call sequence (a) and song parameters (b)*1)

a.	Variants of the great call sequence:
V1	The female sings only one series of LB before the male's BS. This is always the case in typical great call sequences.
V2	The female sings two series of LB before the male's BS.
V3	The female sings three series of LB before the male's BS.
V4	The female sings short barks only (SSB or SFB) until the male's SFB phrase.
V5	The female does not sing at all during the male's great call sequence.
V6	The female does not begin a new series of LB after the male's BS, but, instead, produces SFB only, with or without subsequent SSB.
V7	The female does not begin a new series of LB after the male's BS, but, instead, produces only 1-3 SSB, and then, after a short interval, some more SSB, together with the male's SFB phrase.
V8	The female does not begin a new series of LB after the male's BS, but, instead, produces only a series of SSB, without a short interval before the male's SFB phrase.
V9	The male begins his great call sequence before that of the female, *i.e.* he produces a BS before she begins to produce a first series of LB.
V10	The male inserts his BS too early in the female's series of LB, *i.e.* after less than 12 LB and/or before she begins the acceleration of her LB.
V11	The male inserts a US-II during the female's series of LB, whereupon she shows a 'reaction' (the meaning of 'reaction' in this context: see text).
V12	The male inserts SSB during the female's series of LB, whereupon she shows an immediate 'reaction'.
V13	The male inserts SFB (with or without subsequent SSB) during the female's series of LB, whereupon she shows an immediate 'reaction'.
V14	The female sings a great call sequence (one or several continuous series of LB) without a great call sequence of the male; the male does, however, insert one or several atypical contributions (US-II, SFB, SSB).
V15	The female sings a great call sequence (one or several continuous series of LB) without a contribution (US-II, SFB, SSB) by the male.
V16	The female aborts a series of LB (and, hence, a great call sequence) after the insertion of a US-II by the male.
V17	The female aborts a series of LB (and, hence, a great call sequence) after the insertion of SFB (with or without subsequent SSB) by the male.
V18	The female aborts a series of LB (and, hence, a great call sequence) after the insertion of SSB by the male.
V19	The male omits the US-I during his great call sequence, *i.e.* after his BS he directly proceeds to SFB.
V20	The male omits the SFB phrase during his great call sequence, *i.e.* after his US-I he directly proceeds to SSB or to the final US-II.
V21	The male omits the final US-II during his great call sequence.
V22	The male inserts SFB (with or without subsequent SSB) during a series of LB preceding the BS.

TABLE 3. *(Continued)*

a.	Variants of the great call sequence:
V23	The male inserts SSB during a series of LB preceding the BS.
V24	The male inserts a US-II during a series of LB preceding his BS, and the female responds by beginning a new series of LB (therefore, this US-II is not identical with the ‘initial’ US-II described in section 2.3).
V25	The male aborts a BS, *i.e.* the second phase of the scream is not produced.
V26	After the male’s typical US-I, the female begins one or several additional series of LB, or she continues the ongoing series of LB without acceleration at the time of the US-I. The male does not begin a new great call sequence after this, but he may abort it after his US-I or continue and terminate it more or less completely.
V27	After the male’s typical US-I, the female begins one or several additional series of LB, or she continues the ongoing series of LB without acceleration at the time of the US-I. The male responds by beginning a second great call sequence.
V28	‘Phase-shifted’ great call sequence: the male inserts his BS during the last (usually the second) series of LB of the female’s great call sequence (as a rule, the female sings in synchrony with the neighbouring group in these cases). The female does not begin an additional series of LB after the male’s BS. At the time the female begins the SFB-part of her great call sequence, the male still has to sing the rest of his great call sequence (US-I → SFB → SSB → US-II).
V29	Phase-shifted great call sequence: like V28, but the female does begin an additional series of LB after the male’s BS.
V30	The male aborts his great call sequence after producing his BS (or part of it), but the female does not. The male immediately begins a second great call sequence, which is phase-shifted with regard to that of the female (like V28).
V31	The male aborts his great call sequence after his BS (or part of it), but the female does not. The male immediately begins a second great call sequence, which is phase-shifted with regard to that of the female (like V28), and the female begins an additional series of LB after the male’s second BS.
V32	The male aborts his great call sequence after producing his BS (or part of it), the female begins a new series of LB, and both produce a complete great call sequence.
T	Typical great call sequence (see section 2.3). This is the most common form of the great call sequence in established pairs. In this analysis, the typical great call sequence is defined as a great call sequence which does not correspond to any of the atypical variants V2-V32 defined above. This does not imply that V1 is equivalent to T, but merely that V1 occurs in all typical great call sequences.
b.	Song parameters:
N	The number of great calls attempted by the female per song bout. Series of more than two LB were identified as an attempted great call and also counted. An uninterrupted row of several series of LB was counted only once.
V/N	The number of different variants (V2 to V32) used per attempted great call (N).
V/S	The number of different variants (V2 to V32) used per song bout.

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[1] Abbreviations: BS = bitonal scream; LB = long barks; SSB = short slow barks, more than two notes of this type in sequence; SFB = short fast barks, more than 3 notes of this type in sequence; US = ululating scream phrase, where US-I = variant I, US-II = variant II.

TABLE 4. *Definitions of 19 quantitative duet parameters*[1]

1	Duration of interval between the male's last ascending boom before the beginning of a series of LB and the female's first long bark.
2	Duration of interval between the female's first and sixth long bark in the first series of LB of a great call sequence.
3	Duration of interval between the female's first long bark and the male's next following long or ascending boom.
4	Duration of interval between the female's first long bark and the male's BS.
5	Duration of interval between the male's last long or ascending boom during the female's first series of LB and his BS.
6	Number of long and ascending booms of the male during the female's series of LB and before his BS.
7	Number of short barks of the male after his BS and before his US-I (*i.e.* number of short barks in the BS phrase).
8	Duration of interval between the male's BS and his US-I.
9	Duration of interval between the ascending boom of the male's US-I phrase and the US-I itself.
10	Duration of interval between the male's BS and his ascending boom before his US-I.
11	Number of short barks in the male's US-I phrase.
12	Duration of interval between the male's US-I and the beginning of his SFB phrase.
13	Duration of interval between the beginning of the male's SFB phrase and the female's next long or ascending boom.
14	Duration of interval between the beginning of the male's SFB phrase and his next ascending boom.
15	Duration of interval between the female's long or ascending boom after the SFB phrase and the male's ascending boom.
15a	Duration of interval between the male's ascending boom after the SFB phrase and the female's long or ascending boom. Very rare, because the female's boom usually precedes that of the male.
16	Duration of interval between the ascending boom of the male's US-II phrase and the US-II itself.
17	Number of short barks in the male's US-II phrase.
18	Duration of interval between the male's last US-II before the beginning of a great call sequence and the female's first long bark of the great call sequence.
19	Duration of the great call sequence, defined here as the duration of the interval between the female's first long and the male's final US-II.

