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Behavioural Development of Twin Siamangs (*Hylobates syndactylus*)

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ABSTRACT. Multiple births are very rare among gibbons. The birth of siamang twins at the Zürich Zoo in 1992 therefore presented a valuable opportunity to observe the development of the twins and to contrast it with a survey of previous reports on the development of single offspring of siamang and gibbons of the *lar* group. Furthermore, the hypothesis that the presence of twins among siamang may facilitate the occurrence of helping behaviour (defined as the care of offspring by individuals other than their parents) was re-examined (DIELENTHEIS et al., 1991). The Zürich twins (one male and one female) were observed for a total of 74 hr during their first year of life. The results show that: (1) The twins exhibited more rapid behavioural development than that reported for single offspring. (2) A clear difference between the twins was observed: the female twin developed more rapidly than the male. (3) Neither the twins' father nor their older sister *Rama* was ever observed carrying the twins. The hypothesis of DIELENTHEIS et al. (1991) is hence not supported by the present study, although it is possible that the older sister *Rama* did not carry the twins because she was younger than the juvenile in that study. (4) Siamangs may have a longer maturation period than gibbons of the *lar* group.

Key Words: Behavioural development; Paternal care; Helping behaviour; Multiple offspring; *Hylobates syndactylus*; Siamang; Gibbon; Twins.

INTRODUCTION

Whereas most gibbon species appear to exhibit little paternal care (FISCHER & GEISSMANN, 1990), it is quite pronounced in siamangs: several infant siamangs, both in the wild and in captivity, have been observed being carried by their fathers (ALBERTS, 1983, 1987; CHIVERS, 1974, DIELENTHEIS et al., 1991; LEE, 1976). Such carriage has been reported to begin in the second half of the infant's first year of life and to continue during the second year.

Multiple births are very rare among gibbons and only a few cases are known (GEISSMANN, 1989, 1990). The only published study of gibbon twins was conducted at the Berlin Zoo (DIELENTHEIS et al., 1991), where siamang twins, reared in their natal group, were observed for 11 consecutive days at the age of 0.9 years. This study attempted to determine the influence exerted by the presence of twins on the infant care provided by the various family members. During the observation period, one or both twins were usually carried by their father, but hardly ever by their mother. The juvenile individual in the group was also observed to carry the infants for a considerable amount of time.

Helping behaviour, defined as the care of offspring by individuals other than their parents, is unusual among gibbons (DIELENTHEIS et al., 1991). It has been suggested that the considerable amount of helping behaviour observed in the Berlin siamangs was enhanced by the presence of two infants simultaneously instead of one. Because siamangs normally give

birth to only one offspring, the mother's difficulty in keeping track of two infants and the associated physical stress of carrying both could have resulted in increased opportunities for the juvenile member to carry the siblings (DIELENTHEIS et al., 1991).

In May 1992, the female siamang at Zürich Zoo gave birth to twins, one male and one female (SCHMIDT, 1992). This presented a rare opportunity to test the hypothesis of DIELENTHEIS et al. (1991) regarding the occurrence of helping behaviour in siamangs. Accordingly, the amount of infant care exhibited by the various family members was assessed. As far as paternal care is concerned, it should be noted that the male at Zürich Zoo, unlike the male at Berlin Zoo, had been never observed to carry any of its previous (single) offspring by one of us (GEISSMANN, unpubl. observ.), although this was observed on one exceptional situation (Dr. C. R. SCHMIDT, pers. comm.).

The behavioural development of twin gibbons has not been studied previously. For this reason, in addition to testing the hypothesis mentioned above, a number of other features were observed. This was done in order to compare behaviour between the siblings, as well as to compare data on the development of the twins with published information for single offspring. In previous studies on twins in catarrhine primates, twins have often been reported to be less developed at birth than single offspring, and marked developmental differences between the individual twins or in the way they were treated have repeatedly been noted (GEISSMANN, 1989).

Finally, a comparison of our observations on the development of siamangs with published data for gibbons of the *lar* group was also undertaken, as it has been suggested that the siamang may have a longer maturation period (GROVES, 1972, p. 32).

This study hence attempted to answer the following four questions: 1) How does the development of the twins compare to the development of single offspring? 2) Do the twins differ in their development or in the way they are treated? 3) Do family members other than the mother participate in carrying the twins? 4) How does the development of siamangs compare to that of gibbons of the *lar* group?

MATERIAL AND METHODS

ANIMALS

The age classes proposed by GEISSMANN (1993) for captive gibbons and siamangs were used in this report: infants from 0 to 2 yrs of age; juveniles 2.1 to 4 yrs; subadults 4.1 to 6 yrs; adults more than 6 yrs. The family group studied had the following composition: 1) *Dagobert*, adult male, born at the Dortmund Zoo on October 4, 1979, hand-reared, in Zürich since April 1, 1981, 12.8 yrs old at the beginning of this study; 2) *Chandra*, adult female, born at the Zürich Zoo on December 25, 1976, hand-reared, 15.5 yrs old at the beginning of this study; 3) *Rama*, infant/juvenile female, born at the Zürich Zoo on February 4, 1991, 1.4 yrs old at the beginning and 2.2 years at the end of this study; and 4) *Solok* (male) and *Sasak* (female), twin infants, born on May 2, 1992, 0.2 yrs (10 weeks) old at the beginning and 1.0 yrs (50 weeks) at the end of this study. The twins were easily recognized individually, because only the female infant had a patch of whitish hairs above each eye.

