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BEHAVIOURAL DEVELOPMENT OF A PILEATED GIBBON

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Introduction

The early development of individual gibbons has only rarely been studied in detail. A recent review of the behavioural development of gibbons (Dal Pra and Geissmann, 1994) revealed that (1) most published data stem from anecdotal observations on a few individuals, and (2) most of the few scientific studies specifically dedicated to infant development were carried out on only two species, the white-handed gibbon (*Hylobates lar*) and the siamang (*H. syndactylus*).

It has been suggested that siamangs may have a longer maturation period than gibbons of the *lar* group (Groves, 1972, p. 32). A difference in behavioural development has been supported by a review of data from the literature, but, as mentioned by the authors, this result must be regarded with caution, due to the small size of their samples (Dal Pra and Geissmann, 1994). Clearly, more data are required.

The pileated gibbon is a member of the *lar* group (Geissmann, 1993, 1994, 1995). In spite of its high conservation priority rating (Eudey, 1987), little is known of its reproductive biology (Badham, 1967; Oosterhuis, 1975) or of its behavioural development (Hintermann, 1988, 1989; Srikosamatara, 1980).

During this study, the behavioural development of an infant pileated gibbon reared in its natal group at Zürich Zoo, Switzerland, was studied during its first year of life. The study attempted to answer the following questions:

1. How does the development of the infant pileated gibbon compare to the development of other gibbons of the *lar* group?
2. Does the development of the infant pileated gibbon support the view that the behavioural development of gibbons of the *lar* group differs from that of siamangs?

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 years of age; juveniles 2.1 to 4 years; subadults 4.1 to 6 years; adults more than 6 years. The family group studied had the following composition:

(1) *Iaman*, adult male, wild-born in about 1959, previously at Saarbrücken Zoo, Germany, arrived at Zürich Zoo on 16 November 1982, about 33 years old at the beginning of this study;

(2) *Iba*, adult female, wild-born, imported from Bangkok, adult when arrived at Zürich Zoo on 29 October 1982, at least 15 years old at the beginning of this study;
(3) *Quang*, juvenile male, born at Zürich Zoo on 11 July 1990, 3.1 years old at the beginning and 4.0 years at the end of this study; and
(4) *Tuk*, infant female, born on 26 June 1993, 0.1 years (7 weeks) old at the beginning and 1.0 years (52 weeks) at the end of this study.

Adult female pileated gibbon Iba at Zürich Zoo, 11 April 1994, carrying her female infant Tuk (born on 26 June 1993). The adult male Iaman sits in the background (Photo: Christian Braendle)

All offspring born to this pair were reared by their mother (including, in addition to those present during this study, the males Khmer, 28 Nov. 1984, and Nong, 21 Aug. 1987).

Housing

The family group was kept in an indoor cage (base area 18 m^2, height 5 m), with additional access to an outdoor cage (30 m^2 x 4.6 m) during warm weather. Both cages had ropes in addition to horizontal, vertical and oblique bamboo poles.

Observation Time

The group was observed by one of us (C. B.) from 13 Aug. 1993 to 26 June 1994, i.e. when the infant was aged between 7 and 52 weeks (with gaps when the infant was 16–17 and 36–39 weeks old).

During the observation period, the gibbons were observed between 08:30 and 16:30, in order to cover their activity period effectively. Observation sessions lasted about four hours 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 156 hours.

Method

In order to facilitate comparison, the observation method was largely adopted from Dal Pra and Geissmann (1994). All behavioural variables were collected with the scan sampling method using instantaneous sampling. They were recorded every 30 sec., and the number of occurrences as a percentage of the total number of sample points was used as a direct estimate of the proportion of time for which the behaviour occurred (Martin and Bateson, 1993).

