MASTERARBEIT

DIFFERENTIAL PARENTAL INVESTMENT AND BEHAVIOURAL DEVELOPMENT IN GIBBONS: COMPARISON BETWEEN SIAMANG (*SYMPHALANGUS SYNDACTYLUS*) AND LAR GIBBON (*HYLOBATES LAR*)

VERFASSER:
BAKKALAUREA BIOLOGIAE MANUELA LEMBECK

ZUR ERLANGUNG DES AKADEMISCHEN GRADES EINER
MAGISTRA RERUM NATURAE
(MAG.RER.NAT.)

AN DER NATURWISSENSCHAFTLICHEN FAKULTÄT DER KARL-FRANZENS-UNIVERSITÄT GRAZ
IN ZUSAMMENARBEIT MIT DEM STEIRISCHEN LANDESTIERGARTEN TIERWELT HERBERSTEIN

BETREUUNG
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MITBETREUUNG
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Februar 2009

DANKSAGUNG

Ich möchte mich bei all jenen bedanken, die mich auf vielfältige Weise bei der Durchführung dieser Arbeit unterstützt haben. Zunächst danke ich Prof. Dr. Skofitsch, der mich mit diesem Thema betreut hat und mir stets freie Hand ließ, meine Pläne in die Tat umzusetzen. Weiteres, dem tollen Team der Tierwelt Herberstein, allen voran der Geschäftsführerin, Doris Wolkner-Steinberger, die mich mit offenen Armen empfangen hat, sowie den zoologischen Leitern, Dr. Jochen Lengger und Mag. Thomas Lipp, die mich fachlich unterstützten und durch großes Interesse motivierten. Den Tierpflegern, insbesondere Renate Lederer, möchte ich danken, für ihre Bemühungen und für ihre offene Begeisterung, die sie für „meine“ Affen an den Tag legten und mich allmorgendlich mit Neuigkeiten versorgten. Danken möchte ich auch dem Team des Tiergartens Schönbrunn, besonders Dr. Schwammer, der sofort einverstanden war mit meiner Vorstellung einer vergleichenden Studie, sowie allen Tierpfleger des Affenhauses, die ebenfalls großes Interesse zeigten und alle meine Fragen geduldig beantworteten. Einen ganz besonderen Dank möchte ich Dr. Cornelia Franz aussprechen, da sie mich von Anfang an tatkräftig unterstützte, und sich dabei nicht nur fachlich, sondern auch persönlich sehr engagierte und das Tag und Nacht. Trotz ihres stressigen Alltags, bewundere ich sie für die Ruhe und gleichzeitige Zielstrebigkeit, die sie stets an den Tag legte, sowie ihr Bemühen meine Vorstellungen auszubauen, und dabei für mich neue Blickwinkel zu beleuchten, was für anregende Gespräche sorgte. In dem Zusammenhang möchte ich auch Mag. Elfriede Kalcher für ihre Fähigkeit statistische Fragen auf einfache Weise zu erklären loben, sowie ihre Scharfsinnigkeit auch nach mehreren Diskussionsstunden. Dr. Georg Desch muss ich für die Datenanalyse danken. Meiner Kollegin Marion Fruhmann müsste ich eigentlich an erster Stelle danken, da sie es war, die mich damals für ein Vorstellungsgespräch in Herberstein begeisterte und im Laufe der Zeit zu einer sehr lieben Freundin geworden ist, mit der ich nicht nur allzu oft das Auto, sondern auch alle Höhen und Tiefen der Diplomarbeitszeit gemeinsam teilen konnte. Einen lieben Dank auch an meine Kollegin Wiebke Hoffmann, die ich mit meinem Thema begeistern konnte und die mir ihre Daten zur Verfügung stellte. Ich bedanke mich auch sehr bei meinen Eltern, die mir das Auto über so lange Zeit borgten, geduldige Zuhörer waren und nie an meinen Fähigkeiten zweifelten. Nicht zuletzt muss ich meinen Geschwister und Freunden, insbesondere den Nicht-Biologen, dafür danken, dass sie immer mit viel Humor meinen Geschichten gegenüberstanden und mich auch mal gerne auf den Boden der Tatsachen zurückholten.

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ZUSAMMENFASSUNG

Siamangs und Weisshandgibbons leben in monogamen Familiengruppen, bestehend aus dem adulten Elternpaar sowie 1-3 Jungtieren. Kooperatives Fürsorgeverhalten ist bei monogamen Säugetieren am ehesten zu erwarten, allerdings ist wenig über die Unterschiede im Elterninvestment im Verlauf der Jungenentwicklung bekannt. Unterschiede in den Bedürfnissen des Nachwuchses im Verlauf der Ontogenese, sollten sich demnach auch in unterschiedlichem, elterlichem Rollenverhalten widerspiegeln. Dabei sollten Mütter als primäre Bezugspersonen in den ersten Lebensmonaten das Sicherheitsbedürfnis stillen, wohingegen der Explorationsdrang in späterer Jugend im väterlichen Spielverhalten überwiegt. Diese Annahmen wurden in einer Gruppe von Siamangs (n=4) im Tierpark „Tierwelt Herberstein“, sowie in einer Gruppe von Weisshandgibbons (n=4) im Wiener Zoo „Schönbrunn“, ebenfalls in Österreich, untersucht. Um das Sozialverhalten sowie die Jungenentwicklung beider Spezies zu vergleichen, wurden Daten zum Zeitpunkt gleicher Entwicklungsstufen gesammelt. Darüber hinaus wurde das Siamang Jungtier bis zu einem Alter von 6 Monaten kontinuierlich und ein Jahr später für einen weiteren Monat, beobachtet. Die Ergebnisse befürworten das Modell eines komplementären, elterlichen Rollenverhaltens, das in beiden Spezies offensichtlich wird. Darüber hinaus korreliert das zunehmende Alter des Siamang Jungtieres mit dem abnehmenden Bedürfnis an Körperkontakt mit dem adulten Weibchen, und der Zunahme sozialer Interaktionen in der Gruppe. Väterliche Fürsorge ist vorwiegend in Spielverhalten mit dem Nachwuchs deutlich und wurde wesentlich öfters beobachtet, als mütterliches Spiel. Das adulte Siamang Männchen spielte bevorzugt mit dem juvenilen Weibchen, was sich in höherer Frequenz und längere Dauer gegenüber dem Spiel mit dem adulten Weibchen unterschied. Weiteres wurde das Jungtier, wenn auch selten, vom adulten Männchen getragen. In der Weisshandgibbongruppe spielte das adulte Männchen ebenfalls mehr mit dem Nachwuchs im Vergleich zum adulten Weibchen. Im Gruppenvergleich ergab sich kein signifikanter Unterschied in Spielhäufigkeit und -dauer von adultem Männchen und juvenilen Weibchen. Dennoch investierte das Weisshandgibbon Männchen grundsätzlich weniger Zeit, als das Siamang Männchen in Spiel-, Kontakt- und Fürsorgeverhalten. Artunterschiede werden ebenfalls deutlich in signifikant niedrigeren Raten sozialer Interaktionen in der Gruppe der Weisshandgibbons im Vergleich zu Interaktionshäufigkeiten in der Siamangfamilie. Diese Unterschiede stimmen mit Ergebnissen aus Freiland- und Zooforschung überein, denen möglicherweise Mechanismen intra-spezifischer Nahrungskonkurrenz zu Grunde liegen.

ABSTRACT

Siamangs and lar gibbons live in monogamous family groups consisting of an adult pair and 1-3 offspring. Cooperative care for offspring is expected for monogamous mammals though little is known about the differential parental investment during infant development. Ontogenetic changes in the needs of the infant in respect to security and exploration should be reflected in differential parental investment. Mothers as the primary attachment figures are expected to provide security during the first months of life whereas fathers supply the need for exploration in play behaviour during later infancy. These assumptions are studied in a group of siamangs (n=4) in the wild animal park “Tierwelt Herberstein”, as well as in a group of lar gibbons (n=4) in the Vienna zoo “Schönbrunn”, both Austria, with similar group composition and infants of similar age. In order to compare social behaviour and infant development data for both species were collected at similar developmental stages of the infants. Additionally, the ontogenetic development of the siamang infant was tracked continuously until the age of six months. At the age of about one year, additional data on the infant’s activity budget were collected additionally. The results support a model of complementary parental investment with a higher amount of maternal investment in terms of caring behaviour during early infancy and a higher amount of paternal investment in terms of play behaviour in later juvenile stages in both species. In particular, a correlation between the siamang infant’s increasing age and the decreasing amount of mother – infant body contacts was found, which indicates prospective change in the infant’s integration in social interactions among the family group. Paternal care in the siamang group was mainly obvious in the more frequent play with the offspring compared to the adult female’s contribution. Further the adult male played significantly more often and longer with the juvenile female, than the adult female did and was observed, though rarely, to carry the infant. Similarly, the lar gibbon father was observed to spend more time in offspring – play than the adult female, particularly he played significantly more often and longer with the juvenile female. Nevertheless, the lar gibbon father invested less time in interactions with offspring than the siamang father. These results support the hypothesis of the siamang male to be outstanding among gibbons, as conducting intensive care in offspring rearing. Species differences are reflected in significantly lower rates of social interactions among family members in the lar gibbon group compared to the siamang group. These results are consistent with studies from both, the wild and captivity, possible originating from differing intra-specific feeding competition mechanism.

PUBLICATION

LEMBECK, M., FRANZ, C. Differential Parental Investment and Behavioural Development in Gibbons: Comparison Between Siamang (*Symphalangus syndactylus*) and Lar Gibbon (*Hylobates lar). Mamm. biol. Special issue to volume 73*:23-24

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Siamangs and lar gibbons live in monogamous family groups consisting of an adult pair and 1-3 offspring. Cooperative care for offspring is expected for monogamous mammals though little is known about the differential parental investment during infant development. Ontogenetic changes in the needs of the infant in respect to security and exploration should be reflected in differential parental investment. Mothers as the primary attachment figures are expected to provide security during the first months of life whereas fathers supply the need for exploration in play behaviour during later infancy. These assumptions are studied in a group of siamangs (n=4) in the zoo “Tierwelt Herberstein”, as well as in a group of lar gibbons (n=4) in the Vienna zoo “Schönbrunn”, both Austria, with similar group composition and infants of similar age. In order to compare social behaviour and infant development data for both species were collected at similar developmental stages of the infants. Additionally, the ontogenetic development of the siamang infant was tracked continuously until the age of six months. Results support a model of complementary parental investment with a higher amount of maternal investment in terms of caring behaviour during early infancy and a higher amount of paternal investment in terms of play behaviour in later infancy in both species. Species differences are reflected in significantly lower rates of physical contact and social interactions among family members in lar gibbons compared to siamangs. Accordingly, the siamang father invested more time in interactions with offspring than the lar gibbon father. This tendency is already obvious in significantly more and longer play contacts among the two siamang infants in comparison to the gibbon infants. These findings correspond to data on species differences from the wild which possibly originate in differing intraspecific level of food competition. Variation in the ontogenetic development of offspring in respect to changing demands is further investigated. Siamangs and lar gibbons as typical biparental species cooperate by emphasizing different parental roles tuned to the changing demands of infants during development.

INTRODUCTION

In mammals parental care is an energy costly time investment which is naturally mostly performed by mothers since it is associated with lactation (Bales & French & Dietz 2002). Beside nursing duties females additionally invest in other responsibilities such as carrying or protecting the offspring which may be critical for the infant survival and in return for the female's reproductive success. Such tasks, however, can be performed by individuals others than the mother thus decreasing maternal obligation. In primate societies also other responsibilities than lactation are performed, like carrying. For example siblings act as useful helpers in some twinning *Callitrichidae* species. It has been observed that sibling - infant carrying sometimes even more often occur than mother – infant carrying (Nicolson 1987). Fathers may also invest a lot, e.g. tamarin males almost exclusively care for the offspring with the exception of nursing. Similarly, in the small titi monkey (*Callicebus sp.*), males are known to care intensively for offspring. Relatedness is the basic prerequisite for cooperative infant care and accordingly, paternal infant care is predominantly known from monogamous species. On the other hand, a monogamous breeding system does not self-evidently result in direct male care, as in most pair-bond systems male participation is lacking (vanSchaik & Kappeler 1997). Monogamy is seen as a compromise between male and female reproductive interests and is present in species where infant survival is dependent on active female and male investment (Brotherton & Komers 2003), for example in birds. In only 14% of all primate species monogamy is common (Rutberg 1983, cited in Leighton 1987). Among old world monkeys only in barbary macaques and gibbons, males are known to participate in parental duties (Whitten 1987). Although, gibbons are regarded as a prime example for monogamy, species-specific differences are evident (Fuentes 2001).