[1] Abbreviations: BS = bitonal scream; LB = long barks; SFB = short fast barks; US = ululating scream phrase, where US-I = variant I, US-II = variant II.

various stages of each partner exchange. The chi-square test was used for the comparison of great call variants among stages; only if the expected values were below 5, the Fisher exact probability test was used. For the comparison of quantitative song parameters (N, V/N, V/S) the Mann-Whitney *U* test was used.

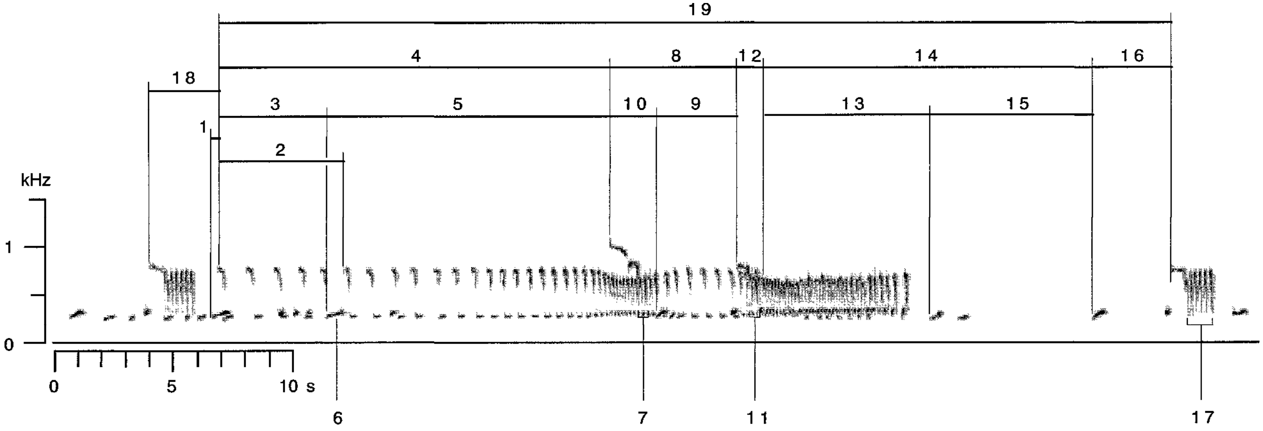

Fig. 4. Quantitative duet parameters: Parameters corresponding to note intervals are indicated above, those which count the number of notes in selected series of notes are indicated below the sonagram of a great call sequence of the pair *Na+Ga*.

2.5. *Quantitative duet parameters*

Only typical great call sequences (T, described above) were analysed in this part of the study. Nineteen quantitative duet parameters were defined in the great call sequence; these definitions are listed in Table 4 and illustrated in a sonagram of a typical great call sequence (Fig. 4). The parameters used in this part of the study included the duration of intervals between specific notes of the great call sequence (15 parameters) and the number of elements in particular series of notes (4 parameters). Time intervals between two notes were measured from the beginning of the first to the beginning of the second note. Time measurements were taken with a stop watch during play backs which were slowed down by a factor of 4. The values of the parameters in the great call sequences of pair *Na+Ga* were statistically compared with those of the pairs *Na+Vr* and *Bh+Ga*. The Mann-Whitney *U* test was used for these comparisons.

2.6. *Interference from neighbouring groups*

At the outset of this study, I had reason to assume that any vocal change in the newly mated pairs might possibly represent evidence for a partner-directed learning effort. Although several studies had described how mated siamangs coordinate their individual song contributions to form duet songs (see Introduction), it had neither been observed nor suspected that pairs may also coordinate their duets songs with those of neighbours in order to form 'supra-duets'. This unexpectedly happened during this study. In addition, the organisation of these supra-duets completely differed in the two study localities. As a result, song changes of a newly mated siamang could possibly occur as a result of an adaptation to the songs of the new mate or to those of the new neighbours. Because there is no way, yet, of predicting how the supra-duets will develop after a partner exchange, it is not possible to predict which variables are more likely of relevance for test of the pair-bonding hypothesis. As a result, the variables have to be examined in retrospect in order to determine whether the confouding effect (adaptation to the songs of neighbours) can be excluded. This assessment is presented in the Discussion.

3. Results

3.1. *General observations on the new pairs*

3.1.1. Pair *Na+Vr*

Immediately after his arrival in Studen (on 14 July 1981, at 19:15), the adult male *Na* was released in the outdoor-cage of the lone female *Vr*. The first copulation of the new pair was observed on 4 Sept. 1981 (*i.e.* 50 days after the arrival of the male *Na*); other copulations followed. Assuming a gestation length of 189-239 days (Geissmann, 1991), conception occurred between 5 Dec. 1981 and 24 Jan. 1982, *i.e.* about 5-6 months after the arrival of *Na*. The male died on 19 May 1982 from a chronic kidney disease. On 1 Aug. 1982, *Vr* gave birth to a healthy female infant which she raised alone.

3.1.2. Pair *Bh+Ga*

Hardly one month after the departure of *Na* from Zürich to Studen, another new pair was formed in Zürich. In the meantime, *Na*'s former partner, the female *Ga*, had been kept alone. During this time, she continued to produce song bouts, without a detectable change in the amount of singing. The animals *Bh* and *Ga* were put together on the morning of 12 Aug. 1981. On 26 Aug. 1981, *Ga* had a premature breech birth (sired by her previous partner *Na*). The female fetus had a body weight of only 152g, whereas the average birth weight of normal siamangs is 551.4 ± 87.5 g ($N = 18$, Geissmann & Orgeldinger, 1995). Assuming a gestation period of 189-239 days (Geissmann, 1991), conception must have occurred not earlier than 30 Dec. 1980, but probably about 1-3 months later. On 30 Sept. 1981 (*i.e.* 35 days after the premature birth and 49 days after the introduction of *Bh* and *Ga*), first copulations were observed in the new pair. Although additional copulations were observed later, the pair produced its first offspring on 21 Jan. 1985, *i.e.* almost 3.5 years after having been brought together.