The first offspring of this pair were also twins (born on September 28, 1984): the first twin was stillborn while the second (*Khao*) lived 8 months prior to dying of cachexia (GEISSMANN, 1991; SCHMIDT, 1992). All intervening offspring born to this pair were

singletons and all were reared by their mother (*Luang*, July 23, 1985; *Nias*, January 10, 1987; *Olong*, September 23, 1988; *Perak*, August 31, 1989; and *Rama*, February 4, 1991).

HOUSING

During the first month of this study (July 1992), the family group was kept in an indoor cage (base area of 18 m² x height of 5 m). On August 6, 1992, they were transferred to an indoor/outdoor cage (18.4 m² x 2.8 m and 40 m² x 5 m, respectively). Because the animals were frequently out of sight in the outdoor cage, the group was kept in the indoor part of the cage during observation sessions carried out after August 6, 1992. All cages had ropes, in addition to horizontal, vertical and oblique bamboo poles.

OBSERVATION TIME

The group was observed by one of us (G.D.P.) from July 8, 1992 to April 15, 1993, i.e. when the twins were aged between 10 and 50 weeks (with gaps in November 1992 and from January to March 1993). Later observations were made only occasionally by T.G. until the twins were 64 weeks old. One week before the beginning of the study, the twins were observed twice for 3 hr in order to define the behavioural variables and the method for collecting data.

During the observation period, the siamangs were observed between 08:30 and 16:30, in order to effectively cover their activity period. Observation sessions lasted about 4 hr and were carried out once per week, alternating between morning and afternoon sessions. For statistical analysis and graphical presentation, data from each morning session have been pooled with those from the following afternoon session.

Total observation time amounted to 73 hr 43 min. Data were collected by a substitute observer briefed by one of us (G.D.P.) when the twins were 26 weeks old.

In previous publications, the age of young hylobatids at attainment of various developmental markers has frequently been measured in months. Because months do not have a uniform duration, weeks have been used throughout the present study. Where necessary, comparative data from the literature have been transformed from months to weeks, assuming that an average month has a duration of 30.4 days or 4.3 weeks.

METHOD

Behavioural variables 1 – 5 and 7 were collected with the scan sampling method using instantaneous sampling (MARTIN & BATESON, 1986). They were recorded every 30 seconds and the number of occurrences in percent of the total number of sample points was used as a direct estimate of the proportion of time for which the behaviour occurred (MARTIN & BATESON, 1986). The behavioural variable 6 was recorded whenever it occurred and was expressed as a function of total observation time. The behavioural variables recorded were as follows: 1) *Away from mother*: the infant is not in physical contact with its mother. 2) *Being carried*: one individual being carried by another, which, while stationary or moving, provides weight-supporting contact with the carried animal(s). It was also recorded each time which twin was carried on the right and which on the left (from the mother's perspective). In order to detect possible side preferences of the twins, this information was only recorded when both the twins were carried simultaneously; when only one infant was carried, it usually occupied a more central position on the mother's belly. 3) *Nipple contact (nursing)*: the infant

holds the mother's nipple in its mouth. It was not specifically recorded whether the infants suckled or not when at the nipple, as sucking movements of the infants' mouth were often not reliably detectable. 4) *Play* (social play): play behaviour exhibited by or involving the infants mainly consisted of the following: a) one animal watches another one and briefly touches it in the region of the hand, the arm or the upper part of the body; and b) one animal lightly bites another anywhere on the body, but is seemingly inhibited because the addressee does not show signs of pain or injury. 5) *Being groomed*: the grooming animal examines, parts and plucks at the hair and/or skin with the hand and sometimes with the lips or teeth. Various items (e.g. particles of dirt or skin flakes) are removed by hand or with the tongue, lips or teeth and usually swallowed. This variable includes only social grooming (allogrooming) and excludes self-grooming (autogrooming). 6) *Being licked*: one individual is licked very briefly once or twice by another (mainly directed towards the receiver's head). This behaviour may correspond to "kiss" as described by LEE (1976). It was not classified as grooming because of its short duration, and because it happened only sporadically and not during grooming sessions. 7) *Agonistic behaviour from Chandra towards Rama*: This behaviour consisted mostly of the mother directing open-mouth threats or bites towards her older daughter *Rama*, and frequently occurred when *Rama* approached the twins. Agonistic behaviour between other group members was ignored.

Inter-individual distances between each twin and between the twins and all other family members (seven distances in all) were estimated and assigned to one of the following three categories: A) less than 20 cm, B) 20 – 100 cm, C) more than 100 cm. These distances were recorded every 5 min with the scan sampling method (instantaneous sampling). The frequency of occurrence of each distance category (A, B, and C) was expressed as a percentage of the total number of sample points.

Finally, the following ten developmental markers were recorded when they were first observed in the twins: complete lack of contact with mother, suspension by one arm, bimanual brachiation, bipedal locomotion, feeding on solid food, play with siblings, being groomed by siblings, grooming (allogrooming), and participation in group calls. Comparative data on the development of singleton siamangs and gibbons of the *lar* group were collected from the literature, and some additional, previously unpublished, observations on siamang infants were kindly made available by Mr. M. ORGELDINGER.

For statistical analysis, nonparametric statistical tests were adapted from CIBA-GEIGY AG (1980). Differences in frequencies of the different behavioural variables between the twins were tested for significance with 2 x 2 Chi-square tests. The same tests were also carried out to compare the data of the first part of the study (weeks 10 – 20) with those of the second part (weeks 22 – 50). In addition, Spearman rank correlation coefficients (r_s) were calculated between each behavioural variable and the twins' age, as a measure of developmental trends.