Gibbon Socioecology

All gibbon species are prevalent in south-east Asian tropical rainforests. During a speciation process the sea level oscillations may have lead to isolated populations. Today almost all species are allopatric, with exception of the siamang (Geissmann 2003). Its habitats are the Sumatran and Malaysian rainforests and overlaps with the white-handed or lar gibbon's (*H. lar*) habitat and also with the agile gibbon (*H. agilis*) (Reichard 2003). The lar gibbon is mostly found in Sumatra and Malaysia, but also in some southeastern regions of Asia's continent, like Burma and Thailand, reaching as far as Southwest-Yunnan in China

(Geissmann 2003). However, recently due to the lack of sightings it is assumed that the lar gibbon became extinct in China (Geissmann 2008).

Gibbons are specialized on ripe fruits in high density, scattered in widespread food patches throughout the home range (Geissmann 2003), whereas the siamang is much more folivorous than other gibbon species (Whitten 1987). In a study of Palombit (1997) the siamang's fruit intake contains about 61%, in lar gibbons 71%. The biggest difference between siamang and lar gibbon is found in analyzing feeding behaviour on leaves: whereas mature leaves are ingested equally often by both species, the siamang feeds on young leaves the fourfold in comparison to the lar gibbon. Morphological adaptations are obvious in molar size and molar chewing surface (Raemaekers 1979, revised in Orgeldinger 1999). Moreover the increased body size of the siamang in comparison to the lar gibbon is regarded as typical for herbivores who need a larger intestine for digestion of leaves with the help of symbiontic bacteria. Frugivore and herbivore nutrition is supplemented with insect consumption (Geissmann 2003).

Gibbons are monogamous, whereas pairs stay together in the range of a few months until one mate's death (Chivers 1974). Sexual dimorphism is lacking and no dominance hierarchy among the adult pair is common, though the female usually leads the group when travelling between various feeding places (Leighton 1987). Fixed home ranges of about 20 to 40 hectares are defended (Geissmann 2003) in ritualized territorial behaviour patterns (Leighton 1987). Species-specific songs are conducted to maintain territory boundaries, but also play a part in gibbon pair-bonding. The quality of social pair bonds is obvious in mate related affiliative behaviour, but also in spatial relations (Orgeldinger 1999). Duetting pairs stay near to each other, are highly active in mutual grooming as well as show a high synchronization in daily behaviour patterns (Geissmann & Orgeldinger 2000).

Explanations for gibbon mating systems are still discussed and several hypotheses reviewed. According to observations on gibbon territorial behaviour, two assumptions become clear: One the one hand researchers assume that the male defends the female, as it has been seen during group encounters, thus monogamy evolved from the male's necessity to guard its mate and protect it from other males. In this case the male can be sure of its paternity, but it is unclear, why males do not defend at least two females' separate ranges, which might be energetically possible for the male (Leighton 1987). Nevertheless, this hypothesis is still disputed. Others argue that the male defends not only the female, but also the territory with its access to food patches (Leighton 1987). Therefore in gibbon societies the female profits not only by the male's support in territory respective food resource defence (Wrangham 1987, revised in vanSchaik & Kappeler 1997), but also by his potential investment in offspring rearing (vanSchaik & Kappeler 1997). Due to the female's time-consuming investment in caring about the offspring over a long period of time, little time is left to defend the territory and the pair's reproductive success would lower (Leighton 1987). According to recent studies ecological factors might be influencing social monogamy in gibbons and support hypotheses assuming more flexibility in gibbon mating system. E.g. the lack of territories and mates can form multi-male gibbon groups, as it is the case in an area on Sumatra, being damaged by fire (Lappan 2007).

Gibbons live in nuclear family groups consisting of the adult pair and 1 to 3 offspring. The inter birth interval is about 2 years and after about 7 month gestation (until 8 months in siamangs) a single infant is born (Geissmann 2003). Twins are very rare and have only been reported in captivity so far (Dal Pra & Geissmann 1994, Dielentheis et. al. 1991). Gibbon young are totally dependent on the mother´s caring behaviour, especially in the first year of life. From the first day on, the infant clings on the mother's stomach until the age of about 15 weeks, when independent locomotion starts (Alberts 1987). From 8 months onward the infant is able to brachiate and at the age of 10 months to walk bipedal (Fox 1972, revised in Orgeldinger 1999). Lactation is usually not finished within the first year and soon before the next infant´s birth the shared sleeping place is given up (Orgeldinger 1999). In fact, much time is spent in rearing the offspring and only five to six young are born over the pair's reproduction lifetime (Tilson 1981, reviewed in Leighton 1987). Sexual maturity is reached at the age of 6 to 8 years for wild populations, whereas in captivity earlier maturity was sometimes observed (Geissmann 1991, reviewed in Geissmann 2003). Usually then the offspring leave its natal group, but sometimes remains until the age of 10 years without being expelled. Life expectancy is estimated for about 25 to 35 years in the wild and up to 50 years in captivity (Geissmann 2003).

Offspring Development

When looking at offspring development Carpenter (1964, reviewed in Bischof 1989) points out that parental cooperative time investment and complementary infant care occurs according to its varying needs for security and exploration during the ontogenetic development. The female as the primary attachment figure meets the needs for security by providing nutrition and protection essential during the first months of life. With increasing age the needs of the infant for security decrease, whereas needs for exploration grow. In socially monogamous groups peers are lacking, thus the adult male or siblings act substitutionally. In contrast to the female, the male meets the needs for exploration in terms of social play. Play behaviour enhance proving strength and satisfies curiosity. Moreover, Carpenter (1964, reviewed in Bischof 1989) argues that with offspring's increasing age, social play gets rougher, loses its bonding character and therefore emphasizes migration behaviour.

Nevertheless, these variations are apparent in investment differences among the adult pair. Though, due to different social and mating systems in primate societies, male-infant relationships offer a lot of flexibility. In particular siamang (*Symphalangus syndactylus*) males feature more caring behaviour than other gibbon fathers, mainly obvious in supporting the female by carrying the infant. Only once, in 1933, a male Hoolock gibbon (*Hylobates hoolock*) has been seen to carry an infant (McCann 1933, cited in Reichard 2003), but this seems to be a unique event, since more sighting reports are lacking. Chivers (1974, cited in Whitten 1987) reported on wild siamang fathers not only carrying their infants in the second half of the first year of life, but also spending up to 78% daily activity budget with caring behaviour. Consequently the siamang gibbon is defined as outstanding in this respect and since then the male is mostly categorized as being an "intensive caretaker" (Whitten 1987). By now only a few sightings of males carrying infants are known and studies in captivity indicate a broad variation, as some siamang fathers were observed to carry their infants (Alberts 1987, Dielentheis et al. 1991) while others did not show any attempt or only in exceptional situations (Dal Pra & Geissmann 1994). Agreement is found in the siamang male to promote playing and exploration of his offspring, starting in the first year mainly by representing the preferred playing partner (Orgeldinger 1999). Nevertheless, group composition concerning presence and age of siblings may influence the distribution of social interactions among the individuals (Nicolson 1987). As some studies indicate, primarily the older sibling is involved in play behaviour with the infant (Dal Pra & Geissmann 1994, Fox 1972).

Further, it has been argued that siamangs may have a longer maturation period than gibbons of the lar group, measured on body size comparison during the infant's first year (Groves 1972). According to Dal Pra & Geissmanns (1994) behavioural study seven of nine behavioural development markers have been observed earlier in gibbon infants of the lar group in comparison to siamang infants, when summarizing past studies.

Socioecology Difference between Siamang and Gibbon

Socioecological theory suggests that species-specific feeding ecology determines social interaction patterns and relationship quality of conspecifics, as it might be the case in gibbons. Therefore patchy distribution and monopolisation of fruit diet should lead to contest competition among lar gibbons, whereas feeding competition in the more folivorous siamang is reduced among individuals of a group, indicating scramble competition (vanSchaik 1989, cited in Dunbar 1993). Further, species differences in social interaction contexts can be referred in various studies, supporting the hypothesis of the larger coherence found in siamang groups in comparison to lar gibbon groups (Fischer & Geissmann 1990). Lar gibbon pairs spend time in physical contact mostly when grooming, whereas siamang pairs spend much more time without grooming, in body contact. Further embraces are observed much more often among siamang pairs, than among lar gibbon pairs, indicating species differences in the more reciprocal and stronger pair bonds in the latter.

Study aim and Hypotheses

The aim of this study is to investigate male and female role allocation in relation to infant development. For the analysis of infant development I focused on a group of siamangs. For analysis of species differences I compared the siamang group with a group of lar gibbons both consisting of an adult pair, a juvenile and an infant, with similar age and gender composition. In order to relate social behaviour to infant development, especially its influence on changing interaction patterns, data on social interactions and spatial relations for both species were collected at similar developmental stages of the infants.

(1) According to the requirements of the infant during the first year of life a higher amount of maternal than paternal investment in terms of caring behaviour is expected in both species. (2) In terms of role allocation the father should spend significantly more time in contact with the juvenile than with the infant if the parents share parental investment. According to the requirements of the juvenile play should be the primary interaction between father and juvenile. (3) In the course of development of the siamang infant it is expected that with age close contacts with its mother decrease and with the father increase indicating the change in the infant's requirements and demands related to parental care.

In respect to species variation it is expected that (4) the lar gibbon father spends less time in close contact with his offspring in comparison to the siamang partner. Further, a higher group cohesion in terms of closer contacts among all group members is expected for the siamang group in comparison to the lar gibbon.

Overall a complementary parental investment with a higher amount of maternal investment in terms of caring behaviour during early infancy and a higher amount of paternal investment in terms of play behaviour in later infancy is expected for both species.

MATERIAL AND METHODS

Systematic and Morphology

The siamang (*Symphalangus syndactylus*) is a member of the family of Hylobatidae, whereas as the only species he belongs to the genus *Symphalangus*, which separation from the other genera occurred 8.6 million years ago (Chatterjee 2006). There are three other genera, which are *Hylobates* or *lar* group (including: *H. lar, H. pileatus, H. agilis, H. muelleri, H. moloch* and *H. klossi*), *Hoolock (H. hoolock)* and *Nomascus* or *concolor* group (including: *N. concolor*, *N. gabriellae*, *N.* sp. cf. *nasutus, N. leucogenys*) (Barndon-Jones 2004, as cited in Chatterjee 2006). Species exhibit no sex-biased body size or canine length, whereas pelage colour can vary. Forelimbs and fingers are extremely extended, which provides not only a facilitated food purchase, but also a very fast type of locomotion, known as brachiation. Thus, the siamang is also able to hang under food patches instead of sitting in the branch as other primates have to. When leaving treetops, bipedal walk is common and exceeds about 10 % of daily activity budget. The malayan word “siamang” means black, which is characterizing its black pelage colour, further it´s scientific name “symphalangus” originates from the greek expression “sym” as together and “phalangus” as phalanges, because most of all siamang individuals’ proximal limbs of the second and third toe, show a dermal conjunction (Hoffmann 1993, Preuschoft 1988, Weber 1928, Wolkin & Mayers 1980, revised in Orgeldinger 1994), as an adaption to arboreal life and locomotion (Geissmann 2003). A special adaptation is found in the siamang’s throat sac, most likely amplifying sound propagation, as it is only inflated while singing (Geissmann 2003).

Subjects

The focal study group on the siamang (Fig. 1) as well as lar gibbon group (Fig. 2) consists of an adult pair and two offspring each (Tab. 1). The siamang group is housed at the wild animal park “Tierwelt Herberstein”, Stubenberg, Austria, the lar group at the zoo “Tiergarten Schönbrunn”, Vienna, Austria.

STUDY GROUP	AGE CLASS AND SEX			
	ad Male	ad Female	juv Female	inf Female
Siamang (*Symphalangus syndactylus*)	Nelson	Yala	Terkina	Suri
Lar Gibbon (*Hylobates lar*)	Robert	Sipura	Semera	Baby*

Tab. 1: Study groups composition. According to the age classes of Geissmann (1993, reviewed in Orgeldinger 1999): as "infantile" at the age of 0-2 years, "juvenile" from 2.1-4 years, "subadult" from 4.1-6 years and "adult" from 6 years on. * No name was given yet at that time.