3.2. Variants of the great call sequence

3.2.1. Partner exchange *Na+Ga* → *Na+Vr*

30 out of 33 recognised variants of the great call sequence occurred during the song bouts of the two pairs resulting from the exchange of the male *Na*. The variants V5, V9 and V12 were not recorded in these song bouts. Two (V1 and T) of the 30 variants which did occur are compatible with the description of typical great call sequences, the 28 other variants were atypical ones.

The relative frequencies of the variants in various stages of the partner exchange, as well as the results of the statistical comparison between the stages are listed in Table 5.

A comparison between songs before the partner exchange and those of the first week after the exchange (comparison B-A1) revealed statistically significant differences ($p = 0.034$) for 5 of the 28 variants classified as atypical great call sequences (*i.e.* variants V6, V7, V14, V17, V28). Of these, variants V6 and V28 increased in their frequency ($p = 0.034$). Eight variants (V6, V23, V24, V28, V29, V30, V31, V32) exclusively occurred during stage A1 and were not observed before or after that stage. Three other variants (V7, V16, V18) exclusively occurred before the partner exchange (stage B).

TABLE 5. *Relative frequencies of variants of the great call sequence (V1-V32, T) and of quantitative song parameters (N, V/N, V/S) in various stages of the partner exchange Na+Ga → Na+Vr, and a statistical comparison of frequencies among various stages of the partner exchange*

Variant	Partner exchange stage				Compared stages			
	B	A1	A2	A3	B-A1	A1-A2	A2-A3	B-A3
V1	0.41	0.45	0.63	0.83	–	–	–	< 0.001
V2	0.19	0.28	0.11	0.06	–	–	–	–
V3	0.12	0.05	–	0.06	–	–	–	–
V4	0.02	0.01	–	–	–	–	–	–
V5	–	–	–	–	–	–	–	–
V6	–	0.20	–	–	< 0.001	< 0.02	–	–
V7	0.05	–	–	–	0.034	–	–	–
V8	0.03	0.01	0.07	–	–	–	–	–
V9	–	–	–	–	–	–	–	–
V10	0.02	0.05	–	–	–	–	–	–
V11	–	0.03	0.11	–	–	–	–	–
V12	–	–	–	–	–	–	–	–
V13	0.02	0.02	–	–	–	–	–	–
V14	0.22	0.06	0.11	0.06	< 0.001	–	–	< 0.05
V15	0.08	0.07	0.19	–	–	–	0.023	–
V16	0.03	–	–	–	–	–	–	–
V17	0.15	0.04	–	0.08	< 0.01	–	–	–
V18	0.03	–	–	–	–	–	–	–
V19	0.10	0.05	0.11	0.08	–	–	–	–
V20	0.02	0.01	–	0.03	–	–	–	–
V21	0.02	0.02	0.07	0.22	–	–	–	< 0.01
V22	0.03	0.01	–	–	–	–	–	–
V23	–	0.01	–	–	–	–	–	–
V24	–	0.01	–	–	–	–	–	–
V25	0.02	0.08	0.11	0.08	–	–	–	–
V26	–	0.02	0.11	0.03	–	–	–	–
V27	–	0.01	–	0.06	–	–	–	–
V28	–	0.16	–	–	< 0.01	< 0.001	–	–
V29	–	0.04	–	–	–	–	–	–
V30	–	0.03	–	–	–	–	–	–
V31	–	0.01	–	–	–	–	–	–
V32	–	0.02	–	–	–	–	–	–
T	0.25	0.36	0.44	0.64	–	–	–	< 0.001

TABLE 5. *(Continued)*

Song parameter	Partner exchange stage				Compared stages			
	B	A1	A2	A3	B-A1	A1-A2	A2-A3	B-A3
N	8.43	8.84	9.00	4.50	–	–	–	< 0.01
V/N	0.78	0.80	0.48	0.64	–	–	–	< 0.01
V/S	6.71	6.89	5.17	5.00	–	–	–	< 0.01

The relative frequency of a variant is defined as its absolute frequency per number of attempted great calls (N). Variants and song parameters are defined in Table 3; the statistical tests are described in the text. Numbers in the last four columns indicate error probabilities (p); if no value is indicated, $p > 0.05$.

A comparison between the songs produced before the exchange with those produced 4 months afterwards (comparison B-A3) revealed significant changes in the frequency of 2 variants corresponding to atypical great call sequences: The frequency of variant V14 had decreased ($p < 0.05$), that of V21 had increased ($p < 0.01$). The two variants corresponding to typical great call sequences (V1, T) had also both increased significantly in their frequency ($p < 0.001$), whereas the three song parameters (N, V/N, V/S) had decreased significantly ($p < 0.01$).

Figure 5 shows the changes in the relative frequency of selected variants of the great call sequence. The examples in the figure demonstrate how differently the frequency of the variants behaved during the partner exchange: V1, V21 and T continuously increased after the exchange. The variants V2, V6 and V28 increased temporarily at the beginning of the exchange and decreased again thereafter, and the frequency of V14 decreased after the partner exchange.

3.2.2. Partner exchange *Na*+*Ga* → *Bh*+*Ga*

26 out of 33 variants of the great call sequence defined above occurred during the song bouts of the two pairs resulting from the exchange of the female *Ga*. The variants V26 through V32 were not recorded in these song bouts. Two (V1 and T) of the 26 variants which did occur are compatible with the description of typical great call sequences, the 24 other variants were atypical.