RESULTS

The observations on each variable are presented separately.

AWAY FROM MOTHER

Figure 1a shows the percentage of time each twin spent out of contact with its mother. There is a gradual decrease in mother-infant contacts as a function of the infants' age, with

a corresponding increase in time spent alone (*Solok*: $r_s = 0.91$, *Sasak*: $r_s = 0.98$, $p < 0.002$ in each case). Only at the beginning of this study did the infants spend 100% of the observation time in contact with the mother; this was observed to occur up to the age of 13 weeks for *Sasak*, and up to the age of 17 weeks for *Solok*. The frequencies with which the twins were alone were compared with the Chi-square test. Overall, the female infant *Sasak* was more frequently alone than the male infant *Solok*; the difference is statistically significant ($p < 0.001$). If the data points in Figure 1a are analysed separately, this difference is significant in 8 out of 11 comparisons (Chi-square test; $p < 0.05$). The 3 exceptions all occurred in the first part of the study (weeks 10, 12 and 18). During occasional, non-quantitative observations, carried out when the twins were 64 weeks old the male twin still appeared to spend more time in contact with its mother than the female twin.

CARRYING

In the first year of life the twins were carried only by the mother, i.e. they were never observed being carried by their father or sister. This was also the case during occasional observations carried out when the twins were older than one year (i.e. up to the age of 64 weeks). The mother frequently carried both twins at the same time when they were 55 weeks old, but in week 64, only the male twin was observed to be carried.

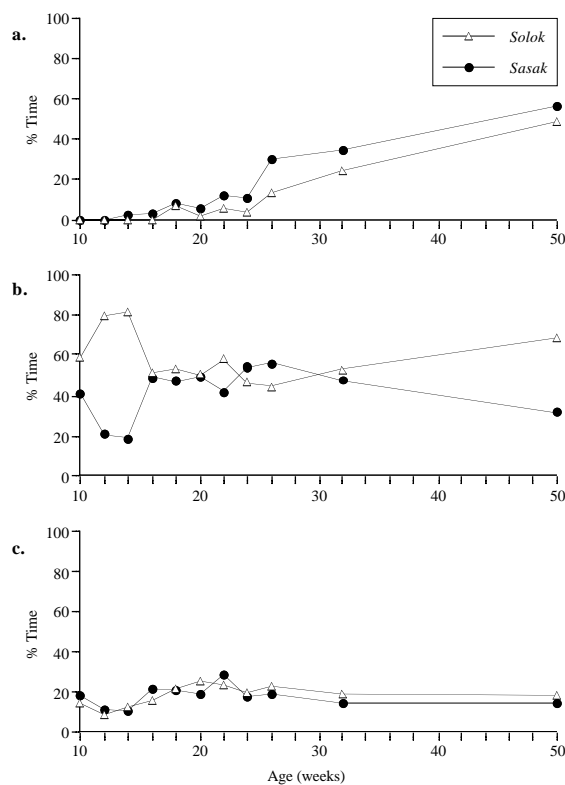


Fig. 1. Percentage of time each twin spent away from the mother (a), was carried on the right side of the mother (b), and spent in contact with the mother nipple (c).

Figure 1b shows the percentage of time each twin was carried on the mother's right side. Because these data were collected only when both twins were carried simultaneously, the frequencies for *Solok* being on the right side are exactly inverse to those for *Sasak*. Overall, *Solok* was more frequently carried on the right side than *Sasak* (Chi-square test; $p < 0.001$). If the data points in Figure 1b are analysed separately, significant differences between the twins are found for 7 out of 11 data points (Chi-square tests, $p < 0.05$). Over the whole study period, the side preference of each twin was not correlated significantly with time ($r_s = -0.44$, $p > 0.05$), but a comparison between the data from the first six observation sessions with those of the last five revealed a significant decrease in side preference (Chi-square test; $p < 0.001$).

NIPPLE CONTACT

Up to the age of 16 weeks the twins were seen nursing only while *Chandra* was resting (i.e. sitting or lying); thereafter, nursing also occurred when she was moving. *Chandra* was never observed to obstruct an infant's attempt to suckle. From the beginning to the end of this study, both twins were also frequently observed to suck their thumbs (and occasionally their great toes).

The percentage of nursing for each twin is shown in Figure 1c. Statistically significant differences in nursing frequency between the twins were found at the age of 16, 20, 22, 32 and 50 weeks (Chi-square test; $p < 0.05$). During the first part of the study, it was not consistently the same twin that spent more time at the nipple, but during the second part, the male twin spent more time at the nipple. If all data are pooled for comparison, no significant difference is found between the twins.

A comparison between the first six data points in Figure 1c and the last five revealed a significant difference only for the male twin (Chi-square test; *Solok*: $p < 0.001$; *Sasak*: $p > 0.05$). The frequency of nursing increased gradually until the twins were 20 – 22 weeks old, and slowly decreased thereafter.

SOCIAL PLAY

The twins were first observed to engage with each other in what resembled play at the age of 12 weeks. Such play was mostly characterised as a series of mutual bites and pushes, and it was sometimes difficult to determine whether the twins were actually playing or whether these bites represented an agonistic reaction to mutual physical obstruction or a strategy to gain more space on the mother. The bites were nevertheless classified as social play.

Figure 2a shows the percentage of time the twins played with each other: there is a gradual increase in the frequency of social play as a function of age ($r_s = 0.92$, $p < 0.002$), and there is a significant difference between first six data points in Figure 2a and the last five (Chi-square test; $p < 0.001$).