Fig. 1: Siamang study group (Photo: Manuela Lembeck)

Fig. 2: Lar gibbon study group (Photo: Manuela Lembeck)

The individuals are categorised to age classes according to Geissmann (1993, reviewed in Orgeldinger 1999: age 0-2 years: infant; age 2.1-4 years: juvenile; age 4.1-6 years: subadult; age more than 6 years: adult), because of a mostly accelerated maturity process in captive groups.

The siamang (*S. syndactylus)* group at Tierwelt Herberstein, Austria consists of *Nelson*, the adult male, at the time of data collection 8 years old, born on 5 September 1998 at Burger´s Zoo, Arnhem, NL, in Herberstein since 1 September 2003, *Yala*, the adult female, also 8 years old at the time of data collection, born on 7 June 1998 at Zoo Zürich, CH, in Herberstein since 3 September 2003, *Terkina,* at the time of data collection 2.4 years, the juvenile female, born on 25 February 2005 in Herberstein, *Suri,* the infant female, 0.1 years (5 weeks at the begin of the study), born on 11 April 2007 in Herberstein.

The lar gibbon *(H. lar)* group at Zoo Schönbrunn, Austria consists of *Robert*, the adult male, at the time of data collection 9 years old, born on 16 January 1998 at Zoo Hellbrunn, Salzburg, A, in Schönbrunn since 26 September 2001, *Sipura*, the adult female, at the time of data collection at least 19 years old (birthplace unknown), in Schönbrunn since 26 April 2002, *Semera*, the juvenile female, at the time of data collection 2.4 years old, born on 6 February 2005 in Schönbrunn, *Baby* (the infant's name was not yet defined), the infant female, at the time of data collection 0.2 years old (8 weeks at the begin of the study), born on 3 July 2007 in Schönbrunn.

Housing

The siamang group is kept in an indoor enclosure (base area 28 m^2 with extern cage gangway 5.9 m^2, height 2.4 m), with two rooms, equipped with platforms, ropes, hammocks and toys (Fig. 3). The smaller room offers the keepers the possibility to separate the group if necessary and the siamangs the possibility to withdraw from visitor's sight. Permanent access to an outdoor enclosure (about 1250 m^2) is provided, in large part a primary forest with high trees enabling the typical gibbon brachiation. Ropes and feeding hideouts enrich the area, as well as a pond bordering one part of the enclosure. Visitors can watch the group from all sights, except one part of the area, so the animals have the opportunity to withdraw.

The lar group is kept in an indoor enclosure (base are 72 m^2, height 3.7 m) with platforms, plants and ropes, whereas the ceiling bar construction provides generous brachiation opportunity (Fig. 4). Permanent access to an island (base area 85 m^2), surrounded by a pond, is given. Visitors can walk around pond with the island, which exhibits dense copse as well as high trunks, connected by ropes. As a result of lacking hideouts on the island or a second room of the indoor enclosure, the lar group is always visible for visitors.

Fig. 3: Siamang enclosure and house (Photo: Manuela Lembeck)

Fig. 4: Lar gibbon enclosure and house (Photo: Manuela Lembeck)

Observation Time

The siamang group was observed from the infant's age of 5th until 61th week of life, from May 16th until October 29th 2007 (5th to 29th week) by me and comparable data for a bachelor thesis were collected from May 6th until June 13th 2008 (56th, 57th and 61st week of the infant's age by my colleague Wiebke Hoffmann. Daily observations were taken between 7 AM and 5 PM, based on past studies (Chivers 1974), as well as according to the siamang daily activity period based on preliminary observations. Total observation time amounted to 75 hours (4496.60 min) per individual, the siamang infant was observed to 78 hours (4700.10 min).

SIAMANG	Date	Week	Observation amount/ per individual
Scan data (whole group)	16.5.-28.5.07	Early infancy (5th, 6th, 7th)	1800 min
	6.5.-13.6.08	Late infancy (56th, 57th, 61st)*	600 min
Focal animal data (whole group)	18.6.07-29.10.07	10th to 29th	2096.60 min
Infant data (all periods)	4.6.07-29.7.07	8th to 29th week	2300.10 min
Period 1	4.6.07 - 17.6.07	8th to 13th	2300.10 min
Period 2	18.07.07-7.9.07	14th to 21st	
Period 3	8.9.07-31.10.07	22st to 29th	

Tab. 2: Overview on siamang group data collection; *Data collected by my colleague Wiebke Hoffmann.

The lar gibbon group was observed during two observation periods, according to the infant's development. Data collection ranged from September 5th 2007 until November 22nd 2007 (9th until 20th of the infant's development week). The first data collection period contains data from September 10th until September 19th (according to the 10th and 11th development week), the second data collection period contains data from November 15th until November 22nd 2007 (the 19th and 20th development week). Total observation time amounted to hours 29 hours (1724.15 min) per individual.

LAR	Date	Week	Observation amount/ per individual
Scan data (whole group)	5.9.07-11.9.07	9th, 10th	1200 min
	15.11.07-20.11.07	19th , 20th	
Focal animal data (whole group)	10.9.07-19.9.07	10th to 29th	1159.15 min
	15.11.-22.11.07	19th to 20th	

Tab. 3: Overview on lar group data collection.

Behavioural Measures

In order to obtain a daily activity budget the scan sampling method (instantaneous sampling) was used. For detailed behavioural analysis focal animal sampling method (continuous recording) was applied (Martin & Bateson 2007). Scan sampling was performed in the siamang group from May 16th until May 28th 2007, as well as from May 6th until June 13th 2008 and in the lar group from September 5th until November 20th, as 5-min samples points of each individual. The following behavioural categories were noted:

(1) *Locomotion*: Describes any movement, like brachiating, climbing or walking bi- or quadruped, as well as the infant's crawling, walking and climbing efforts respectively.

(2) *Resting*: sitting, laying or hanging awake or asleep, while not moving or being moved (e.g. carried).

(3) *Feeding*: feeding on material from the natural environment e.g. seeds, leaves and grass, as well as drinking from the pond or consuming prepared food from the keeper. Foraging behaviour, e.g. plucking leaves and chewing movements or nipple contact by the infant (as milk intake cannot be checked) is also assigned to this behavioural category.

(4) *Allogrooming*: manipulation of the fur of a conspecific in order to remove detritus or parasites by using the fingers or passive as being groomed. Autogrooming, i.e. grooming own body, is excluded.

(5) *Social-Play*: Activity patterns from different contexts that are altered in forms and temporal sequencing appear exaggerated and seem to follow no apparent immediate purpose, often accompanied by a play-fac, performed by at least two individuals. E.g. play-chase each other or showing play-wrestle, pull, push, slap etc.

(6) *Care*: defined as carrying, inspecting and retrieving the infant or the infants attempt to hold on to someone in need of support, also including licking or embracing behaviour among other family members.

(7) *Contacting*: Friendly motivated movements towards another individual, by placing the hand on another conspecific or nibbling on the others limbs. Grabbing or pulling someone when passing by.

(8) *Agonistic/Submissive*: Agonistic display is obvious in slapping, kicking or sometimes biting, but (in comparison to play behaviour) combined with staring and open-mouth threat. Sometimes approach already causes displacing someone, which was noted as submissive display. Other behavioural patterns are turning away or avoiding someone, or drawing back or side step.

(9) *Self-directed*: Includes auto-play with or without an object, or just exploring an object by manipulating it with its fingers or toes, as well as auto-grooming or finger-/toe – suckling.

(10) *Others*: Including singing, food theft or sexual related performance, as well as other rare activities.

Focal animal samples from the siamang group were collected from June 18th to October 29th 2007 and from the lar group from September 10th to November 24th 2007. Focal animal sampling was adapted to a focal dyad observation, which means the monitoring of two individuals at the same time. Two dyads per gibbon group of the same composition were chosen and maintained throughout the study: adult male - juvenile female and adult female - infantile female, resulting in parallel individual focal data. Distribution of observation sessions per day were chosen randomly with the same amount for each dyad group per day. During 30-min sample observation periods all social interactions between the two focal animals, as well as interactions of one of the focal animals with other group members, were recorded. Other behavioural variables were neglected except those of both infants: whenever the mother-infant dyad was observed all infant behavioural patterns were recorded continuously to get more information on its developmental stage (see detailed ethogramm in appendix) as divided in three periods in the siamang infant. Throughout focal animal sampling scan sampling for inter-individual distances was applied in order to investigate spatial relations. The proximity of two individuals was assigned to one of the following four categories: "body contact", "one-arm length", "less than 5 meters", "more than 5 meters".

Finally, variables indicating infant development stage were noted whenever they were observed (adapted from Dal Pra & Geissmann 1994; Braendle & Geissmann 1997): (I) Partial independence from mother (hang on cage bars in contact with mother), (II) Complete lack of contact with mother, (III) Suspension by one arm, (IV) Bimanual brachiation, (V) Bipedal locomotion, (VI) Feeding on solid food, (VII) Initiating play with siblings, (VIII) Being groomed by siblings, (IX) Grooming (allogrooming), (X) Participation in group calls.

Data Recording and Analysis

Data recording was conducted by means of a digital voice tracer (Philips Voice Tracer 7655). For statistical analysis Microsoft Excel and SPSS were used. As a result of low sample size statistical analysis was limited. 2 x 2 PEARSON CHI-SQUARE TESTS were applied to analyze scan data from the activity budget and the inter-individual distance. LEVENE'S TEST for equality of means was applied for focal animal data, whereas only among each defined observation dyad. Due to parallel focal individual observations in dyads, it was not possible to compare individual data statistically. Therefore, data of all social interaction of pair combinations within 30-min-observation units were analyzed and averaged over all units.

For the infant data analysis, LEVENE'S TEST for equality of means was chosen and ANOVA (Analysis of Variance) combined with DUNNETT'S T3 as Post Hoc test used to compare the infant's behaviour in relation to age between the respective observation periods. SPEARMAN CORRELATION COEFFICIENT (r_S) between age of the infant and distance to the other group member was applied. All statistical tests were computed with a significance level of 0.05, except from SPEARMAN RANK CORRELATION COEFFICIENT, which was applied with a significance level of 0.01.

RESULTS

1. ACTIVITY BUDGET

In the following chapter the siamang's daily activity budget is calculated to investigate a general time management on all behavioural categories. Data of the male and the female individuals of both species are compared in order to analyze differences in biparental investment.

Chi-Square (X^2) Tests are applied to analyze observed frequencies scan data among each group but also between both groups and individuals of both groups.

1.1. SIAMANG'S ACTIVITY BUDGET

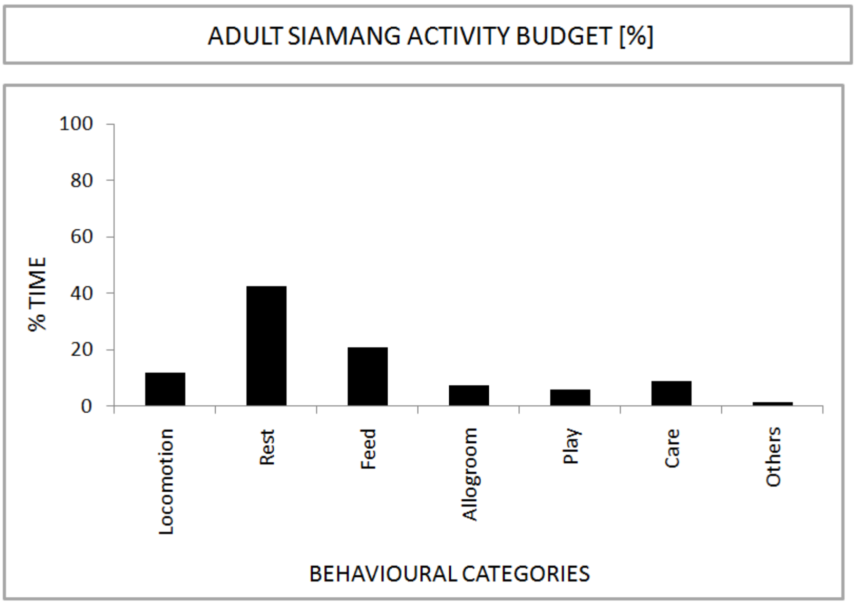

Fig. 1: Adult siamang activity budget expressed in percentage of time [%], N = 2.

The adult pair in the siamang group spends most of its time with resting behaviour (42.7 %), followed by feeding (21.0 %) and locomotion display (12.1 %) (Fig. 1). In social context caring behaviour is observed for 9.0 %, allogrooming for 7.6 % and playing behaviour for 6.0 % of observation time, 1.6 % is spent with other behaviour patterns.