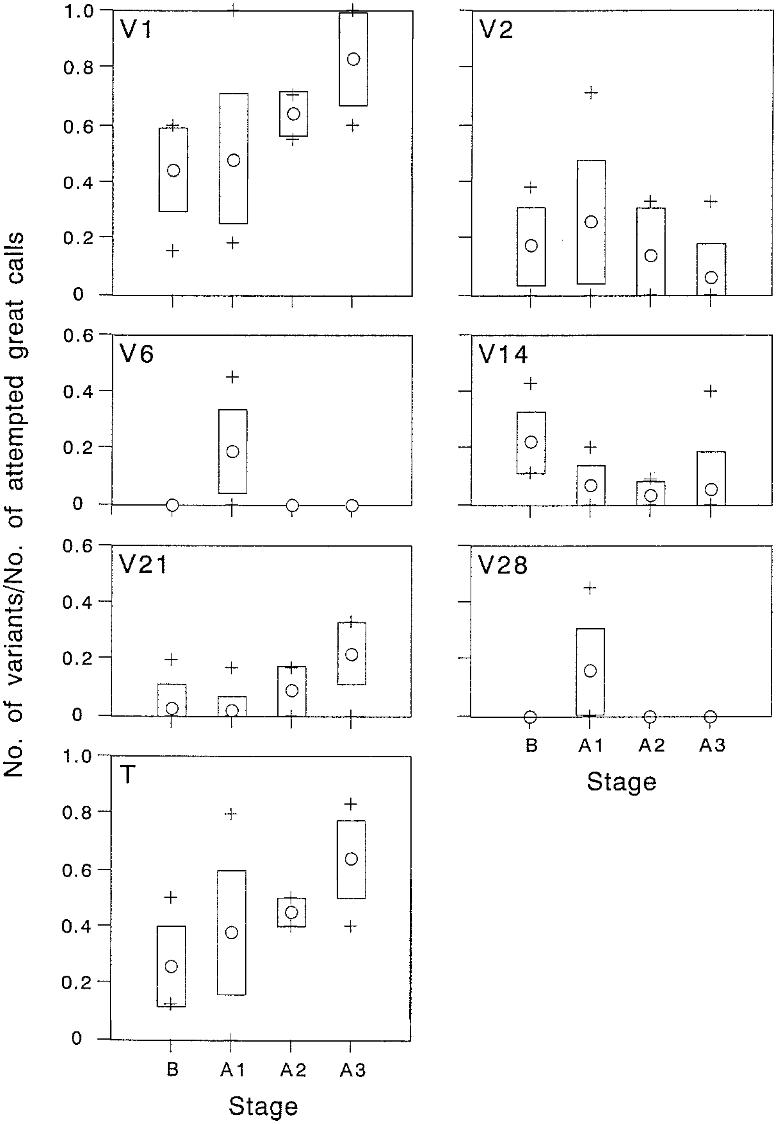

Fig. 5. Relative proportion of selected variants of the great call sequence during various stages of the partner exchange *Na+Ga* → *Na+Vr*. B = stage before the partner exchange; A1-A3 = stages after the partner exchange. Symbols: circles = mean values, boxes = standard deviations, crosses = mimimum and maximum values.

TABLE 6. *Relative frequencies of variants of the great call sequence (V1-V32, T) and of quantitative song parameters (N, V/N, V/S) in various stages of the partner exchange Na+Ga → Bh+Ga, and a statistical comparison of frequencies among various stages of the partner exchange*

Variant	Partner exchange stage				Compared stages			
	B	A1	A2	A3	B-A1	A1-A2	A2-A3	B-A3
V1	0.41	0.72	0.82	0.80	< 0.001	–	–	< 0.001
V2	0.19	0.11	0.05	0.12	–	–	–	–
V3	0.12	0.02	–	0.01	< 0.01	–	–	< 0.001
V4	0.02	0.01	–	–	–	–	–	–
V5	–	0.01	–	–	–	–	–	–
V6	–	0.01	–	–	–	–	–	–
V7	0.05	0.01	0.06	0.11	–	–	–	–
V8	0.03	0.07	–	0.02	–	0.011	–	–
V9	–	0.02	–	–	–	–	–	–
V10	0.02	0.07	–	0.06	–	0.006	0.017	–
V11	–	0.04	0.04	0.01	–	–	–	–
V12	–	0.01	–	–	–	–	–	–
V13	0.02	–	0.02	–	–	–	–	–
V14	0.22	0.07	0.06	0.05	< 0.01	–	–	< 0.001
V15	0.08	0.04	0.04	0.02	–	–	–	–
V16	0.03	0.05	0.04	0.03	–	–	–	–
V17	0.15	0.03	0.02	0.02	< 0.01	–	–	< 0.001
V18	0.03	–	–	–	–	–	–	–
V19	0.10	–	–	–	< 0.001	–	–	< 0.001
V20	0.02	–	0.01	0.01	–	–	–	–
V21	0.02	0.02	0.04	0.05	–	–	–	–
V22	0.03	0.03	0.02	0.01	–	–	–	–
V23	–	0.01	–	–	–	–	–	–
V24	–	0.02	0.03	–	–	–	–	–
V25	0.02	–	–	0.02	–	–	–	–
V26	–	–	–	–	–	–	–	–
V27	–	–	–	–	–	–	–	–
V28	–	–	–	–	–	–	–	–
V29	–	–	–	–	–	–	–	–
V30	–	–	–	–	–	–	–	–
V31	–	–	–	–	–	–	–	–
V32	–	–	–	–	–	–	–	–
T	0.25	0.46	0.74	0.56	< 0.001	< 0.02	< 0.01	< 0.001

TABLE 6. *(Continued)*

Song parameter	Partner exchange stage				Compared stages			
	B	A1	A2	A3	B-A1	A1-A2	A2-A3	B-A3
N	8.43	14.88	16.83	16.00	< 0.01	–	–	< 0.01
V/N	0.78	0.46	0.31	0.31	–	–	–	–
V/S	6.71	7.05	4.33	2.88	–	–	–	< 0.05

The relative frequency of a variant is defined as its absolute frequency per number of attempted great calls (N). Variants and song parameters are defined in Table 3; the statistical tests are described in the text. Numbers in the last four columns indicate error probabilities (p); if no value is indicated, $p > 0.05$.

The relative frequencies of the variants in various stages of the partner exchange, as well as the results of the statistical comparison between the stages are listed in Table 6.

A comparison between song bouts before the partner exchange and those of the first 20 days after the exchange (comparison B-A1) revealed statistically significant differences ($p < 0.01$) for 4 of the 24 variants classified as atypical great call sequences (*i.e.* variants V3, V14, V17, V19). All 4 variants decreased in their frequency. Five atypical great call sequences (variants V5, V6, V9, V12, V23) occurred exclusively during stage A1 and were not observed before or after that stage. Two other variants (V18, V19) occurred exclusively before the partner exchange (stage B). Both variants which corresponded to the definition of typical great call sequences (V1, T) increased significantly in frequency ($p < 0.001$), this also applied to the song parameters N ($p < 0.01$) and N/S ($p < 0.05$).