Chandra was not observed to play with her twin offspring, although she was observed to play with *Rama*. The twins' father was observed to play with the infants only during the last two observation sessions, i.e. when they were 50 weeks old (Fig. 2b), and he played more frequently with the male twin (Chi-square test; $p < 0.001$).

From the age of 14 weeks onwards, the twins were also observed playing with their older sister *Rama*. At the beginning, play was almost invariably initiated by *Rama*, who approached the infants and either seized the arm of one sibling or playfully bit some part of its body. This happened more frequently when the twins were away from their mother.

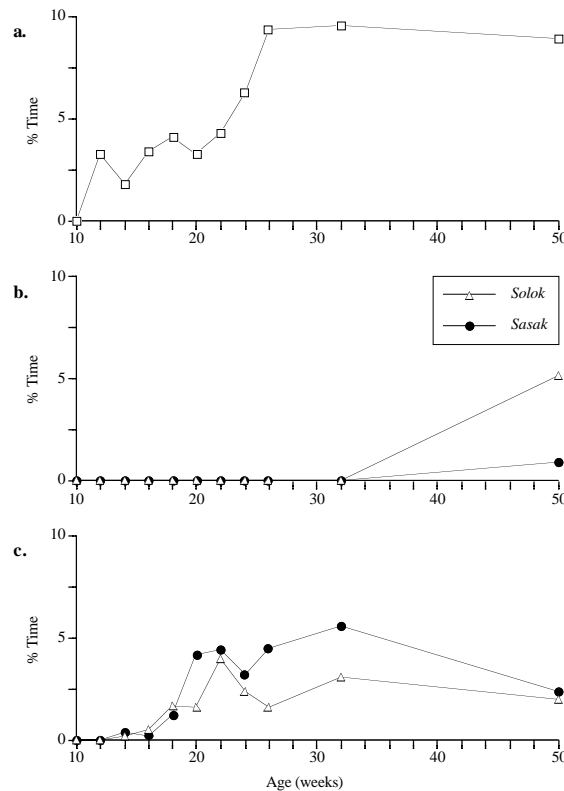


Fig. 2. Percentage of time the twins played with each other (a) and percentage of time each twin played with its father (b) and its older sister (c).

The twins themselves often tried to touch *Rama* or to attract her attention by stretching one arm toward her, when they were on or close to *Chandra*. They did this less frequently when they were away from their mother. Instead, they tried to return to their mother as fast as possible if *Rama* approached them.

Because of repeated interventions by *Chandra* (see below), *Rama* played with her siblings only for short periods of time at the beginning of the study. These periods then became longer as the twins became older (*Solok*: $r_s = 0.79$, *Sasak*: $r_s = 0.83$, $p < 0.01$ in each case). The frequencies at which the twins played with *Rama* are shown in Figure 2c. The overall difference between the twins is statistically significant (Chi-square test; $p < 0.001$); *Rama* and *Sasak* played significantly more often together than did *Rama* and *Solok*. If the data points in Figure 2c are analysed separately, a significant difference is found only when the twins were aged 20, 26 and 32 weeks (Chi-square test, $p < 0.05$).

BEING GROOMED

At the beginning of this study, both *Dagobert* and *Rama* were already allowed by *Chandra* to groom the infants, albeit only for brief periods of time. *Chandra* remained the main groomer of the twins during the whole observation period.

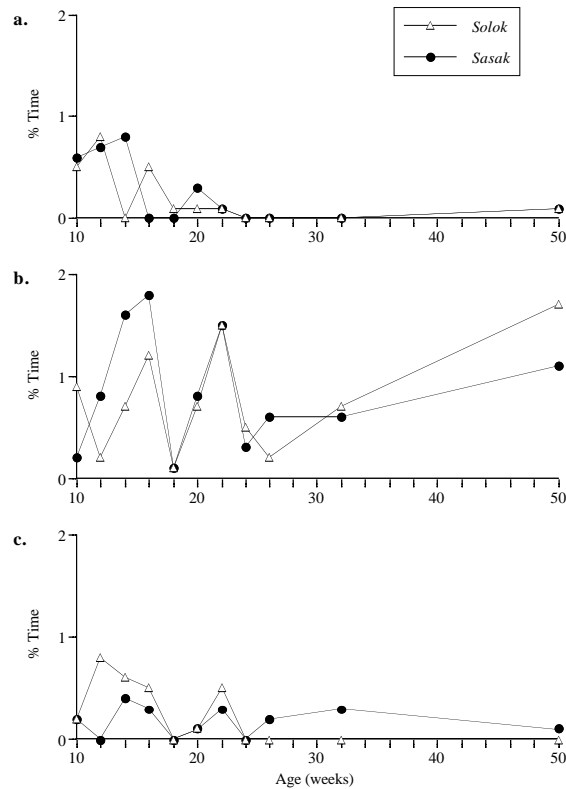


Fig. 3. Percentage of time each twin was groomed by its father (a), its mother (b) and its older sister (c).

The percentages of time that *Dagobert*, *Rama* and *Chandra* spent grooming the twins are shown in Figure 3. None of the family members showed a significant preference for one particular twin ($p > 0.05$) when data for the whole study period were compared. This also applied when data for each point in Figures 3a – c were analysed separately, with two exceptions: the older sister *Rama* groomed the male twin more frequently than the female twin in week 12, and the father groomed the female twin more frequently in week 14 (Chi-square tests; $p < 0.05$). For each family member, the first 6 data points in Figures 3a – c were compared with the last 5. *Dagobert* was found to groom both twins more frequently in the first part of this study than in the second part (Chi-square test; *Solok*: $p < 0.001$; *Sasak*: $p < 0.05$), and *Rama* groomed the male twin more frequently during the first part of the study than in the second part ($p < 0.05$). For *Chandra*, no significant differences were found. None of the grooming frequencies between a twin and another family member was significantly correlated with the twins' age, except for the decreasing frequency of grooming between the male twin and his older sister *Rama* ($r_s = -0.75$, $p < 0.05$).