The behavioural variables recorded were as follows:

(1) *Rest*: The infant is lying or sitting in a stationary posture.
(2) *Locomotion*: The infant is exhibiting any type of locomotor movement.
(3) *Feed*: The infant is biting, mouthing or consuming solid food.
(4) *Away from mother*: The infant is not in physical contact with its mother.
(5) *Being carried*: The infant is being carried by another animal, which, while stationary or moving, provides weight-supporting contact with the carried animal.
(6) *Physical contact*: The infant is in physical contact with, but not being carried by, the mother.
(7) *Play* (social play): Play behaviour 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 since the bitten animal does not show signs of pain or injury. Only play behaviour exhibited by or involving the infant was recorded. (It is sometimes difficult to determine whether a gibbon is actually playing or whether its bites represent agonistic behaviour. In case of uncertainty,

these bites were classified as social play.)
(8) *Groom*: 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). Only grooming behaviour exhibited by or involving the infant was recorded.
(9) *Agonistic behaviour*: Open-mouth threats or bites directed from one animal towards another. Not only instances of agonistic behaviour involving the infant were recorded, but also those directed from Iba towards the juvenile Quang. A more detailed description of the variability of these behavioural patterns can be found in Baldwin and Teleki (1976: *H. lar*) and Orgeldinger (1994: *H. syndactylus*).

Inter-individual distances between all four family members (six distances in all) were estimated and assigned to one of the following three categories: (A) less than 20 cm; (B) 20–100 cm; and (C) more than 100 cm. These distances were recorded every five min with the scan sampling method (instantaneous sampling). The frequency of occurrence of each distance category (A, B, 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 infant: (1) Partial independence from mother (infant hangs on cage bars in contact with mother), (2) complete lack of contact with mother, (3) suspension by one arm, (4) bimanual brachiation, (5) bipedal locomotion, (6) feeding on solid food, (7) initiating play with siblings, (8) being groomed by siblings, (9) grooming (allogrooming), and (10) participation in group calls.

For statistical analysis, we used the statistical software *StatView*, version 4.02 (Abacus Concepts), with a significance level of 0.05. Spearman rank correlation coefficients (r_S) were calculated between each behavioural variable and the infant's age, as a measure of developmental trends.

Results

Changes in the Frequency of Behavioural Variables

Unless noted otherwise, the frequency of a behavioural variable was not correlated with the infant's age.

Figure 1 shows a gradual decrease in the percentage of time the infant spent resting as a function of the infant's age ($r_S = -0.97$, $P < 0.0001$), with a corresponding increase in time spent in locomotion and feeding on solid food ($r_S = 0.97$, $P < 0.0001$, and $r_S = 0.68$, $P < 0.004$, respectively).

Similarly, Figure 2 shows a decrease in the percentage of time the infant was carried by the mother ($r_S = -0.93$, $P < 0.0001$), while the time it spent away from the mother increased correspondingly ($r_S = 0.94$, $P < 0.0001$). The time the infant spent in contact with the mother without being carried seemed to follow a more complex pattern, increasing considerably when the infant was 14–18 weeks old, and decreasing slowly thereafter (Fig. 2). Only at the beginning of this study (up to an age of 12 weeks) did the infant spend 100% of the observation time in contact with the mother.