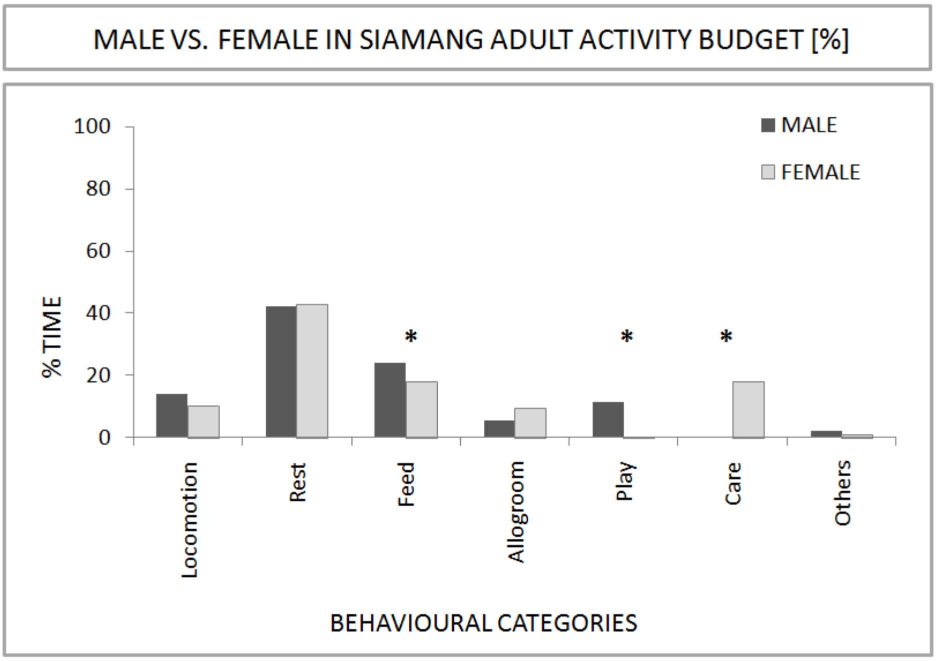

Fig. 2: Comparison between the adult male's and the adult female's activity budget in the siamang group expressed in percentage of time, N =2; X^2 – test (*$p < 0.05$).

In parental activity budget a significant difference is found in feeding (male: 24.2 %, female: 17.9 %), whereas the most distinctive differences are obvious in playing and caring behaviour: the adult male spends significantly more time with play (11.6 %) compared to the female (0.3 %) and the adult female spends more time with caring behaviour (17.9 %), in comparison to the adult male who does not show any (0.0 %; Fig. 2; X^2 - test: 105.460, df = 6, $p < 0.001$).

1.1.1. INTER-INDIVIDUAL DIFFERENCES AMONG THE GROUP MEMBERS

INDIVIDUAL'S ACTIVITY BUDGET IN THE SIAMANG GROUP [%]				
BEHAVIOUR	FOCAL ANIMALS			
	Adult male	Adult female	Juvenile female	Infantile female
Locomotion	14.03	10.15	20.54*	0.90*
Rest	42.39*	42.99*	30.06*	78.81*
Feed	24.18*	17.91	23.21*	0.30*
Allogroom	5.67	9.55*	7.74	2.39*
Play	11.64*	0.30*	14.29*	0.00*
Care	0.00*	17.91*	0.00*	17.61*
Others	2.09	1.19	4.17*	0.00

Tab. 1: Comparison of activity budget among the siamang group members expressed in percentage of time [%], N = 4; X^2 – test (*$p < 0.05$).

In the siamang group, the juvenile female spends significantly more time in locomotion in comparison to the infant who is significantly more time resting in comparison to the other group members (Tab. 1; X^2 - test: 462.931, df = 18, $p < 0.001$). In feeding both, adult male and juvenile female, spend significantly more time compared to the infantile female amount. In social context the adult female invests significantly more time in allogrooming and caring, than the other individuals. The adult male as well as the juvenile female is significantly more often observed in social-play than the adult female and the infant. Other behavioural patterns are only significantly more often observed in the juvenile female's activity budget.

1.1.2. COMPARISON OF ACTIVITY BUDGETS BETWEEN EARLY INFANCY AND LATE INFANCY

In the following section the siamang's daily activity budget at two different points of data collection, at early infancy (5th, 6th and 7th developmental week) as well as at late infancy (56th, 57th and 61st week) is compared in order to investigate changes in time budget.

EARLY VS. LATE INFANCY IN ADULT SIAMANG ACTIVITY BUDGET [%]			
BEHAVIOUR	INFANCY PERIOD		X^2
	early	late	Sign.
Locomotion	12.09	15.23	n.s.
Rest	42.69	48.31	n.s.
Feed	21.04	20.49	n.s.
Allogroom	7.61	11.84	*
Play	5.97	1.69	*
Care	8.96	0.75	*
Others	1.64	1.69	n.s.

Tab. 2: Comparison of the adult's activity budget between early and late infancy among the siamang group members expressed in percentage of time [%], N = 2; X^2 – test (*p < 0.05).

In early infancy data collection period the siamang group spends significantly less time in allogrooming behaviour context (Tab. 2; X^2 - test: 60.676, df = 6, p < 0.001). In later infancy differences are obvious in significant decrease in time spent playing and caring.

EARLY VS. LATE INFANCY IN ADULT SIAMANG ACTIVITY BUDGET [%]									
	Adult male			Adult female			Juvenile female		
BEHAVIOUR	early	late	X^2	early	late	X^2	early	late	X^2
Locomotion	14.03	16.42	n.s.	10.15	14.02	n.s.	20.54	31.23	*
Rest	42.39	51.49	*	42.99	45.08	n.s.	30.06	33.09	n.s.
Feed	24.18	20.15	n.s.	17.91	20.83	n.s.	23.21	18.96	n.s.
Allogroom	5.67	7.46	n.s.	9.55	16.29	*	7.74	5.95	n.s.
Play	11.64	2.99	*	0.30	0.38	n.s.	14.29	8.18	*
Care	0.00	0.00	n.s.	17.91	1.52	*	0.00	0.00	n.s.
Others	2.09	1.49	n.s.	1.19	1.88	n.s.	4.16	2.59	n.s.

Tab. 3: Comparison of individual activity budgets at early infancy and at late infancy in the siamang group expressed in percentage of time [%], N = 4; X^2 – test (*p < 0.05).

The adult male's daily activity behaviour changes from early to late infancy in a significant increase in resting amount, as well as in a significant decrease in time spent playing (Tab. 3; X^2-test: 19.645, df = 5, p < 0.001). The adult female's allogrooming amount increased significantly, as the time spent caring decreased significantly in late infancy (X^2 - test: 45.671, df = 5, p < 0.001). The juvenile's daily activity budget changes significantly in terms of increased locomotion in late infancy and decreased amount of play (X^2 - test: 15.015, df = 5, p < 0.010).

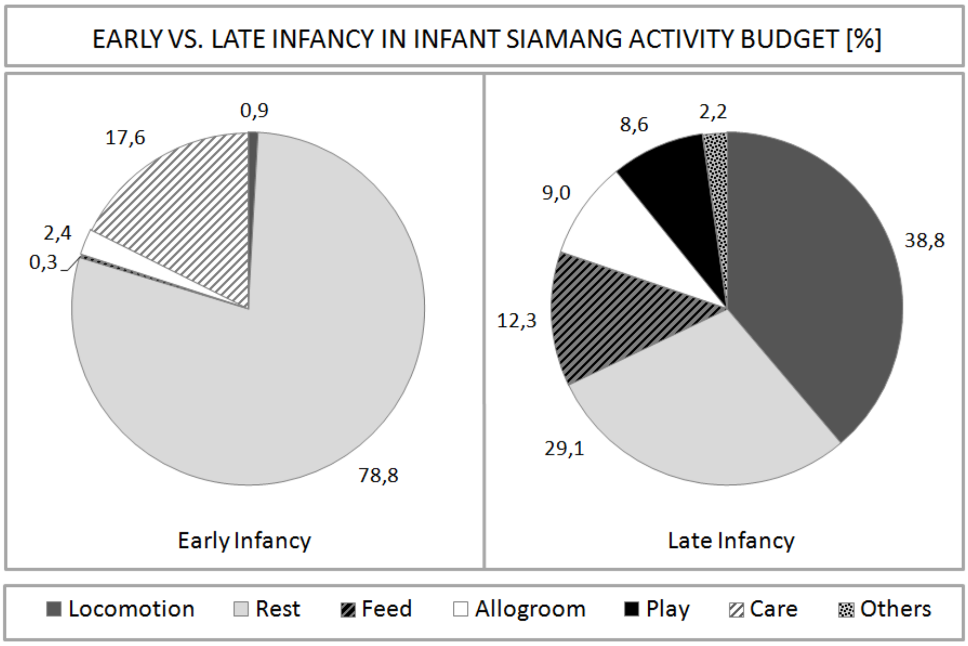

Fig. 3: The siamang infant's actvity budget at early infancy compared with late infancy activity budget expressed in percentage of time [%], N = 1; X^2 – test ($p < 0.05$); *are not drawn in, because significant differences are found between all behavioural categories.

In terms of behaviour there are significant differences in all behavioural aspects between both stages of age of the infant (Fig. 3; X^2 - test: 462.931, df = 18, p < 0.001). In early infancy the infant is observed to locomote in about 0.9 % of time, whereas in late infancy the infant spends more than 38 % of time with locomotion. Resting behaviour decreases remarkably (from 78.8 % in early infancy to 29.1 % in late infancy), as well as care-related display from 17.6 % to 0.0 %. Time spent with feeding increases from 0.3 % to 12.3 %, as well as playing behaviour (from 0.0 % o 8.6 %). The infant's amount of allogrooming also gains 6.4 % of time in late infancy as well as activity in other behaviour (from 0.0 % to 2.2 %).

The siamangs of my study group never sleep alone. According to scan data analysis in the morning and evening hours when individuals are still or already at their sleeping places it becomes obvious that, sleeping partners did not change over observation time. This is expressed in 100 % body contact between the adult male and juvenile female, as well as between the adult female and the infantile female.

1.2. Lar Gibbon’s Activity Budget

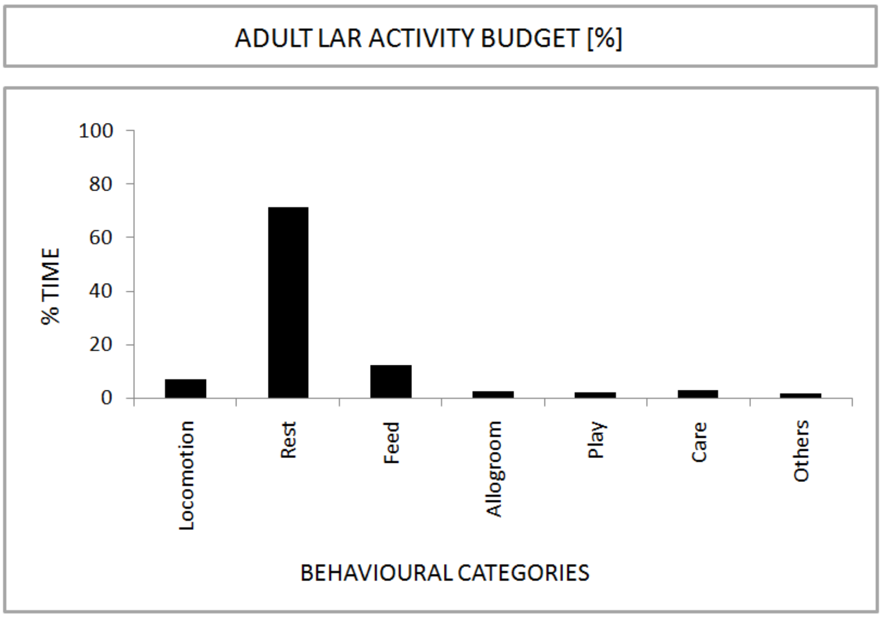

Fig. 4: Adult lar gibbon activity budget expressed in percentage of time [%], N = 2.

The adult pair in the lar group spends most of the time resting (71.4 %) followed by feeding time (12.2 %) and locomotion (7.0 %; Fig. 4). In social interaction context most of the time is spent with caring behaviour (3.1 %) and allogrooming (2.4 %). Play only amounts to 2.2 % in daily activity budget and other behavioural patterns to 1.7 %.