During the study period the twins themselves were never observed to exhibit grooming behaviour.

INFANT LICKING

Licking was exhibited only by the mother and was always directed at the twins. It typically consisted of a single lick on the infant's faces (similar to a kiss) and did not seem to

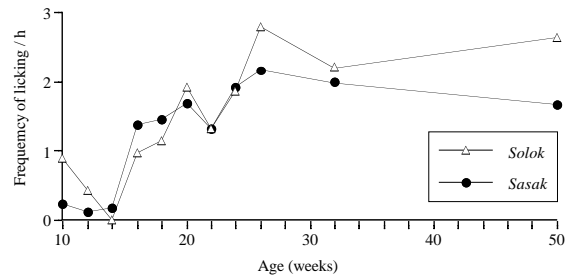


Fig. 4. Frequency with which each twin was licked by its mother.

have any cleaning function. Figure 4 shows the frequencies with which *Chandra* licked the twins. No significant preference for one of the twins was found (Chi-square test; $p > 0.05$). The frequency of licking appeared to increase over the study period (*Solok*: $r_s = 0.93$, $p < 0.002$; *Sasak*: $r_s = 0.81$, $p < 0.01$). A comparison of the first six data points with the last five showed a significant increase for both infants (Chi-square test; $p < 0.05$).

AGONISTIC BEHAVIOUR DIRECTED BY *CHANDRA* TOWARDS *RAMA*

At the beginning of this study, *Chandra* frequently intervened whenever *Rama* came close to the twins or tried to touch them. The mother's interventions consisted of directing open-mouth threats or bites towards *Rama*, pushing her away or moving away from *Rama*. The frequencies of *Chandra*'s open-mouth threats towards *Rama* are shown in Figure 5. Threats became less frequent in the course of the study period ($r_s = -0.71$, $p < 0.05$): a comparison of the first six data points in Figure 5 with the last five revealed a statistically significant difference (Chi-square test; $p < 0.01$).

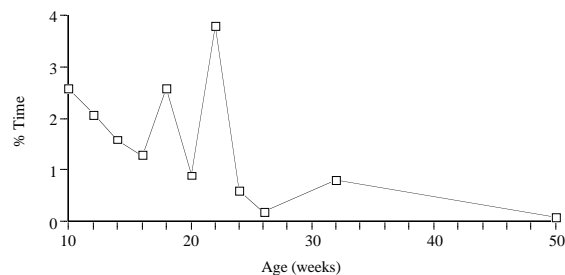


Fig. 5. Percentage of time *Chandra* directed agonistic behaviour at *Rama*.

DISTANCES

Chandra was never observed more than 20 cm away from her twin offspring until they were 24 weeks old (see Fig. 6b). In addition, the twins always remained closely together (< 20 cm) up to the age of 24 weeks (see Fig. 6a). As a result there was no difference between the twins in their distances from other family members. Only when the twins began to move around separately did these distances begin to differ (see Fig. 6b – d). A gradual reduction of the distances between the twins and *Dagobert* as well as between the twins and *Rama* was observed until the twins were 22 weeks old; during this period the frequency of the shortest

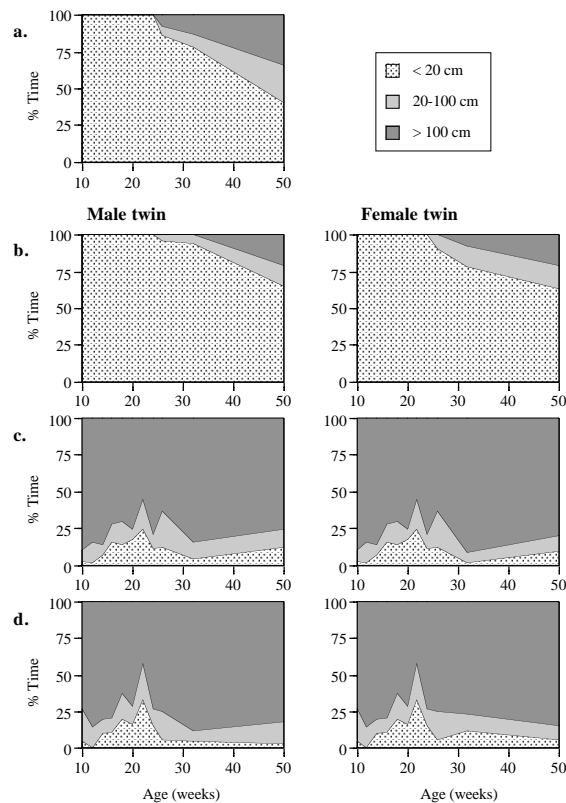


Fig. 6. Average distance between the twins (a), and between the twins and their mother (b), their father (c) and their older sister *Rama* (d), as expressed by the frequency of three distance classes. In (b – d), *Solok* is shown left and *Sasak* right.

distance class (< 20 cm) increased whereas the longest distance class decreased (> 100 cm). The frequency of the intermediate distance class (20 – 100 cm) remained relatively constant throughout the study.

In the later sessions, when the twins were 32 – 50 weeks old, *Rama* was more frequently observed to be close (< 20 cm) to *Sasak* than to *Solok*.