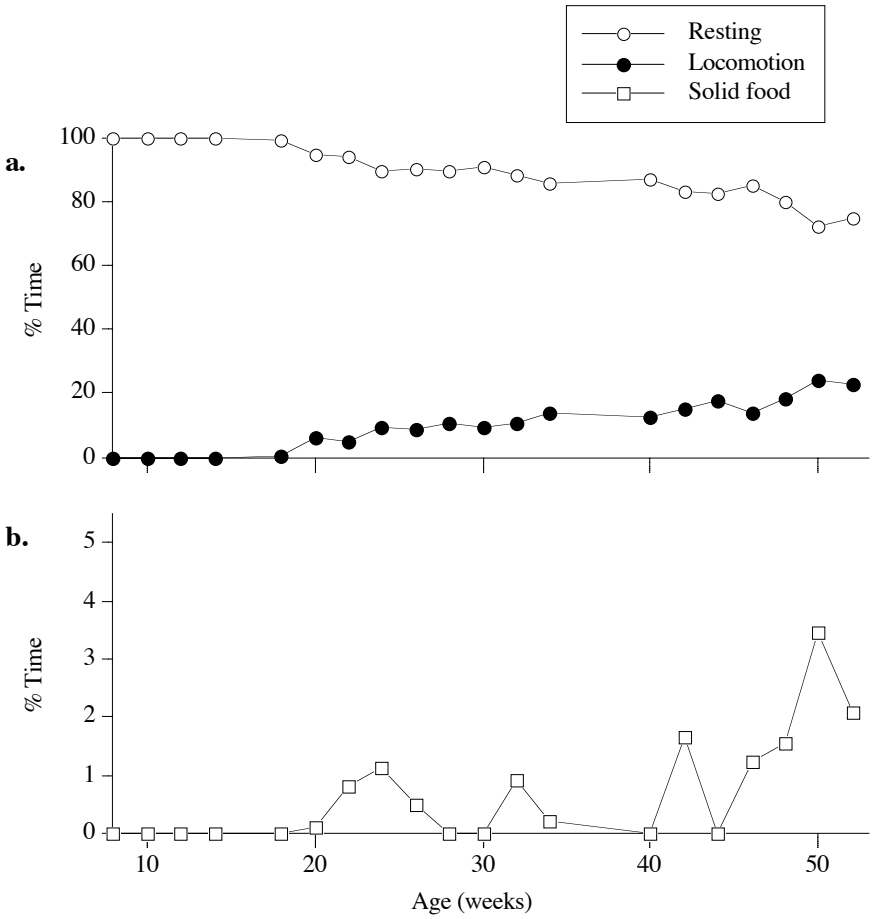

Figure 1. Percentage of time the infant was resting (a), performed locomotion (a), and was biting, mouthing or consuming solid food (b). Notice that scales of the vertical axis are different in (a) and (b).

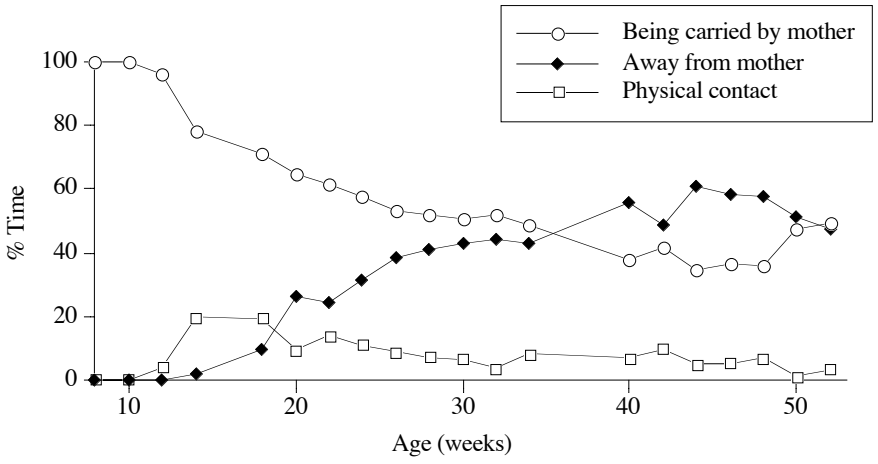

Figure 2. Percentage of time the infant was carried by the mother, spent away from the mother, or spent in contact with the mother, without being carried.

During this study, the infant was never observed being carried by its father, but when the infant was 29 weeks old, it was first observed being carried by its older brother Quang. The percentage of time the infant was carried by its brother reached its highest level (1.4%) in the following week and decreased slightly afterwards.

The percentage of time the mother directed agonistic behaviour at Quang remained relatively stable during the study period and was correlated neither with the infant's age nor with the frequency with which Quang carried the infant. Early during this study (week 11), Iba already let Quang come close to the infant and gently touch it. She only intervened whenever he tried to handle it roughly or started a mock-attack. The mother's interventions consisted of directing open-mouth threats or bites towards Quang, and occasionally chasing him.