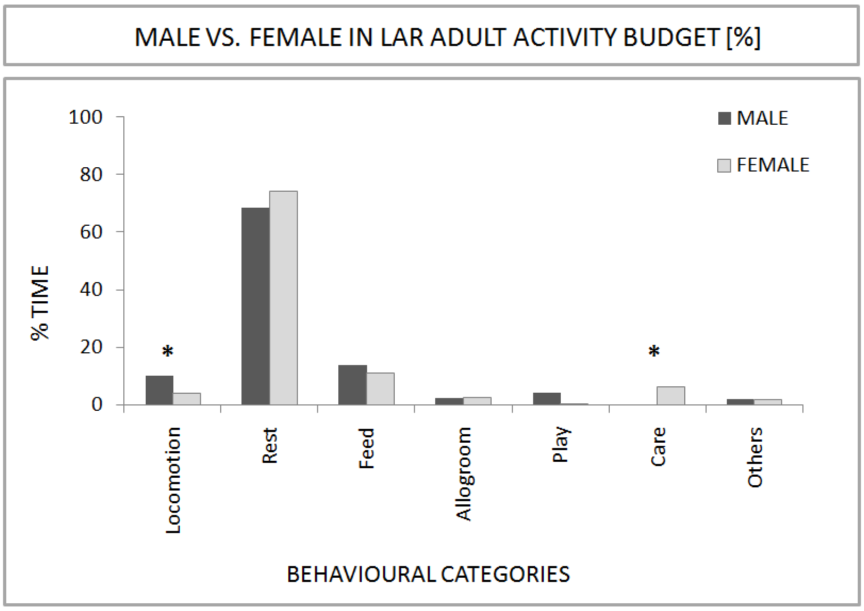

Fig. 5: Comparison between the adult male’s and the adult female’s activity budget in the lar group expressed in percentage of time, N =2; X^2 – test (*p < 0.05).

In the lar study group activity budget does not vary much among the individuals of the adult pair (Fig. 5; X^2 - test: 27.776, df = 6, $p < 0.001$). A significant difference is found in a higher amount of the adult female's caring behaviour (6.1 %) in comparison to the adult male (0.0 %). The adult male spends significantly more time in locomotion (10.0 %) than the adult female (3.9 %).

1.2.1. INTER-INDIVIDUAL DIFFERENCES AMONG THE GROUP MEMBERS

INDIVIDUAL'S ACTIVITY BUDGET IN THE LAR GROUP [%]				
BEHAVIOUR	FOCAL ANIMALS			
	Adult male	Adult female	Juvenile female	Infantile female
Locomotion	10.04	3.93*	17.47*	9.42
Rest	68.56	74.24	46.29*	73.99
Feed	13.54	10.92	18.34*	4.48*
Allogroom	2.18	2.62	4.37*	0.00*
Play	3.93	0.44	4.80*	0.00*
Care	0.00*	6.11*	0.00*	2.24
Others	1.75*	1.75*	8.73*	9.87*

Tab. 4: Comparison of activity budget among the lar group members expressed in percentage of time [%], N = 4; X^2 – test (*$p < 0.05$).

The adult female in the lar group spends significantly less time with locomotion than the juvenile female, who is significantly less often resting (Tab. 4; X^2 - test: 136.186, df = 18, $p < 0.001$). The infant spends significantly less time feeding as well as playing, in comparison to the juvenile female. The juvenile female invests significantly more time allogrooming compared to the infant. In caring behaviour context the adult female spends significantly more time with caring behaviour than the adult male and the juvenile female. The offspring, both the juvenile and the infantile female, invest significantly more time with other behavioural patterns than the adult pair.

According to scan data analysis the lar gibbon group members never sleep in close proximity to each other, except the adult female and the infant. Further, the choice of sleeping place is obviously flexible due to frequent changes observed.

1.3. Spatial Relations

During scan data sampling inter-individual spatial relations were collected as a measure of relationship quality among the group members.

1.3.1. Siamang

SPATIAL RELATION BETWEEN SIAMANG GROUP MEMBERS IN ACTIVITY BUDGET [%]					
ADULT MALE	DISTANCE BETWEEN INDIVIDUALS	ad M	ad F	juv F	inf F
	body contact	-	11.78	21.08*	11.78
	≤ one arm length	-	30.22	26.81	30.21
	≤ 5 m	-	41.69	43.67	41.70
	> 5 m	-	16.31	8.44*	16.31
ADULT FEMALE		ad M	ad F	juv F	inf F
	body contact	11.78*	-	22.22*	99.71*
	≤ one arm length	30.82*	-	21.62*	0.29*
	≤ 5 m	41.09*	-	40.84*	0.00*
	> 5 m	16.31*	-	15.32*	0.00*
JUVENILE FEMALE		ad M	ad F	juv F	inf F
	body contact	21.08	21.92	-	21.32
	≤ one arm length	26.51	21.62	-	22.22
	≤ 5 m	43.98	41.14	-	41.14
	> 5 m	8.43*	15.32	-	15.32
INFANTILE FEMALE		ad M	ad F	juv F	inf F
	body contact	11.78*	99.71*	21.32*	-
	≤ one arm length	30.82*	0.29*	22.52*	-
	≤ 5 m	41.09*	0.00*	40.84*	-
	> 5 m	16.31*	0.00*	15.32*	-

Tab. 5: Spatial relation between siamang group members in activity budget [%], N = 4; X^2 – test (*$p < 0.05$).

The adult male in the siamang group is observed to spend significantly more time in body contact with the juvenile female and significantly less time more than five meters away from her (Tab. 5; X^2 - test: 23.972, df = 6, p = 0.001). The adult female spends significantly more time in body contact and in less than one arm length distance to the infant than to the adult male and the juvenile female. She also spends significantly more time in less than five meters and more than five meters distance to the adult male and the juvenile female compared to the infant. The juvenile female is observed to stay significantly less often more than five meters away from the adult male than she does with the adult female and the infant. The infantile female is observed to spend significantly more time in body contact with the adult female and significantly less time in less than one arm length, than to the adult male and the juvenile female. Further she spends significantly more time less than five and more than five meters away from the juvenile female and the adult male, than with the adult female.

1.3.2. Lar Gibbon

SPATIAL RELATION BETWEEN LAR GIBBON GROUP MEMBERS
IN ACTIVITY BUDGET [%]

	DISTANCE BETWEEN INDIVIDUALS	ad M	ad F	juv F	inf F
ADULT MALE	body contact	-	0.44*	6.12*	0.44*
	≤ one arm length	-	2.62*	11.79*	3.06*
	≤ 5 m	-	72.92	61.57*	72.92
	> 5 m	-	24.02	20.52	23.58
ADULT FEMALE		ad M	ad F	juv F	inf F
	body contact	0.44*	-	11.79*	92.58*
	≤ one arm length	3.06*	-	9.17*	4.80
	≤ 5 m	72.05*	-	69.43*	2.62*
	> 5 m	24.45*	-	9.61	0.00*
JUVENILE FEMALE		ad M	ad F	juv F	inf F
	body contact	5.24*	11.79	-	13.10
	≤ one arm length	10.92	8.30	-	7.86
	≤ 5 m	66.38	70.30	-	69.43
	> 5 m	17.46*	9.61	-	9.61
INFANTILE FEMALE		ad M	ad F	juv F	inf F
	body contact	0.44*	94.31*	13.54*	-
	≤ one arm length	3.93	5.68	8.30	-
	≤ 5 m	71.62*	0.00*	68.12*	-
	> 5 m	24.01*	0.00*	10.04*	-

Tab. 6: Spatial relation between lar group members in activity budget [%], N = 4; X^2 – test (*$p < 0.05$).

Also in the lar group the adult male spends significantly more time in body contact and in less than one arm length with the juvenile female than with the adult female and the infant, as well as significantly less time less than five meters away from the juvenile female (Tab. 6; X^2 - test: 45.752, df = 6, $p < 0.001$). The adult female in the lar group is observed to spend significantly more time in body contact with the infant than with the adult male and the juvenile female, with whom she spends significantly more time in less than one arm length and less than five meter spatial relation distance (X^2 - test: 547.810, df = 6, $p < 0.001$). Further she spends significantly less time more than five meters away from the infant than to the adult male. The juvenile female spends significantly more time in body contact and less time in more than five meters distance to the adult male (X^2 - test: 17.472, df = 6, p =

0.008). The lar gibbon infant spends significantly more time in body contact with the adult female and than with the adult male and the juvenile female. Moreover it spends significantly more time in less than five meters and more than five meters distance with the adult male and the juvenile female than with the adult female.

1.4. Species Comparison

Scan data of both species are compared in order to find out if there are differences in general activity budgets. Further, analysis on social and non-social behaviour is conducted in order to compare female and male parental care in both species. Spatial relations among individuals of both family groups are also compared to investigate if there are species-specific differences concerning group coherence, expressed in varying inter-individual distances between the species. Moreover, inter-individual distances between the study groups while feeding and resting, is compared.

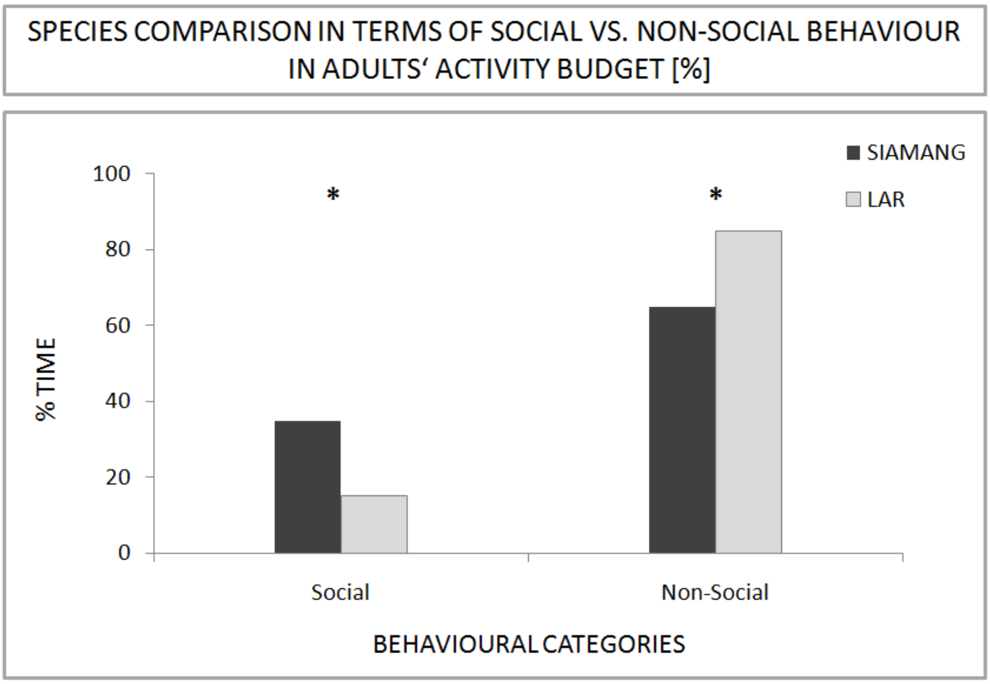

Fig. 6: Percentage of time both adult pairs spend with non-social behaviour and social interactions. “Social interactions” contains the following behavioural categories: Allogrooming, Play, Care, Contact and Agonistic behaviour; “Non-social Behaviour” contains: Locomotion, Resting, Feeding, Others and Self-directed behaviour. N = 4; X^2 – test (*$p < 0.05$).

According to Figure 6 (X^2 - test: 33.486, df = 1, p < 0.001), social interactions among group members are significantly more often observed in the siamang group (34.9 %), than in the lar gibbon group (15.2 %). Thus, the latter spends 84.8 % of total observation time in non-social actions, which differs significantly from the siamang family (65.1 %).

SPECIES COMPARISON IN TERMS OF SOCIAL VS. NON-SOCIAL BEHAVIOUR IN ACTIVITY BUDGET [%]						
	ADULT MALE			ADULT FEMALE		
	siamang	lar	X^2	siamang	lar	X^2
SOCIAL	31.94	16.39	*	37.91	13.93	*
NON-SOCIAL	68.06	83.61	*	62.09	86.07	*

Tab. 7: Percentage of time the adult male and the adult female of each observation group spends with non-social behaviour and social interactions. “Social interactions” contains the following behavioural categories: Allogrooming, Play, Care, Contact and Agonistic behaviour; “Non-social Behaviour” contains: Locomotion, Resting, Feeding, Others and Self-directed behaviour. N = 4; X^2 – test (*p < 0.05).