DEVELOPMENTAL MARKERS

The first occurrences of these markers are summarised in Table 1, together with comparable observations collected from earlier studies on the development of single offspring in siamangs and gibbons of the *lar* group.

Locomotion: During the whole study, *Chandra* was very protective towards her infants: when they began climbing alone, she often placed her hand on their backs if they were in danger of falling down, and she always stayed very close to them. When the infants became more competent in climbing, *Chandra* was frequently observed moving away from one of the twins (normally *Sasak*) for a distance of a few meters while carrying the other twin. A few seconds later, she usually returned to the abandoned infant, which had begun to move towards her,

Table 1. Age (in weeks) when ten developmental markers were first recorded in singleton siamangs and gibbons of the *lar* group (as reported in previous studies), and in the twin siamangs observed in the present study.

Developmental marker	Data from previous studies on singletons		This study
	Gibbon ¹⁾	Siamang	Siamang twins
1. Partial independence from mother (hangs on cage bars in contact with mother)	9 (BERKSON, 1966) 9 (IBSCHER, 1964, 1967)	9 (FOX, 1977)	≤8 (both twins)
Mean	9	9	≤8
2. Complete lack of contact with mother	6 (CRANDALL, 1946a, b) 12 (BENCHLEY, 1938a, 1938b) 13 (BERKSON, 1966) 14 (BRODY & BRODY, 1974) 14 (HINTERMANN, 1988, 1989) 15+16, n=2 (LINKE, 1988) 17 (STEINER, 1949) 18 (IBSCHER, 1964, 1967) 22 (ROBERTS, 1983)	13** (THETFORD, 1991) 14 (ALBERTS, 1987) 14 + 15, n=2 (ORGEL-DINGER, 1989a, 1989b, pers. comm.) 15 (LEE, 1976) 20+22, n=2 (FOX, 1977)	12 (female) 16 (male)
Mean	15	16	14
3. Suspension by one arm	13* (RUMBAUGH, 1965) 22 (BERKSON, 1966) 30* (LINKE, 1988)	24 (FOX, 1977)	20 (female) 22 (male)
Mean	22	24	21
4. Bimanual brachiation	10-18*, n=4 (BREZNOCK et al., 1979) 12* (RUMBAUGH, 1967b) 14 (BRODY & BRODY, 1974) 14-16, n=7 (BREZNOCK et al., 1979) 22 (CRANDALL, 1946a) 22* (WELT & WELKER, 1963) 26 (BERKSON, 1966) 32 (LINKE, 1988) 31-34* (LINKE, 1988, 1989) 39 (ROBERTS, 1983)	35 (FOX, 1977)	30 (both twins)
Mean	21	35	30
5. Bipedal locomotion	24 (LINKE, 1988) 26* (WELT & WELKER, 1963) 26-27* (LINKE, 1988, 1989) 39 (BERKSON, 1966) 39 (ROBERTS, 1983) 41* (RUMBAUGH, 1966, 1967b) 43* (SAWINA & OPACHOWA, 1981) 44 (IBSCHER, 1964) 65 (CRANDALL, 1946a)	43 (FOX, 1977)	32<x<50 (both twins)
Mean	39	43	32<x<50
6. Feeding on solid food	10-15*, n=4 (BREZNOCK et al., 1979) 11+17, n=2 (IBSCHER, 1964) 15 (HINTERMANN, 1988) 16-20, n=7 (BREZNOCK et al., 1979) 17 (BERKSON, 1966) 17 (CRANDALL, 1946a, b) 17, n=3 (MARTIN et al., 1979) 17 (ROBERTS, 1983) 19 + 29, n=2 (LINKE, 1988) 26 (STEINER, 1947, 1949) 35* (LINKE, 1988)	9 (FOX, 1977) 12 (ALBERTS, 1983) 13** (THETFORD, 1991) 13 + 15, n=2 (ORGEL-DINGER, 1989a, pers. comm.)	16 (both twins)
Mean	19	12	16
7. Play with siblings	16 (IBSCHER, 1964) 30 (ROBERTS, 1983)	15 (ORGELDINGER, 1989a) 43 (FOX, 1977)	12 (between twins) 14 (with older sister)
Mean	23	29	13
8. Being groomed by siblings	9 (ROBERTS, 1983)	4 (ORGELDINGER, pers. comm.) 22 (FOX, 1977)	≤8 (both twins)
Mean	9	13	≤8
9. Grooming (allogrooming)	26 (BERKSON, 1966)	36 (ORGELDINGER, pers. comm.) 54 (FOX, 1977)	Not observed until the end of this study (50 weeks)
Mean	26	45	-
10. Infant calling (throat sac inflated)	-	23 (ORGELDINGER, pers. comm.) 35 + 39, n=2 (FOX, 1977)	12 (both twins)
Mean	-	32	12

1) Species: *Hylobates lar* (BERKSON, 1966; CRANDALL, 1946a, 1946b; MARTIN et al., 1979; ROBERTS, 1983; SAWINA & OPACHOWA, 1981; WELT & WELKER, 1963); *H. lar* x *H. moloch* (RUMBAUGH, 1965, 1966, 1967b); *H. moloch* (BENCHLEY, 1938a, 1938b; at least the infant's mother was of that species, judging from the photographs); *H. muelleri* (BRODY & BRODY, 1974; LINKE, 1988, 1989); *H. pileatus* (HINTERMANN, 1989); *H. pileatus* x *H. lar* (IBSCHER, 1964, 1967; STEINER, 1947, 1949). BREZNOCK et al. (1979) reported on two groups of gibbons: their sample of mother-reared animals (n=7) was *H. lar*, the sample of hand-reared gibbons included two *H. lar* and two *H. pileatus*. * hand-reared; ** reared by foster mother; n = 1 in all studies except where noted otherwise.

showing signs of distress. At the end of the study period, both twins were capable of bimanual brachiation and bipedal locomotion.