The percentages of time that Iaman, Quang and Iba spent grooming the infant and playing with it are shown in Figures 3a and 3b, respectively. The mother remained the main groomer of the infant during the whole observation period. The father was never observed to groom the infant, and Quang was observed doing so rarely and only towards the end of the study period (weeks 42 and 50).

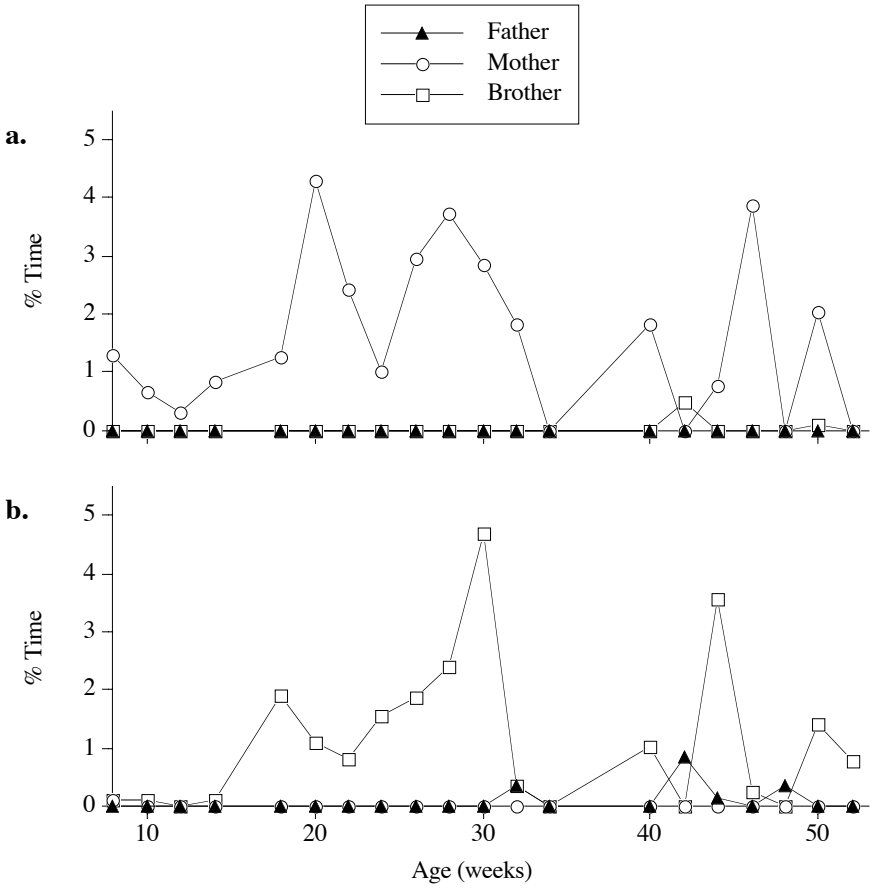

Figure 3. Percentage of time the various family members spent grooming the infant (a) or playing with the infant (b).