A comparison between the songs produced before the exchange with those produced 4-8 months afterwards (comparison B-A3) revealed significant changes in the frequency of 6 variants corresponding to atypical great call sequences: The frequency of variants V3, V14, V17 and V19 had decreased ($p < 0.001$). In contrast, the two variants corresponding to typical great call sequences (V1, T) had both increased significantly in their frequency ($p < 0.001$); again, this also applied to the song parameter N ($p < 0.01$).

Figure 6 shows the changes in the relative frequency of selected variants of the great call sequence. In order to facilitate the comparison, the variants are the same as those chosen from the exchange *Na+Ga* → *Na+Vr* (Fig. 5). Again, the frequency of different variants changed quite differently: V1 and T increased immediately after the partner exchange and then remained on the

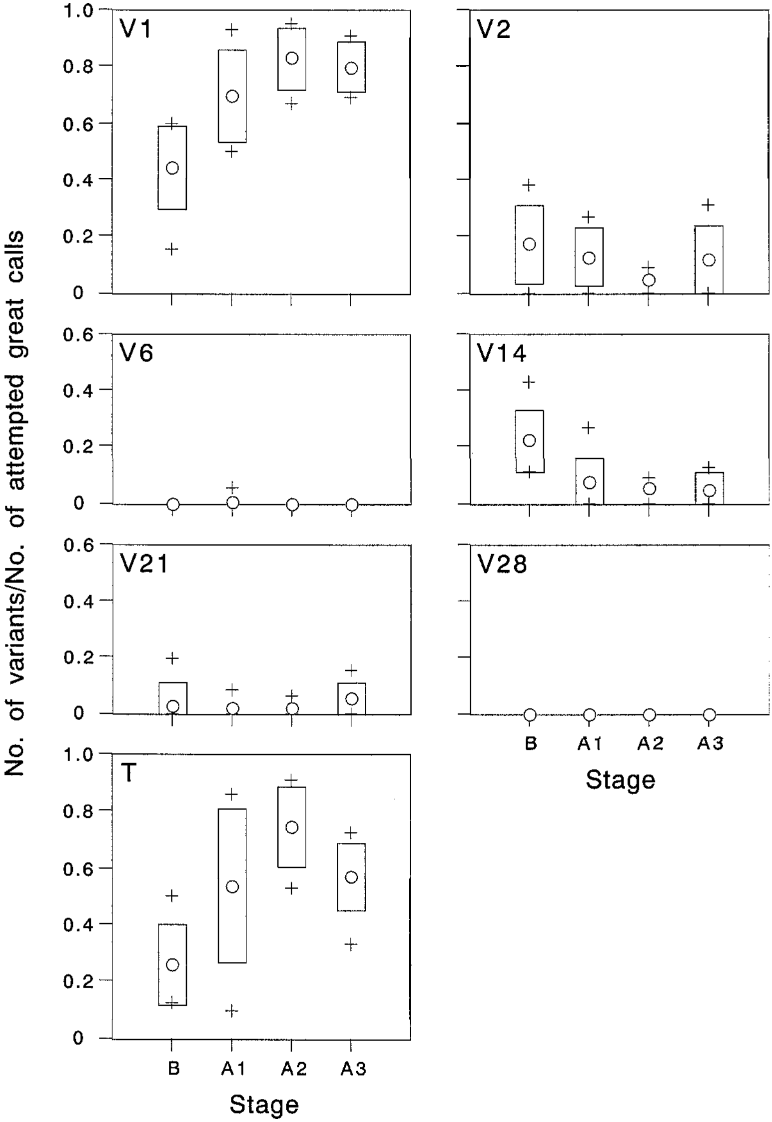

Fig. 6. Relative proportion of selected variants of the great call sequence during various stages of the partner exchange *Na+Ga* → *Bh+Ga*. B = stage before the partner exchange; A1-A3 = stages after the partner exchange. Symbols: circles = mean values, boxes = standard deviations, crosses = mimimum and maximum values.

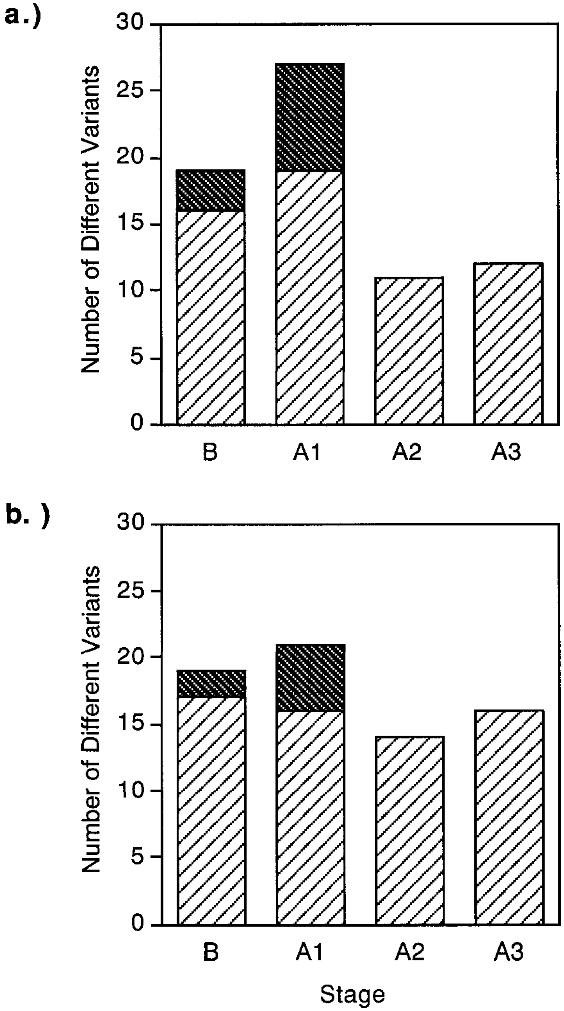

Fig. 7. Absolute number of different variants of the great call sequence used during various stages of partner exchanges *Na*+*Ga* → *Na*+*Vr* (a.) and *Na*+*Ga* → *Bh*+*Ga* (b.). The dark upper segments of the bars represent variants used exclusively in one stage of that particular partner exchange. B = stage before the partner exchange; A1-A3 = stages after the partner exchange.

new level. The variants V2 and V14 decreased after the exchange. Variant V6 occurred rarely and only immediately after the partner exchange. The variant V21 remained more or less constant, whereas V28 did not occur at all.