Feeding behaviour: From the age of 12 weeks onward, both twins were observed biting and chewing solid items such as leaves and apples, but it was impossible to determine whether they swallowed the food or not. The first time they were seen consuming solid food with certainty was at the age of 17 weeks. At about the same time, they were first observed to attempt taking food away from the mother. *Chandra* and the other family members were never observed to take food from the twins.

Infant calling: Both twins clung to their mother during song bouts of the family group. At the age of 12 weeks, they could already clearly be observed to inflate their throat sacs during these loud vocalisations, but through the glass front of the cage it was impossible to hear whether the infants were actually vocalising. When they were 16 weeks old, their mouths could clearly be seen to be opened during the song bouts in the typical fashion of singing siamangs, i.e. while their throat sacs were inflated. The infants appeared to vocalise mainly at the beginning of great call sequences (see GEISSMANN, 1984; and HAIMOFF, 1981).

DISCUSSION

GENERAL OBSERVATIONS ON THE TWINS' DEVELOPMENT

Feeding behaviour: The data of the present study confirm those of BERKSON (1966) and FOX (1977), who observed attempts of gibbon and siamang infants to take food from the mother at about the same time as when they first began eating solid food.

Self-directed orality: Thumb-, finger- or toe-sucking has repeatedly been observed in young captive gibbons and siamangs, in both hand-reared and in mother-reared animals (BREZNOCK et al., 1979; FOX, 1977; IBSCHER, 1967; RUMBAUGH, 1965, 1966, 1967a, b). Self-directed orality was exhibited by the twins from the beginning to the end of the present study.

Infant grooming: The father *Dagobert* groomed the infants significantly less frequently in the second part of the study than in the first part. This decrease in grooming frequency can possibly be explained as a loss of interest in his offspring as the "novelty" effect wore off.

Infant licking: "Licking", as defined in the present study, is probably identical to "kissing", as reported by LEE (1976), in spite of the following differences: whereas this behaviour was only directed from the mother towards her infants in the present study, it was also shown by the father towards his infant in LEE's study (1976). It should be mentioned that that father frequently carried the infant, unlike the siamang father in the present study. In addition, LEE (1976) reported a constant frequency of licking during her observations. In contrast to her report, licking occurred with increasing frequency during the present study. Both the function of licking as well as the reason for its increase in frequency are unclear. Licking does not appear to have a cleaning function, because it is not usually repeated. Instead it may serve as a signal directed from the care-giving animal towards the infant. The observer had the impression that licking was frequently shown when an infant returned to the mother.

Distances: The initial increase in the frequency of the shortest distance (< 20 cm) between the twins and their older sister *Rama*, and between the twins and their father *Dagobert* probably reflect a gradual reduction in the mother's protectiveness of her infants. The frequency of the shortest distance class between the twins and other family members decreased again after the age of 22 weeks, possibly as a result of their growing independence. In addition, it appeared that the father had lost interest in his offspring by that time. Both twins, after achieving motor independence from the mother, still remained close to her and close to each other (< 20 cm) up to the age of 24 weeks and began to move around independently thereafter.

COMPARISON BETWEEN TWIN AND SINGLETON SIAMANGS

For eight of the ten developmental markers reviewed some information is now available for both twin and singleton siamangs (Table 1). The majority of these markers (seven out of eight) were attained earlier by the twins than by singletons, suggesting that the twins of the present study developed faster than singletons, although this result must be viewed with caution because the development of only a few siamang infants has been studied to date.

The beginning of social play between an infant and its older siblings is probably influenced by the mother, which may tend to protect the infant from the rough play of older animals. Because the twins had the same age, they were less likely to hurt each other when playing, and, hence, there was less reason for the mother to intervene. This may explain why the twins began to play earlier than single offspring.

The older sister *Rama* frequently tried to touch the twins and to play with them. The frequency of the mother's agonistic reactions to these attempts decreased with time. The reduction in the mother's protectiveness may be due to the twins' growing mobility; it may have become increasingly difficult for the mother to constantly keep track of, and defend, both twins. This may have further advanced the onset of the twins' play behaviour directed at older siblings as compared to singletons of siamangs (and gibbons) observed in previous studies.

COMPARISON BETWEEN THE TWINS

The female twin *Sasak* totally abandoned the mother's body for the first time at the age of 12 weeks; the male *Solok* did the same about one month later, at the age of 16 weeks. *Sasak* spent more time alone than her twin brother during most of the period covered by this study. Moreover, *Sasak* was observed playing with her older sister *Rama* more frequently than *Solok*. The frequency of being alone and the frequency of playing with *Rama* show a similar increase over time in both twins (Figs. 1a & 2c), except that the female twin always appears to be several weeks ahead of the male in her development. Nonetheless, no marked difference in body size between the twins was observed.

Because carrying two infants simultaneously represented an additional burden on the mother, she may have neglected or otherwise encouraged one of the twins, probably the stronger one, to leave her body earlier than usual.

The two twins received about the same amounts of grooming from the various family members. Although the mother tended to be less protective towards one of the twins (especially during the second part of the study), this did not appear to influence the amount of grooming directed towards that twin.