The adult siamang male spends significantly more time with social interactions than the adult lar male, who spends significantly more time with non-social behavioural patterns (Tab. 7; X^2 - test: 10.772, df = 1, p = 0.001). The adult siamang female invests significantly more time in social behaviour than the adult lar female, who spends significantly more time with non-social behaviour (X^2 - test: 23.821, df = 1, p < 0.001).

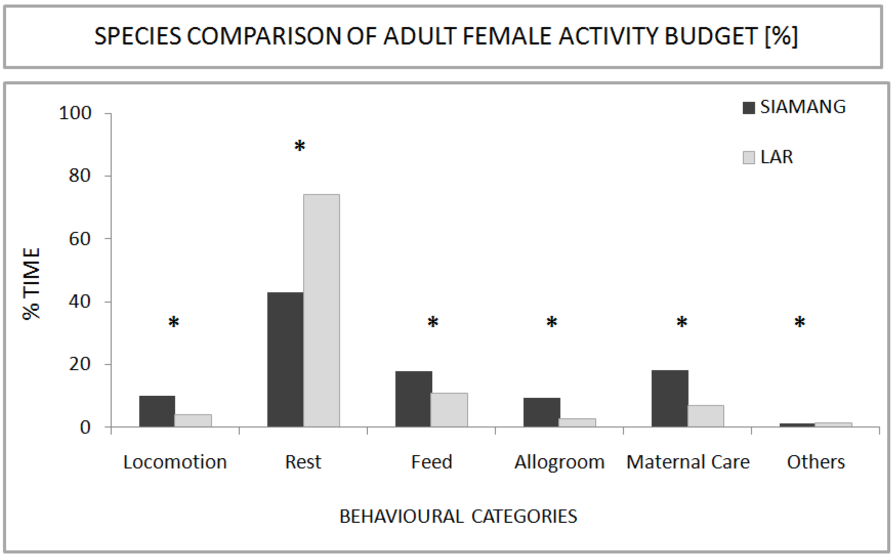

Fig. 7: Percentage of time the adult female of each observation group spends in daily activities. “Maternal care” contains the following behavioural categories: play, care, contacting behaviour. N = 2; X^2 – test (*p < 0.05).

When comparing the activity budget of the adult females of both groups significant differences are obvious in all behavioural categories except for the category “other” behaviours (Fig. 7; X^2 - test: 57.437, df = 5, $p < 0.001$). The siamang adult female spends significantly more time locomoting (10.1 %) in comparison to the lar adult female (3.9 %). Further, the siamang adult female invests significantly more time in feeding (17.9 %) than the lar adult female (10.9 %), as well as in allogrooming (siamang adult female: 9.6 %, lar adult female: 2.6 %). The lar adult female spends significantly more time resting (74.2 %) than the siamang adult female (43.0 %), who invests significantly more time in maternal caring behaviour (18.2 %) compared to the lar adult female (7.0 %).

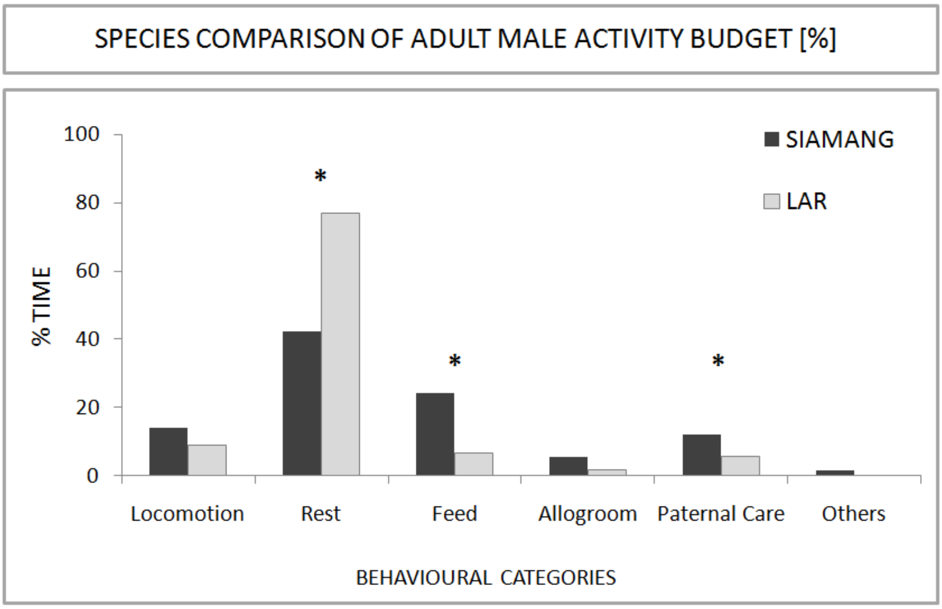

Fig. 8: Percentage of time the adult male of each observation groups spend in daily activities. “Paternal care” contains the following behavioural categories: play, care, contacting behaviour. N = 2; X^2 – test ($*p < 0.05$).

As seen in Figure 8, significant differences are found in resting behaviour (siamang male: 42.4 %, lar male: 77.0 %), as well as in feeding (siamang male: 24.2 %, lar male: 6.6 %) (X^2 - test: 45.420, df = 5, $p = 0.001$). In terms of paternal care the siamang male spends significantly more time (12.2 %) with the offspring than the lar male does (5.7 %).

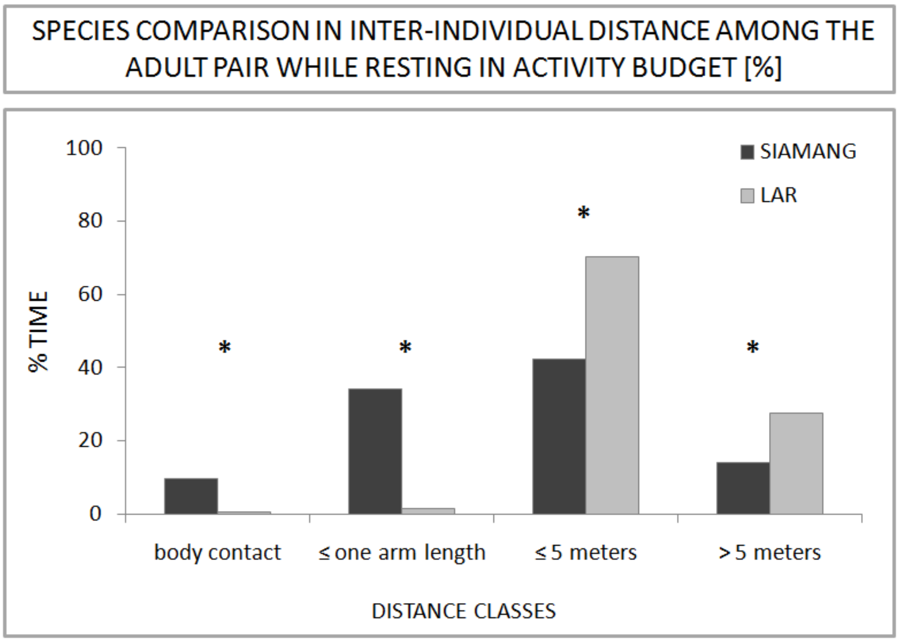

Fig. 9: Species comparison of spatial relation among the adult pairs while resting in activity budget expressed in percentage of time [%], N = 4; X^2 – test (*$p < 0.05$).

The adult pair in the siamang group spends more time near to each other while resting than the adult lar pair, reflected in significant differences in all spatial relation classes (Fig. 9; X^2 -test: 155.937, df = 3, $p < 0.001$). The siamang adult pair spends significantly more time in body contact (9.6 %) compared to the adult lar pair (0.6 %), as well as in one arm length (siamang: 34.1 %, lar: 1. %). The adult lar pair is resting significantly more often in less than five meter distance (70.3 %) than the adult siamang pair does (42.3 %). Significant differences are also found among the siamang pair spending less time in more than five meters away from each other (14 %) than the lar adult pair (27.5 %).

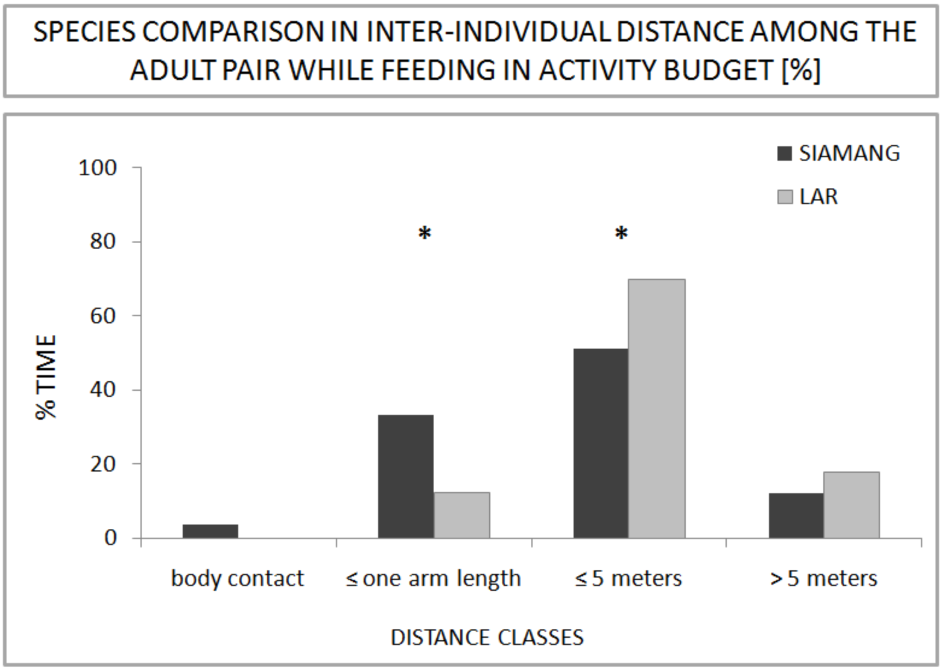

Fig. 10: Species comparison of spatial relation among the adult pairs while feeding in activity budget expressed in percentage of time [%], N = 4; X^2 – test (*p < 0.05).

According to Figure 10 significant differences between the adult pair in the siamang group compared to the adult pair in the lar group are found in the spatial relation categories "one arm length" and "less than five meters" (X^2- test: 11.772, df = 3, p = 0.008). The siamang pair spends significantly more time less than one arm length to each other (33.3 %) in comparison to the lar pair (12.5 %), who spends significantly more time in less than five meters distance to each other (69.6 %) than the siamang pair (51.1 %) while feeding.

SPECIES COMPARISON IN INTER-INDIVIDUAL DISTANCE BETWEEN THE INANTS AND OTHER GROUP MEMBERS [%]				
	INTER-INDIVIDUAL DISTANCE	SIAMANG INFANT	LAR INFANT	X^2
ADULT MALE	body contact	10.27	1.07	*
	≤ one arm length	27.05	6.41	*
	≤ 5 m	52.40	63.52	
	> 5 m	10.28	29.00	*
ADULT FEMALE	body contact	98.53	96.32	
	≤ one arm length	1.47	2.80	
	≤ 5 m	0.0	0.88	
	> 5 m	0.0	0.0	
JUVENILE FEMALE	body contact	18.73	6.67	*
	≤ one arm length	28.09	10.63	*
	≤ 5 m	45.48	66.31	*
	> 5 m	7.70	16.39	*

Tab. 8: Adult female - infant, adult male - infant and juvenile female - infant spatial relation differences among each family group expressed in percentage of time [%]. Data from 10th, 11th, 19th and 20th development weeks of both species are integrated in this analysis. N = 2; X^2 – test (*$p < 0.05$).

The comparison of mother-infant spatial relation between the siamang and the lar gibbon infant show no significant difference in any of all spatial relation classes (Tab. 9; X^2 - test: 4.748, df = 2, $p = 0.093$). However, a significant difference between the species becomes evident comparing the distance classes among the fathers and the infants (X^2 - test: 133.291, df = 3, $p < 0.001$). The siamang infant spends significantly more time in body contact and in less than one arm length distance with its father than the lar gibbon infant does. The lar infant is significantly more often observed more than five meters away from the adult male, in comparison to the siamang infant and its father.