The absolute number of different variants used during various stages of both partner exchanges are shown in Fig. 7. Both new pairs produced more variants and more new variants during the stage immediately after the partner exchange (A1) than during any other stage. The difference in the number of different variants used during each stage is statistically significant only for the exchange *Na*+*Ga* → *Na*+*Vr* (Chi-square test, df = 3, $p < 0.05$), but not for the exchange *Na*+*Ga* → *Bh*+*Ga* ($p > 0.05$).

3.3. Quantitative duet parameters

3.3.1. Partner exchange *Na*+*Ga* → *Na*+*Vr*

The mean values for all duet parameters are listed in Table 7. A statistically significant change was only found for parameter 13 ($p < 0.01$); this interval was shorter after the partner exchange than before. This change could, however, be due to a difference in individual song characteristics of the exchanged females *Ga* and *Vr*. No evidence for changes was found in the song bouts of the male *Na*. Only as a trend, a change could be discerned in parameter 16 ($p < 0.1$), this interval appeared to be shorter after the partner exchange than before.

3.3.2. Partner exchange *Na*+*Ga* → *Bh*+*Ga*

The mean values for all duet parameters are listed in Table 7. Only 17 parameters are included in this comparison. Parameters 3 and 15 could often not be determined reliably in the songs of pair *Bh*+*Ga* and had to be excluded from this part of the study.

A statistically significant change was found for 11 of 17 parameters examined: parameters 2, 4, 5, 8, 9, 11, 14, 16, 17 and 19 ($p < 0.01$), and parameter 6 ($p < 0.05$). Three of these changes concerned the number of notes in series of vocalisations; two of them had higher values after the exchange (parameters 6 and 11) and one had lower values (parameter 17). The other 8 parameters concerned intervals, all of which were shorter after the partner exchange.

All changes could be due to the difference in individual song characteristics of the exchanged males *Na* and *Bh*, with one exception (described below). The great call sequence of *Na* was longer than that of his successor (and son) *Bh*, which is reflected in the longer duration of some of the corresponding intervals. One change, however, cannot be explained as a direct result of

TABLE 7. *Mean values of 19 quantitative duet parameters for three siamang pairs and statistical comparison (Mann-Whitney U test) of these values during two partner exchanges (i.e. Na+Ga → Na+Vr and Na+Ga → Bh+Ga)*

Duet parameter	Pair						Comparison between pairs	
	Na+Ga		*Na+Vr*		*Bh+Ga*		*Na+Ga* → *Na+Vr*	*Na+Ga* → *Bh+Ga*
	Mean	*N*	Mean	*N*	Mean	*N*		
1	5.056	16	4.418	17	2.477	17	NS	NS
2	4.978	16	5.084	18	4.118	15	NS	< 0.01
3	2.692	9	3.903	10	–	–	NS	–
4	15.785	16	14.056	17	10.709	16	NS	< 0.01
5	10.455	8	8.789	10	2.058	10	NS	< 0.01
6	1.267	15	1.250	16	2.182	11	NS	< 0.05
7	2.071	14	1.566	9	1.538	13	NS	NS
8	5.265	16	5.245	19	4.797	17	NS	< 0.01
9	3.162	16	3.130	10	2.636	13	NS	< 0.01
10	2.103	16	2.131	10	2.183	13	NS	NS
11	2.533	15	2.286	14	5.583	12	NS	< 0.01
12	0.941	16	1.088	13	1.502	13	NS	NS
13	7.209	15	8.749	12	7.268	10	< 0.01	NS
14	13.983	15	13.090	12	8.112	13	NS	< 0.01
15	6.699	15	4.428	11	–	–	NS	—
16	3.022	16	2.897	17	2.830	13	NS	< 0.01
17	7.400	15	7.588	17	6.077	13	NS	< 0.01
18	10.576	16	13.560	15	17.747	16	NS	NS
19	35.322	15	34.078	12	24.429	13	NS	< 0.01

The last two columns indicate the error probabilities of statistically significant differences. Parameters are note intervals (in s), except parameters no. 6, 7, 11 and 17, which count the number of notes in selected series of notes. Parameters 3 and 15 could not be determined reliably in pair *Bh+Ga*. Definitions of parameters see Table 4. *N* = number of analysed typical great call sequences; NS = not significant.

the new male's individual song characteristics: After the partner exchange, the initial interval between the female's long barks was shorter (parameter 2); this can only be explained as a change in the female's (*Ga*) singing behaviour.

3.4. Interactions between the groups

The neighbouring siamang groups of this study did not only coordinate the beginning and the end of their song bouts among each other, they also tended to coordinate their respective great call sequences in a group-specific mode of overlap. The resulting stable patterns of elaborate trio and quartet song bouts and their development during the partner exchange will be described in more detail in a future study. In Zürich, the vocal coordination between the focal pair and the neighbouring male before the partner exchange resulted in specific trio great call sequences (*i.e.* with 3 singers) which did not correspond to typical great call sequences (T). The trio great call pattern in Zürich consisted of three instead of only two series of long barks by the focal female *Ga*. During the first one, the neighbouring male *Bh* inserted his bitonal scream, during the second one her mate *Na* inserted his bitonal scream, and during the third one *Na* added a ululating scream (US-I).

During two song bouts, the neighbouring male was confined to the sleeping box. In this situation, the two groups could hear each other less clearly and little vocal coordination was possible between them. During these two song bouts, the focal group's proportion of typical great call sequences (T) rose to 40 and 50%, respectively, as compared to an average 19% during 5 song bouts when the neighbouring male was not confined to his sleeping box (Chi-square test, df = 1, $p < 0.03$).

In Studen, on the other hand, the two neighbouring groups developed a different type of vocal coordination. The two groups consisted of one pair (*Bb*+*Ra*) and the solitary female (*Vr*) before the partner exchange and two pairs (*Bb*+*Ra* and *Na*+*Vr*) after the exchange. Both groups tended to sing their great call sequences in near synchrony. As a result, the coordinated trio songs (before the partner exchange) and quartet songs (after the partner exchange) were compatible with the typical great call sequences (T) described above (section 2.3).