CARRYING AND HELPING

In the siamang group studied, the twin offspring were never seen being carried either by their father or by their older sister *Rama*. Although many studies confirm that male siamangs typically carry their offspring at some stage of their development (ALBERTS, 1983, 1987; CHIVERS, 1974; DIELENTHEIS et al., 1991), the male at the Zürich Zoo has been observed carrying his offspring only in exceptional situations (see Introduction). The unusual presence of two offspring simultaneously, instead of only one, did not induce a change in this behavioural characteristic. It should be noted that the Zürich male was born in captivity and hand-reared, whereas the male in the study of DIELENTHEIS et al. (1991) was presumably wild-born and, therefore, mother-reared at least during his earliest infancy (Mr. R. OPITZ, pers. comm. to T.G.).

Because the twins' older sister also failed to exhibit any infant carrying, this study does not confirm the hypothesis that the presence of multiple offspring may facilitate the occurrence of infant-carrying by non-parental family members (DIELENTHEIS et al., 1991). This result, however, should be regarded with caution, for the following reasons: the only available non-parental family member (*Rama*) was an infant only 1.4 yrs old at the beginning of the study and a 2.2-yr-old juvenile at the end. By contrast, the male in the study of DIELENTHEIS et al. (1991) was a 2.7-yr-old juvenile. This age difference may have led to different results in the two studies, because the infant *Rama* may not have been strong enough to carry one of the twins, or because she was too young to develop an interest in infant-carrying, i.e. a behaviour which is normally exhibited only by adult siamangs.



Fig. 7. The twins at the age of 59 days (June 30, 1992), with the female infant clinging to the mother's lower leg while being carried in an unusual position.

The absence of helping behaviour in the present study does not appear to result from the mother being overly protective: as soon as the twins were beginning to climb unaided, *Chandra* was observed to leave one of them (mostly *Sasak*) for brief periods of time, as if to accustom the infant to her absence. If the twins' older sister *Rama* tried to approach the lone twin, *Chandra* usually threatened her, but as the twins grew older the mother's open-mouth threats became less frequent. During the final observation sessions, *Sasak* was frequently observed climbing alone far away from the mother, which did not show any reaction when *Rama* approached the twin. The observer had the impression that *Chandra* would have tolerated any attempt by *Rama* to carry *Sasak*. Interestingly, *Chandra* reacted more aggressively when *Rama*'s attentions were directed towards the male infant *Solok*.

When only one twin was carried, it commonly occupied a central position on the mother's belly. On the other hand, when both twins were carried simultaneously, one was carried on the left and the other on the right. The male *Solok* was carried more often on the right and the female *Sasak* on the left, particularly up to the age of 15 weeks. Apparently, the twins exhibited a distinct side preference, especially during the first months of life. The limited ability of the infants to move during their first months of life could have promoted their constant position on the mother's body.

Chandra was never observed to have any problem in carrying two infants simultaneously, in contrast to some reports on other twins in catarrhine primates (GEISSMANN, 1989). Because the twins were already two months old at the beginning of this study, it is possible that the mother experienced carrying problems before that time. This is supported by the observation that, during the pilot phase to this study and early on in the study itself, the twins were occasionally carried in potentially dangerous positions (Fig. 7).

COMPARISON BETWEEN GIBBONS AND SIAMANGS

The ages at attainment of developmental markers in captive siamangs and gibbons of the *lar* group are reviewed in Table 1. For nine of the ten markers examined, some information is available for both gibbons and siamangs. If only singletons are considered, seven of nine markers are attained earlier by the gibbons; the siamangs are earlier for one variable, and for another there is a tie.

From a comparison of the body measurements taken of one gibbon and one siamang (both hand-reared) during their first year of life (RUMBAUGH, 1967a), GROVES (1972) tentatively suggested that the siamang may have a longer maturation period than gibbons of the *lar* group. The present review also suggests a difference between gibbons and siamangs in their behavioural development. As mentioned above, this result must be regarded with caution, due to the small size of the samples. If the data for the twins are added to the siamang sample, the difference between gibbons and siamangs is less distinct: gibbons are earlier in five markers, siamangs in three (1 tie).

CONCLUSIONS

1) Comparison of the data collected in this study with those from earlier studies suggests that the twins developed faster than single siamang offspring. Following a hypothesis of DIELENTHEIS et al. (1991), this may be a consequence of the decreased protectiveness of the mother, which may reflect the difficulty of constantly keeping track of two offspring simultaneously.

- 2) Comparison between the twins suggests that the female *Sasak* had a developmental advance of about 4 weeks over her twin brother *Solok*, i.e. leaving her mother earlier and more frequently, and playing more frequently with her older sister *Rama*. It is possible that one of the twins was stimulated by its mother to leave her sooner because she may have been more inclined to be temporarily free of at least one infant.
- 3) Neither the twins' father nor their older sister *Rama* was ever observed carrying the twins. Hence, this study fails to support the hypothesis that the presence of multiple offspring may facilitate the occurrence of infant-carrying exhibited by a non-parental family member in siamang (DIELENTHEIS et al., 1991). It is possible, however, that the twins' older sister *Rama* did not carry the twins because she was so young (younger than the juvenile in the study of DIELENTHEIS et al., 1991). It is unlikely that the lack of carrying behaviour exhibited by *Rama* can be attributed to the reluctance of the mother to let her daughter carry one of the twins.
- 4) A comparison of the developmental data appears to support the hypothesis that siamangs have a longer maturation period than gibbons of the *lar* group (GROVES, 1972), but only if the twins are not added to the siamang sample.

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