In comparison of juvenile female - infant spatial relations, differences are also found (X^2 - test: 85.654, df = 3, $p < 0.001$). In general the siamang infant spends more time near to its sister then the lar gibbon infant does, which is reflected in the siamang infant spending significantly more time in body contact and less than one arm length distance than the lar infant does. The lar infant is significantly more often observed in less than five meters distance and also more than five meters away compared to the siamang infant and its father.

SPECIES COMPARISON OF THE INFANTS' ACTIVITY BUDGET [%]

BEHAVIOUR	SIAMANG INFANT	LAR INFANT	X^2
Locomotion	0.90	9.4	*
Rest	78.81	74.0	
Feed	0.30	4.5	*
Allogroom	2.4	0.0	*
Care	17.6	2.2	*
Contact	0.0	3.6	*
Self-directed	0.0	6.3	*

Tab. 10: Species comparison of the infants' activity budget expressed in percentage of time [%], N = 2; X^2 – test (*$p < 0.05$).

According to Table 10, significant differences are found in all behavioural categories between both infants except for resting (X^2 - test: 100.855, df = 6, $p < 0.001$). The lar gibbon infant spends significantly more time locomoting, feeding, contacting and with self-directed behaviour compared to the siamang infant, which is significantly more often involve in allogrooming and caring behaviour.

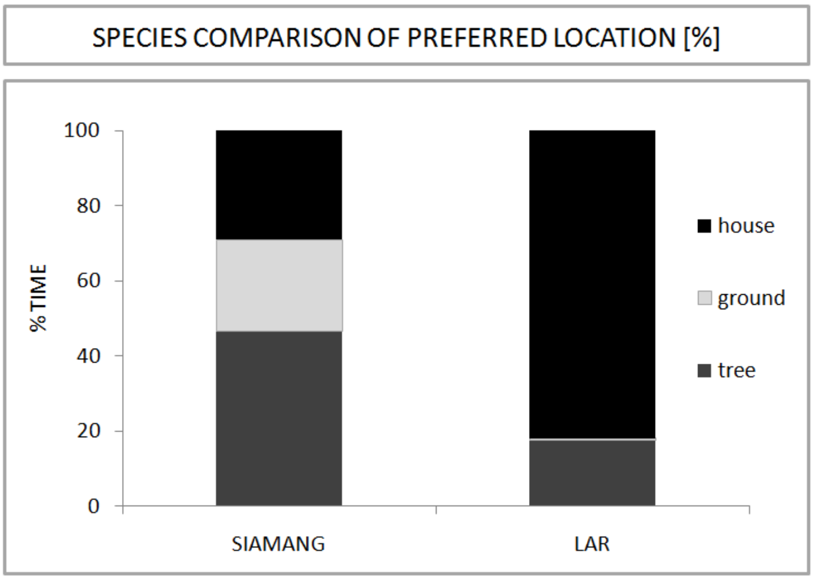

Fig. 10: Species comparison of preferred location at the infant's age of 10th, 11th, 19th and 20th week, expressed in percentage of time [%], N = 8; X^2 – test (*$p < 0.05$) *are not drawn in, because significant differences are found between all categories.

The siamang group is observed to spend significantly more time in the trees (46.56 %) than the lar gibbon group (17.47 %) and on the ground (24.50 %) than the lar gibbon group (0.66 %), which spends significantly more time in the house (81.88 %) than the siamang family (28.94 %) (Fig. 10; X^2 - test: 645.462, df = 2, $p < 0.001$).

2. SOCIAL BEHAVIOUR

To investigate differences in parental investment social behaviour is analyzed from focal animal data among both species. If parental care is present, differences in male and female behaviour directed to the infant are expected. Grooming and contacting behaviour in adults and offspring interactions among each group is compared in order to find out if there are further differences, possibly related to parental role behaviour. For analysis, Levene's Test for equality of variances and T-test for equality of means is applied so as to compare averaged data from all combination pairs among each dyad.

2.1. SOCIAL BEHAVIOUR AMONG THE SIAMANG GROUP

2.1.1. PLAY

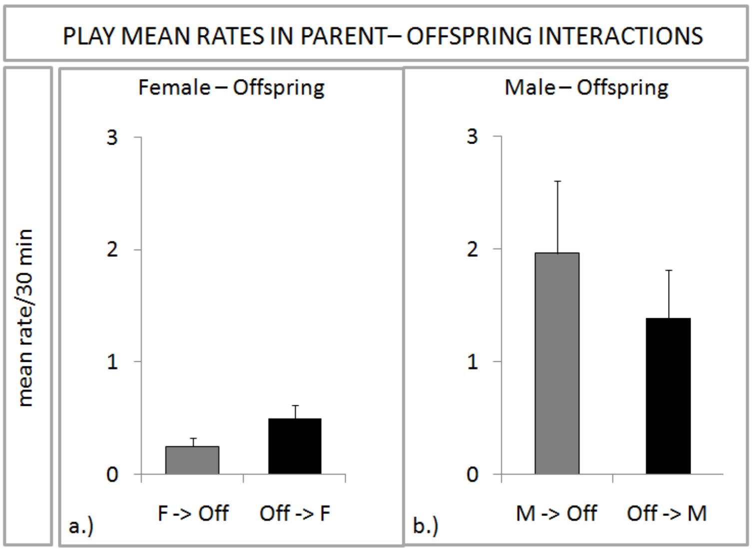

Fig. 11: Mean play rates/30 min between adult female and offspring (**a**) (N = 3) and between adult male and offspring (**b**) (N = 3) in the siamang group."F" = adult female, "M" = adult male, "Off" = Offspring (juvenile and infantile female). Interaction initiator and recipient roles are represented by arrows. T-test for equality of means (*$p < 0.05$), bars indicate the standard error of the mean.

Neither differences are found in playing rates between the adult female initiating play (0.25±0.08 rates/30 min) and the offspring initiating play (0.50±0.18 rates/30 min) in adult female – offspring interactions (Levene's test for equality of variances: F = 5.039, p = 0.026; T-test for equality of means: df = 94.383, p = 0.203; Fig. 11a), nor between adult male initiating playing rates (1.96±0.65 sec/30 min) and offspring initiating (1.39±0.43 sec/30 min) in adult male – offspring interactions (Levene's test for equality of variances: F = 2.370, p = 0.126; T-test for equality of means: df = 144, p = 0.465; Fig. 11b).

In terms of playing duration regarding initiator and recipient roles, no significant differences are found, both in adult female – offspring (Levene's test for equality of variances: F = 3.142, p = 0.078; T-test for equality of means: df = 125.674, p = 0.322) and adult male – offspring interactions (Levene's test for equality of variances: F = 0.714, p = 0.400; T-test for equality of means: df = 124.274, p = 0.340).

COMPARED INTERACTION PAIRS	**MEAN RATE/30'**	**MEAN DURATION/30'**
ad M + juv F	5.38±1.34	5.43±0.81
ad F + juv F	0.15±0.07	1.94±0.91
T-TEST (SIGN.)	*	*

Tab. 11: Mean playing rate and duration per 30 min observation units ± standard error of the mean in adult male - juvenile female interactions in comparison to adult female - juvenile female interactions in the siamang group. N = 4; T-test for equality of means (*p < 0.05).

Play occurs significantly more often between the adult male and the juvenile female than between the adult female and the juvenile female in the siamang group (Tab. 11; Levene's test for equality of variances: F = 37.752, p < 0.001; T-test for equality of means: df = 71.388, p < 0.001). Play duration differs in respect to significantly longer sessions in adult male - juvenile female interactions than in adult female - juvenile female plays (Levene's test for equality of variances: F = 2.888, p = 0.091; T-test for equality of means: F = 141.194, p = 0.005).

<u>ad M → juv F</u> vs. <u>ad F → juv F</u>

In detail, the adult male initiates signifcantly more often playing with the juvenile female (1.89±0.66 rates/30 min) than the adult female does (0.00±0.00 rates/30 min; Levene's test for equality of variances: F = 26.456, p < 0.001; T-test for equality of means: F = 71.000, p = 0.005). The adult male initiated plays last also significantly longer (2.25±0.62 sec/30 min) than adult female initiated plays (0.00±0.00 sec/30 min; Levene's test for equality of variances: F = 247.153, p < 0.001; T-test for equality of means: F = 72.000, p < 0.001).

COMPARED INTERACTION PAIRS	MEAN RATE/30’	MEAN DURATION/30’
ad F + inf F ad M + inf F	0.39±0.11 0.36±0.12	1.37±0.40 1.34±0.42
T-TEST (SIGN.)	**n.s.**	**n.s.**

Tab. 12: Mean playing rate and duration per 30 min observation units ± standard error of the mean in adult female – infantile female interactions in comparison to adult male - infantile female interactions in the siamang group. N = 4; T-test for equality of means (*p < 0.05).

No differences are found between adult female - infant and adult male – infant play, both in rates (Levene’s test for equality of variances: F = 0.004, p = 0.949; T-test for equality of means: df = 188, p = 0.866) and durations (Levene’s test for equality of variances: F = 0.15, p = 0.904; T-test for equality of means: df = 188, p = 0.954; Tab. 12).

2.1.2. CARE

COMPARED INTERACTION PAIRS	MEAN RATE/30’	MEAN DURATION/30’
ad F + inf F ad M + inf F	3.06±0.36 0.18±0.05	3.41±0.54 1.15±0.41
T-TEST (SIGN.)	*	*

Tab. 13: Mean caring rate and duration per 30 min observation units ± standard error of the mean in adult female - infantile female interactions in comparison to adult male - infantile female interactions in the siamang group. N = 4; T-test for equality of means (*p < 0.05).

Caring display is performed significantly more often in adult female – infantile female interactions than in adult male – infantile female interactions (Levene’s test for equality of variances: F = 152.340, p < 0.001; T-test for equality of means: df = 97.574, p < 0.001; Tab. 13). Differences are also found in significantly longer caring duration in adult female – infantile interactions than in adult male – infantile female encounters (Levene’s test for equality of variances: F = 2.163, p = 0.143; T-test for equality of means: df = 174.204, p = 0.001).

COMPARED INTERACTION PAIRS	MEAN RATE/30’	MEAN DURATION/30’
ad F + inf F	3.06±0.36	3.41±0.54
ad F + juv F	0.02±0.02	0.01±0.01
T-TEST (SIGN.)	*	*

Tab. 14: Mean caring rate and duration per 30 min observation units ± standard error of the mean in adult female - infantile female interactions in comparison to adult female - juvenile female interactions in the siamang group. N = 4; T-test for equality of means (*p < 0.05).

Caring behaviour is observed significantly more often in adult female – infantile female interactions compared to adult female – juvenile female interactions (Tab. 14; Levene’s test for equality of variances: F = 171.708, p < 0.001; T-test for equality of means: df = 96.170, p < 0.001) and also lasts signifcantly longer (Levene’s test for equality of variances: F =31.431, p < 0.001; T-test for equality of means: df = 97.850, p < 0.001)

2.1.3. GROOM

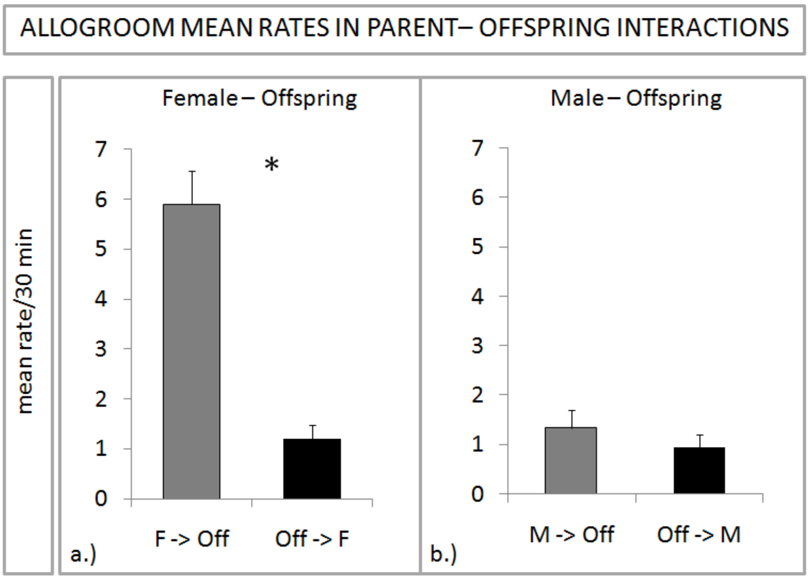

Fig. 12: Mean allogroom rates/30 min between adult female and offspring (**a**) (N = 3) and between adult male and offspring (**b**) (N = 3) in the siamang group.“F” = adult female, “M” = adult male, “Off” = Offspring (juvenile and infantile female). Interaction initiator and recipient roles are represented by arrows. T-test for equality of means (*p < 0.05), bars indicate the standard error of the mean.