4. Discussion

4.1. Variants of the great call sequence

Originally, the author had expected to find a particularly high proportion of typical great call sequences (T) in the songs of the established pair *Na*+*Ga*. This pair, however, had developed a stable pattern of vocal interactions with the neighbouring male *Bh*. Because of this stable trio pattern, typical great call sequences were very rare in Zürich before the partner exchange (T = 25%). In the two song bouts during which the neighbouring male was less audible (because he was confined to the sleeping box), the established pair's proportion of typical great call sequences rose to 40 and 50%, respectively, as compared to 19% when the neighbour was in the adjacent cage. An even higher proportion may have occurred if the neighbouring male had been kept further away from the focal pair. The low proportion of typical great call sequences in the established pair *Na+Ga* does not imply that this pair did not coordinate its sequences. On the contrary, the low proportion occurred because the pair, in addition, coordinated its great call sequences with those of the neighbouring male *Bh*. This resulted in a duet structure which, albeit stable, was rated as atypical according to the definitions adopted at the outset of this study.

In Studen, the new pair *Na+Vr* and the neigbouring pair gradually developped a stable pattern of vocal interaction, as well. This pattern, however, differed from the one observed in Zürich: These pairs produced quartet great call sequences in near synchrony. In contrast to the pattern produced by the trio in Zürich, the quartett pattern in Studen was compatible with the typical great call sequence produced by mated siamang pairs (as described in section 2.3). Yet, during the first stage after the partner exchange (A1), the proportion of typical great call sequences reached only 36% (stage A1) and climbed above 50% only during the last stage (A3).

After the partner exchange in Zürich, the proportion of typical great call sequences almost immediately rose to 46% (stage A1) and was already well above 50% during stage A2. In contrast to the situation in Studen, this new pair (*Bh+Ga*) had no adult neighbours. Apparently, the female *Ga* very quickly accepted the new male as her duetting partner.

If new pairs experience difficulties in synchronising their duets, this should result in atypical great call sequences which are absent or rare in established pairs. Exactly this occurred in both new pairs observed during the present study. The new pairs in Zürich and Studen both used a higher diversity of variants of the great call sequence immediately after the partner exchange than during any other stage before or after the exchange (Fig. 7), although the difference is statistically significant for only one of the exchanges (*Na+Ga* → *Na+Vr*). In addition, eight out of 28 atypical variants of the great call sequence (29%) observed in the songs of the male *Na* occurred only immediately after the partner exchange (*i.e.* in phase A1). Similarly, 5 out of 24 atypical variants (21%) in the songs of the male *Bh* occurred only just after the partner exchange. Again, the increase in the diversity of the great call sequence appears to be slightly higher in the new pair *Na*+*Vr* than in the new pair *Bh*+*Ga*.

This difference may be explained by the differential familiarity among the newly mated individuals. The newly-paired siamangs *Bh*+*Ga* in Zürich were not complete strangers, because they both had ample opportunity to hear each others' songs from the adjacent cage before being brought together as a pair. In contrast, *Na*+*Vr* came from two different zoos and were kept in the same cage immediately after *Na*'s arrival in Studen.

A large part of the observed changes in qualitative duet parameters can either be explained as individual song characteristics introduced by a newly mated animal into the duet song of its partner, or as the result of newly established or lost vocal relationships to neighbouring siamang groups. At least one vocal change of the male *Na*, however, appears to represent an active adaptation to the duets with his new mate. After the partner exchange, the male *Na* frequently omitted his US-II at the end of the great call sequence (V21). Instead, his new partner (*Vr*) frequently produced a US-II there. She had already produced these screams when she sang together with the pair in the adjacent cage, *i.e.* before the arrival of *Na*. In contrast to this female, *Na*'s previous mate *Ga*, like most other siamang females, was never heard to utter any ululating screams. After the partner exchange, *Na* began to omit his US-II, possibly in order to avoid the atypical occurrence of two ululating screams at the end of the great call sequence.

Maples *et al.* (1989) reported that the proportion of incomplete (and thus atypical) great call sequences in the songs of a newly formed pair of siamangs decreased from 76 to 21% during the 13 weeks following the pair's introduction to one another. The observations of these authors cannot be compared directly to those of the present study for the following reasons: In the former study, typical great call sequences were defined much more broadly (accepting many variants as typical which are here recognised as being atypical). There were no neighbouring pairs in the study of Maples *et al.* (1989), and, at least the female of that study (age: 6.5 years) had no proper duetting experience, because she had always been living in her family group prior to that study. The male had lived together with a female when he was about 6 years old (it is unknown whether that pair ever duetted), but he was kept in isolation for 12 years afterwards. As a result, the vocal changes observed by these authors could, at least in part, be of ontogenetic origin.

4.2. *Quantitative duet parameters*

Similar to the changes in qualitative duet parameteres, most of the observed changes in quantitative duet parameters are probably due to individual song characteristics of the newly mated animals. Evidence for an active adaptation of one mate to the other was found only in the new pair *Bh*+*Ga*: The rhythm of the long barks at the beginning of a great call (quantitative parameter 2) was slower when the female *Ga* sang with *Na* than when she sang with the new male *Bh*. Because the new male inserted his bitonal screams earlier in the series of barks than *Na* (parameter 4), *Ga* had a shorter time span at her disposal for reaching her first climax. She possibly tried to compensate for this by attacking her great calls at a faster rhythm when she was singing with *Bh*. By doing so she reached the first climax earlier, which was necessary in order to synchronise the climax with *Bh*'s bitonal scream.

4.3. *Strengthening the pair bond*

Dawkins (1976) and Maynard Smith (1977) suggested that pair-bonding could be strengthened by an individual demanding a preliminary effort of each new partner prior to copulation. An individual which remains together with its mate (for consecutive mating seasons) gains reproductive success without further investment, whereas individuals that change mates must invest again with each new partner. Wickler (1980) applied this hypothesis to duet songs: An individual which has to invest time and energy in order to learn the song of another individual is less likely to desert its mate. This investment has the advantage of not being transferable: A rival taking over a territory cannot benefit from the investment of his predecessor, as he could, had the latter invested in nest building, food provisions, or — through a long courtship behaviour — in sexual readiness of its mate. In addition, the demanding partner can control the learning investment at any time through a test (*i.e.* a duet song) and may, by doing so, also ask for a certain amount of time investment.

In some species, duets typical of established pairs have been reported to occur only after a considerable time period of exercising (Robinson, 1979, p. 395; Wickler, 1980; Farabaugh, 1982; Geissmann, 1986; Maples *et al.*, 1989).