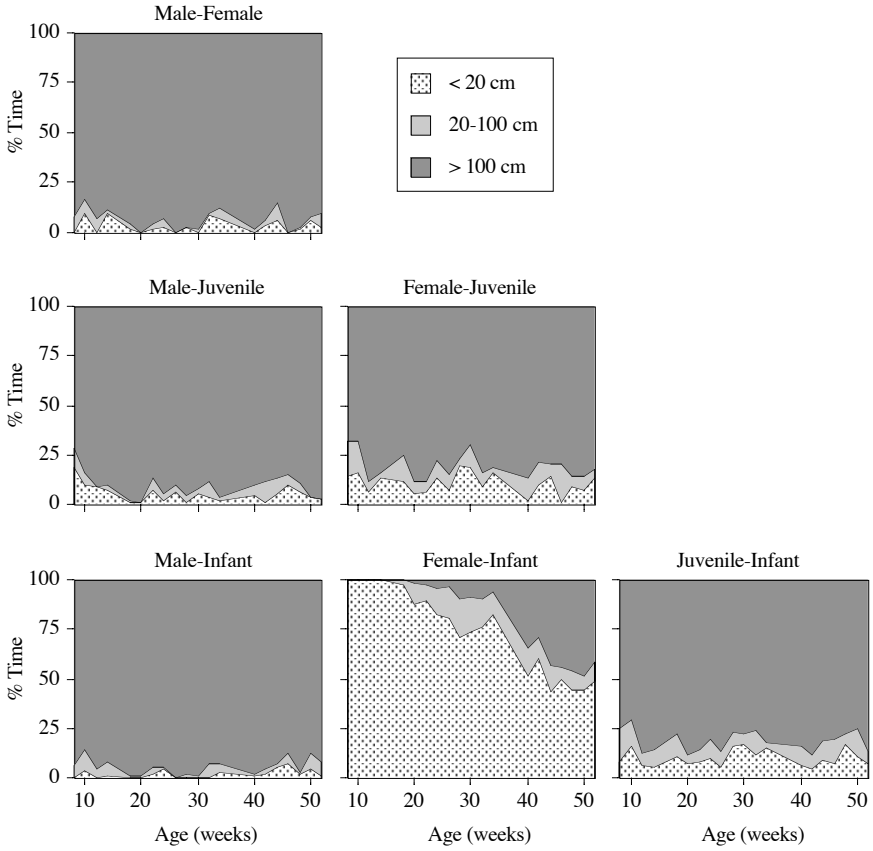

Figure 4. Average distances among all family members, as expressed by the frequency of three distance classes.

From the beginning of this study onwards, the infant was also observed playing with Quang (Fig. 3b). Play was almost invariably initiated by Quang, who became the infant's main partner for playing when the infant was 18 weeks old. Excepting one brief occasion at the beginning of this study (week 8), Iba was not observed to play with the infant, although she was observed doing so with Quang. The infant's father was rarely observed to play with the infant, and only during the second half of this study, starting in week 32.

During the study period, the infant itself was never observed to exhibit grooming behaviour or agonistic behaviour towards other family members, and no clear agonistic behaviour was ever observed being directed at the infant. The infant directed play behaviour exclusively towards its older brother. These occasions were rare (beginning with week 27).

Only once (week 19) was the mother observed to apply a single lick on the infant's face (similar to a kiss); this licking behaviour did not seem to have any cleaning function. From the beginning of this study until the infant was 31 weeks old, it was frequently observed to suck its thumbs

(and twice its great toes). The parents were observed copulating twice during the second half of the study (weeks 43 and 45), without any disturbance from their offspring.

Iba was never observed more than 20 cm away from the infant until it was 14 weeks old (Fig. 4). There is a gradual decrease in the proportion of the shortest distance class (< 20 cm) between the mother and the infant, and a corresponding increase in the proportion of the longest distance class (> 100 cm) ($r_S = –0.94$, $P < 0.0001$ and $r_S = 0.96$, $P < 0.0001$, respectively). No clear trend was observed in the inter-individual distances among the other group members (Fig. 4).

Developmental Markers

The first occurrences of these markers in the pileated gibbon studied here are summarised in Table 1, together with comparable observations from earlier studies on the behavioural development of siamangs and gibbons of the *lar* group.

During Tuk's early attempts at climbing, Iba was protective towards her infant and often held it with one hand if it was in danger of falling down (week 12). Even at the age of 19 weeks, the infant was still well guarded by its mother, who never withdrew more than one metre from the infant. At the age of 17 weeks, the infant was capable of bimanual brachiation, but its dexterity at this showed considerable improvement only at the age of 21 weeks. Even then, Iba was never more that 5 m away from the infant. At 27 weeks, Tuk displayed typical bipedal locomotion.

From the age of 12 weeks onward, the infant was observed biting and chewing solid food items such as leaves and fruits, but it was impossible to determine whether it swallowed the food or not. At the age of 20 weeks, Tuk developed pronounced interest in solid food, and in week 21, she was first observed to attempt taking food away from her mother, without success: after Tuk bit into the item (a piece of carrot) several times, Iba held it away from her reach. The first time Tuk was seen consuming solid food with certainty was at the age of 25 weeks, but it is likely that she had consumed solid food earlier.

The adult pair produced duet songs on about 60% of 20 observation days. Early during this study, Tuk kept clinging to its mother during songs. The infant did not show signs of excitation, but rather seemed to be slightly confused. When she had become more independent, she was repeatedly observed to continue her ongoing activities during her parents' song bouts, seemingly without being influenced by the song. Tuk was never observed to vocalise during the song bouts. Even her juvenile brother only once tried to participate during a song bout of his parents (week 12). He produced short phrases during the second half of the great call sequences (Geissmann, 1993), but soon stopped singing and was not heard again during this study.

Discussion

General Observations on the Infant's Development

The behavioural development of the pileated gibbon observed during this study was largely comparable to that reported for other gibbon species of the *lar* group, with the exception of grooming behaviour: Tuk was first

Table 1. Age (in weeks) when 10 developmental markers were first recorded in gibbons of the *lar* group and siamangs (extracted from the review in Dal Pra and Geissmann, 1994), and in the pileated gibbon observed in the present study.[1]

Developmental marker		*lar* group	*Hylobates pileatus*	*Hylobates syndactylus*	*Hylobates syndactylus* (twins)
1. Partial independence from	Mean	9	11	9	≤8
mother (hangs on cage	Range	9			≤8
bars in contact with her)	Sample size	2	1	1	2
2. Complete lack of	Mean	15	12	16	14
contact with mother	Range	6–22		13–22	12–16
	Sample size	10	1	7	2
3. Suspension by one arm	Mean	22	17	24	21
	Range	13–30			20–22
	Sample size	3	1	1	2
4. Bimanual brachiation	Mean	21	17	35	30
	Range	10–39			30
	Sample size	12	1	1	2
5. Bipedal locomotion	Mean	39	27	43	32<x<50
	Range	24–65			32<x<50
	Sample size	9	1	1	2
6. Feeding on solid food	Mean	19	25	12	16
	Range	10–35		9–15	16
	Sample size	17	1	4	2
7. Play with siblings	Mean	23	27	29	13
	Range	16–30		15–43	12–14[2]
	Sample size	2	1	2	2
8. Being groomed by	Mean	9	42	13	≤8
siblings	Range			4–22	≤8
	Sample size	1	1	2	2
9. Grooming (allogrooming)	Mean	26	>52	45	>50
	Range			36–54	>50
	Sample size	1	1	2	2
10. Infant calling	Mean	–	>52	32	12
	Range			23–39	12
	Sample size		1	3	2

[1] Species in samples of the *lar* group include: *H. lar*, *H. lar* x *H. moloch*, *H. moloch*, *H. muelleri*, *H. pileatus*, *H. pileatus* x *H. lar*. Some studies summarising data from several animals did not indicate a mean age but a range at which the animals attained a particular developmental marker. In order to calculate mean age, we used these minimum and maximum values and counted them as a sample size of two.

[2] Between twins: 12 weeks; with older sibling: 14 weeks.

observed being groomed by a sibling at the age of 42 weeks, whereas Roberts (1983) observed this for an infant *H. lar* at the age of nine weeks. Whereas Berkson (1966) observed allogrooming behaviour of an infant *H. lar* at the age of about 26 weeks, Tuk was never observed to exhibit any grooming behaviour, although it was groomed by other family members. Likewise, some siamang infants were observed to groom during their first year of life, whilst others were not (Table 1). Possibly, grooming in infant groups shows so much individual variability that it is less suitable for use as a developmental marker.

Infant grooming was almost exclusively provided by the infant's mother, whereas her juvenile brother initiated most of the play behaviour involving the infant. Interactions between Tuk and her father were particularly rare, confirming the result of an earlier study on pileated gibbons (Hintermann, 1988).

Whereas the inter-individual distance between the mother and the infant continuously increased after the infant was 14 weeks old, distances among other family members did not seem to follow a recognisable trend.