The siamang, however, appears to be the first species shown to meet all three requirements of Wickler's (1980) pair-bonding hypothesis (see

Introduction): All animals were adult before the partner exchange and exhibited a stable song pattern. The songs of the established pair *Na+Ga* exhibited a clear, pair-specific structure. The partner exchange led initially to a drastic, but temporary disorganisation of the song, and later to a permanent restructuration of several song characteristics in both new pairs. Stabilization of the duet structure preceded reproduction. First copulations in both new pairs were observed 49-50 days after pair formation and conceptions in both new pairs occurred only after stage A3 of this study (at least 5 months after pair formation).

Many of the duet characteristics permanently changed after the partner exchange. At least two of the observed changes could not result simply from the new combination of individual-specific song characteristics.

1. After the partner exchange, the male *Na* frequently omitted the second ululating scream (US-II) at the end of the great-call sequences (V21), possibly, because his new mate (*Vr*) would already produce a ululating scream at the same point of the sequence. *Na*'s former mate (*Ga*), on the other hand, was never heard to produce a ululating scream.
2. Female *Ga* attacked her great calls at a higher speed (*i.e.* with shorter intervals between her barks) after the partner exchange (quantitative parameter 2). She may have done so in order to go faster through the first acceleration phase of her great call. Her new partner (*Bh*) used to insert his bitonal screams earlier in the great call than her previous one (*Na*). By reaching the first climax in her great call earlier, the female may have made sure that her new mate's early bitonal scream would still occur in synchrony with the first climax, as it typically does in siamang duets.

It appears reasonable to interpret these changes as partner-directed learning efforts. Not only is the pair-bonding hypothesis supported by the findings of this study, it also explains why the considerable complexity of duetting relationships observed in siamangs may have evolved. The relatively simple vocal interaction occurring during the great call sequence of gibbons of the *lar* group and the *concolor* group (*i.e.* one female great call phrase followed by one male coda phrase) probably does not require a major learning effort, if any. More complex duet rules may be necessary before a substantial learning effort can be demanded from a partner.

This study does not *prove* that duetting in siamangs strengthens the pair bond, because demonstration of a direct relationship between the pair bond strength and the quality of duetting is still lacking. Moreover, this study is based on a sample size of only two partner exchanges and needs further support from observations on wild siamangs.

In contrast to the siamang duet songs analysed in this paper, the duet songs of some other species are apparently not compatible with the pair-bonding hypothesis, either because pair specific duets were found to consist of the addition of individual-specific characteristics instead of a vocal adaptation between mates, because duet repertoires and duet precision did not change following a change in mates, because there was no evidence of duet practise and improvement during pair integration, or because duet amelioration did not appear to be a necessary precondition to pair establishment and copulation (Arrowood, 1988; Müller, 1994; Levin, 1996).

Lamprecht (1970) suggested that siamang songs did not serve a single function, but rather multiple functions. Marshall & Marshall (1976) proposed that different selection pressures act on male and female repertoires in gibbon duets, and Gittins (1978) postulated different functions for the various song contributions of family members in gibbon groups. Possibly, different parts of the same individual's duet contribution may also differ in function, as has been demonstrated for duets in birds (Sonnenschein & Reyer, 1983) and as has been suggested for duets of white-handed gibbons, *H. lar* (Goustard, 1985).

It is unlikely that the pair-bonding hypothesis represents the only function of siamang songs. For instance, it fails to explain the loudness of these vocalisations. The latter suggests that siamang songs also serve functions in the context of territoriality and/or mate attraction.

The discovery of supra-duets occurring between neighbouring siamang pairs was an unexpected finding. It produced a confouding effect with the duet synchronisation between newly mated siamangs and may have substantially reduced the number of variables which clearly represented positive evidence for a partner-directed learning effort (as compared to a neighbour-directed learning effort). A similar study on siamang groups which have no neighbours at close distance may produce fewer ambiguous results for the vocal variables under comparison.

4.4. Advertising the pair bond

The pair-bonding hypothesis has additional implications: If duetting has to be learned by a newly mated pair, the duet song should provide information on the strength of the pair bond. Advertising the presence of a strong pair bond should be advantageous in territorial defence, because a potential rival may find it easier to take-over a territory or a mate from a less well established pair.

If at least one of the mates has to adapt its song to that of its partner through a process of learning, the degree of that adaptation can be heard in the song and provides an estimate for the duration of time since the pair was formed. Therefore, a potential rival should be able to judge the quality of a pair bond by the quality of the pair's duet song and to estimate the difficulties and his chances of success if he was attempting to take over a mate or a territory from that pair.

Both the daily number of song bouts and the daily singing duration at the Studen Zoo nearly doubled after the partner exchange (Geissmann, 1986). At least as a trend, a similar increase was also observed after the partner exchange in Zürich. An increase in singing frequency was also observed in newly formed pairs of wild *H. pileatus* (Srikosamatara & Brockelman, 1983; Brockelman & Srikosamatara, 1984). If newly formed pairs are going through a critical learning phase and have to face a higher pressure from rivals, then they should be under a selective pressure to keep their learning phase as short as possible. This might be one of the reasons why new pairs duet more than established pairs.

Under the pair-bonding hypothesis, on the other hand, an animal requesting a learning investment from its partner in order to reduce the risk of being deserted, may *not* be interested in minimizing the learning phase. "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" (Geissmann, 1986).

If newly mated pairs attract competitors by their imperfect duets, this should also reduce the probability of mate desertion in established pairs, because deserting animals would necessarily produce imperfect duets with their next partner, at least during the initial phase of the partnership. This represents a second mechanism explaining how duetting may strengthen a pair bond. It differs from Wickler's (1980) pair-bonding hypothesis, but the two mechanisms do not exclude each other. This second hypothetical mechanism assumes that (1) new pairs need to learn to coordinate their duets, and (2) imperfect duets of new pairs attract more unmated competitors than duet songs of well established pairs. The first assumption applies to siamang songs, as shown in this study. The second assumption has not been tested yet. This could be achieved with playback experiments in the field.

If pairs with a particularly well coordinated duet are less exposed to threats by competitors, this should result in a selective pressure on pairs to optimise the stability of their duet coordination. This selective pressure may have contributed to remarkably stable great call sequences exhibited by established siamang pairs (as shown in Geissmann, in press b), even though their duets are much more complex than those of gibbons of the *lar* group or the *concolor* group.

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