Self-directed orality was exhibited by the infant from the beginning of the present study until it was 31 weeks old. Thumb-, finger- or toe-sucking appears to be a common element in behavioural repertoire of young captive gibbons and siamangs (see list of references in Dal Pra and Geissmann, 1994, p. 336).

'Infant licking' or 'kissing' occurred quite regularly during two studies on siamangs (Dal Pra and Geissmann, 1994; Lee, 1976), but it was observed only once during this study. The function of this behaviour is unclear.

Whereas infants and juveniles of the siamang, the hoolock and gibbons of the *concolor* group frequently contribute simple phrases to the song bouts of their parents (Geissmann, unpublished data), the infant of this study was never heard to vocalise during the songs, and even its juvenile brother was heard only once to utter a few phrases. Infant and juvenile song contributions may be less common in gibbons of the *lar* group. Possibly, immature animals are inhibited from singing in some of these species.

Carrying and Helping

Intensive paternal caretaking is a behavioural pattern frequently occurring in monogamous species (Kleiman, 1977). In our study group of pileated gibbons, the infant was never seen being carried by its father. This observation is in conformity with earlier gibbon studies suggesting that its occurrence differs among species. Whereas fathers in most gibbon species appear to exhibit little paternal care (Fischer and Geissmann, 1990), it is quite pronounced in siamangs (Alberts, 1983, 1987; Chivers, 1974; Dielentheis *et al.*, 1991; Lee, 1976), although the behaviour was found to be absent in some siamang family groups (Dal Pra and Geissmann, 1994; Orgeldinger, 1994; Palombit, 1992). Such carrying has been reported to begin in the second half of the infant's first year of life and to continue during the second year.

In contrast to the infant's father, her older brother *Quang* was repeatdly

observed carrying her during the second half of this study, albeit for brief periods of time only. Helping behaviour, defined as the care of offspring by individuals other than their parents, appears to be particularly common in monogamous mammals (Kleiman, 1977), but has only rarely been observed in gibbons. Our observation on helping behaviour is described and discussed in more detail a separate report (Geissmann and Braendle, in prep.).

Comparison between Gibbons and Siamangs

In the present study, the inter-individual distances were recorded with the same method as in a previous study on the development of siamang twins (Dal Pra and Geissmann, 1994). A comparison shows that the siamang twins still remained in close proximity to their mother (less than 20 cm) during 100% of the observation time until they were 24 weeks old, whereas the pileated gibbon only did so until it was 14 weeks old. At the age of 50 weeks, the siamang twins spent only about 21% of their time farther than 1 m away from their mother, whereas the pileated gibbon at the same age maintained this distance for more than 40% of the time. This comparison suggests that the pileated gibbon developed independence from its mother earlier than the siamang twins, although the latter were already thought to show a more rapid behavioural development than that reported for single offspring in siamangs. The difference between these two case studies does not, however, necessarily indicate a species-specific feature; it could be due to individual differences.

Dal Pra and Geissmann (1994) found that seven out of nine developmental markers are attained earlier by the gibbons than by siamangs, but only if the data for siamang twins are ignored. Adding the results of our study on the pileated gibbon to their data set, however, changes the mean values for the *lar* group just enough to make a clear distinction between the two samples less obvious (Table 1). Now, six of the nine markers are attained earlier by the gibbons of the *lar* group (nos. 2–5, 7, 9); the siamangs are earlier for three variables (nos. 1, 6, 8). Marker no. 10 (infant calling) may not be used to imply developmental differences, as discussed above.

The siamang sample is particularly small (only one or two individuals for seven of ten markers). Additional observations on the behavioural development of single-born siamangs would considerably improve the reliability of any conclusions that can be drawn from a comparison between siamangs and gibbons of the *lar* group.

Conclusions

1. The infant ‘s behavioural development was largely comparable to that reported for other gibbon species of the *lar* group (except that this infant was being groomed rarely and was never observed to exhibit grooming behaviour itself).
2. The hypothesis that siamangs have a longer maturation period than gibbons of the *lar* group is not reliably supported, possibly due to insufficiently large samples.

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