As seen in Figure 12a, the adult female is significantly more often (5.89±0.67 rates/30 min) initiating a grooming session, than the offspring does (1.20±0.27 rates/30 min; Levene’s test for equality of variances: F = 60.593, p < 0.001; T-test for equality of means:

df = 92.601, p < 0.001). There is no significant difference between the adult male initiating grooming sessions (1.33±0.37 rates/30 min) and the offspring initiating (0.95±0.25 rates/30 min; Levene's test for equality of variances: F = 1.712, p = 0.193; T-test for equality of means: df = 144, p = 0.410; Fig. 12b).

In terms of allogrooming duration, the adult female is grooming significantly longer, when being the active one (9.72±1.10 sec/30 min), in comparison to the offspring grooming its mother (3.56±0.77 sec/30 min; Levene's test for equality of variances: F = 9.354, p = 0.003; T-test for equality of means: df = 125.140, p < 0.001). Grooming interactions last significantly longer when the male initiates it (6.18±1.15 sec/30 min), than in interactions, when the offspring is grooming its father (3.13±0.68 sec/30 min; Levene's test for equality of variances: F = 20.285, p < 0.001; T-test for equality of means: df = 117.437, p = 0.024).

COMPARED INTERACTION PAIRS	MEAN RATE/30'	MEAN DURATION/30'
ad F + juv F	3.75±0.60	8.74±1.11
ad M + juv F	1.63±0.40	5.10±0.83
T-TEST (SIGN.)	*	*

Tab. 15: Mean allogrooming rate and duration per 30 min observation units ± standard error of the mean in adult female - juvenile female interactions in comparison to adult male - juvenile female interactions in the siamang group. N = 4; T-test for equality of means (*p < 0.05).

Grooming is significantly more often observed in adult female – juvenile female interactions than in adult male – juvenile female interactions (Levene's test for equality of variances: F = 14.918, p < 0.001; T-test for equality of means: df = 123.823, p = 0.004), as well as last significantly longer in adult female – juvenile female interactions than in adult male – juvenile female interactions (Levene's test for equality of variances: F = 3.253, p = 0.073; T-test for equality of means: df = 133.251, p = 0.010; Tab. 15).

ad M → juv F vs. *ad F → juv F*

When regarding initiator and recipient roles, significant differences are obvious in the adult female's significantly higher rates in grooming the juvenile female (3.29±0.58 rates/30 min) than the adult male does (1.33±0.38 rates/30 min; Levene's test for equality of variances: F = 14.981, p < 0.001; T-test for equality of means: df = 103.321, p = 0.006). No significant difference is computed in grooming durations.

COMPARED INTERACTION PAIRS	MEAN RATE/30'	MEAN DURATION/30'
ad M + juv F ad M + inf F	1.63±0.40 0.05±0.02	5.10±0.83 0.43±1.18
T-TEST (SIGN.)	*	*

Tab. 16: Mean allogrooming rate and duration per 30 min observation units ± standard error of the mean in adult male - juvenile female interactions in comparison to adult male - infantile female interactions in the siamang group. N = 4; T-test for equality of means (*p < 0.05).

Differences are also found in significantly more frequent grooming bouts in adult male – juvenile female interactions than in adult male – infantile female interactions (Levene's test for equality of variances: F = 41.857, p < 0.001; T-test for equality of means: df = 71.488, p < 0.001), as well as in significantly longer sessions in adult male – juvenile female interactions than in adult male – infantile encounters (Levene's test for equality of variances: F = 120.715, p < 0.001; T-test for equality of means: df = 78.985, p < 0.001; Tab. 16).

2.1.4. CONTACT

ad F + inf F vs. *ad F + juv F*

Contacting behaviour is observed significantly more frequent in adult female – infantile female encounters (0.94±0.19 rates/30 min) than in adult female – juvenile female's (0.02±0.01 rates/30 min; Levene's test for equality of variances: F = 58.365, p < 0.001; T-test for equality of means: df = 94.920, p < 0.001). Further differences are obvious in significantly longer contacting durations in adult female – infantile female interactions (3.21±0.62 sec/30 min) than in adult female – juvenile female interactions (0.05±0.04 sec/30 min; Levene's test for equality of variances: F = 76.592, p < 0.001; T-test for equality of means: df = 94.695, p < 0.001).

ad M + inf F vs. *ad M + juv F*

Significant differences are observed in higher contacting frequencies among the adult male and the infantile female (0.93±0.25 rates/30 min) than in adult male – juvenile female interactions (0.09±0.03 rates/30 min; Levene's test for equality of variances: F = 26.578, p < 0.001; T-test for equality of means: df = 74.644, p = 0.001). Contacting lasts also significantly longer in adult male – infantile female interactions (4.06±1.00 sec/30 min) than in adult male – juvenile female's (0.50±0.33 sec/30 min; Levene's test for equality of variances: F = 28.865, p < 0.001; T-test for equality of means: df = 87.694, p = 0.001).

2.2. SOCIAL BEHAVIOUR AMONG THE LAR GIBBON GROUP

2.2.1. PLAY

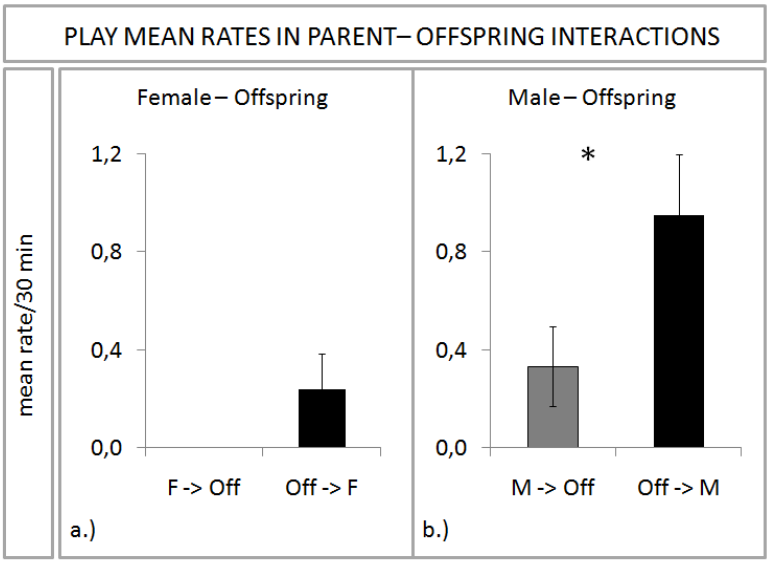

Fig. 13: Mean play rates/30 min between adult female and offspring (**a**) (N = 3) and between adult male and offspring (**b**) (N = 3) in the lar group."F" = adult female, "M" = adult male, "Off" = Offspring (juvenile and infantile female). Interaction initiator and recipient roles are represented by arrows. T-test for equality of means (*p < 0.05), bars indicate the standard error of the mean.

No significant difference is found in playing rate between adult female initiated (0.00±0.00 rates/30 min) and offspring initiated play (0.24±0.17 rates/30 min; Levene's test for equality of variances: F = 7.643, p = 0.007; T-test for equality of means: df = 41.000, p = 0.168; Fig. 13a). In adult male – offspring plays, offspring initiated plays (0.95±0.24 rates/30 min) are significantly more frequently observed than adult male initiated (0.33±0.16 rates/30 min; Levene's test for equality of variances: F = 13.996, p < 0.001; T-test for equality of means: df = 65.168, p = 0.042; 13b).

In adult female – offspring playing sessions, differences in duration are obvious in significantly longer offspring initiated plays (0.30±0.14 sec/30 min) compared to adult female initiated (0.00±0.00 sec/30 min; Levene's test for equality of variances: F = 21.342, p < 0.001; T-test for equality of means: df = 41.000, p = 0.045). In adult male – offspring plays, no significant difference is found between adult male and offspring initiated playing durations.

COMPARED INTERACTION PAIRS	MEAN RATE/30'	MEAN DURATION/30'
ad M + juv F	1.23±0.33	2.01±0.53
ad F + juv F	0.03±0.03	0.40±0.40
T-TEST (SIGN.)	*	*

Tab. 17: Mean playing rate and duration per 30 min observation units ± standard error of the mean in adult male - juvenile female interactions in comparison to adult female - juvenile female interactions in the lar group. N = 4; T-test for equality of means (*p < 0.05).

Adult male – juvenile female plays are observed significantly more often than play between adult female and juvenile female (Levene's test for equality of variances: F = 55.043, p < 0.001; T-test for equality of means: df = 39.440, p = 0.001; Tab. 17). Differences are also obvious in significantly longer playing sessions among adult male – juvenile female interactions, compared to adult female – juvenile female's (Levene's test for equality of variances: F = 13.903, p < 0.001; T-test for equality of means: df = 72.544, p = 0.018).

ad M → juv F vs. *ad F → juv F*

In detail the adult male initiates significantly more often play with the juvenile female (0.33±0.16 rates/30 min) than the adult female does (0.00±0.00 rates/30 min; Levene’s test for equality of variances: F = 15.087, p < 0.001; T-test for equality of means: df = 39.000, p = 0.046). Plays with the juvenile female also last signficantly longer when the adult male initates it (1.10±0.43 sec/30 min) compared to the adult female initiating a play with the juvenile female (0.00±0.00 sec/30 min; Levene’s test for equality of variances: F = 28.377, p < 0.001; T-test for equality of means: df = 39.000, p = 0.015).

COMPARED INTERACTION PAIRS	**MEAN RATE/30’**	**MEAN DURATION/30’**
ad F + inf F	0.22±0.17	0.23±0.13
ad M + inf F	0.00±0.00	0.00±0.00
T-TEST (SIGN.)	**n.s.**	**n.s.**

Tab. 18: Mean playing rate and duration per 30 min observation units ± standard error of the mean in adult female - infantile female interactions in comparison to adult male - infantile female interactions in the lar group. N = 4; T-test for equality of means (*p < 0.05).

No significant differences are found, both in rates (Levene’s test for equality of variances: F = 6.441, p = 0.013; T-test for equality of means: df = 39.000, p = 0.211) and durations (Levene’s test for equality of variances: F = 14.822, p < 0.001; T-test for equality of means: df = 39.000, p = 0.084), between adult female – infantile female plays and adult male – infantile female plays (Tab. 18).

2.2.2. CARE

COMPARED INTERACTION PAIRS	**MEAN RATE/30’**	**MEAN DURATION/30’**
ad F + inf F	4.90±0.84	2.61±0.41
ad M + inf F	0.00±0.00	0.00±0.00
T-TEST (SIGN.)	*****	*****

Tab. 19: Mean caring rate and duration per 30 min observation units ± standard error of the mean in adult female - infantile female interactions in comparison to adult male - infantile female interactions in the lar group. N = 4; T-test for equality of means (*p < 0.05).

Significant differences are obvious in higher caring rates in adult female – infantile female interactions compared to rates in adult male – infantile female interactions (Levene's test for equality of variances: F = 50.252, p < 0.001; T-test for equality of means: df = 39.000, p < 0.001; Tab. 19). In terms of durations, adult female – infantile female caring sessions last significantly longer than in adult male – infantile female interactions (Levene's test for equality of variances: F = 38.711, p < 0.001; T-test for equality of means: df = 39.000, p < 0.001).

COMPARED INTERACTION PAIRS	MEAN RATE/30'	MEAN DURATION/30'
ad F + inf F ad F + juv F	4.90±0.84 0.00±0.00	2.61±0.41 0.00±0.00
T-TEST (SIGN.)	*	*

Tab. 20: Mean caring rate and duration per 30 min observation units ± standard error of the mean in adult female - infantile female interactions in comparison to adult female - juvenile female interactions in the lar group. N = 4; T-test for equality of means (*p < 0.05).

According to Table 20, caring in adult female – infantile female interactions is significantly more often observed than in adult female – juvenile female's (Levene's test for equality of variances: F = 50.252, p < 0.001; T-test for equality of means: df = 39.000, p < 0.001), as well as caring sessions last significantly longer (Levene's test for equality of variances: F = 38.711, p < 0.001; T-test for equality of means: df = 39.000, p < 0.001).

2.2.3. GROOM

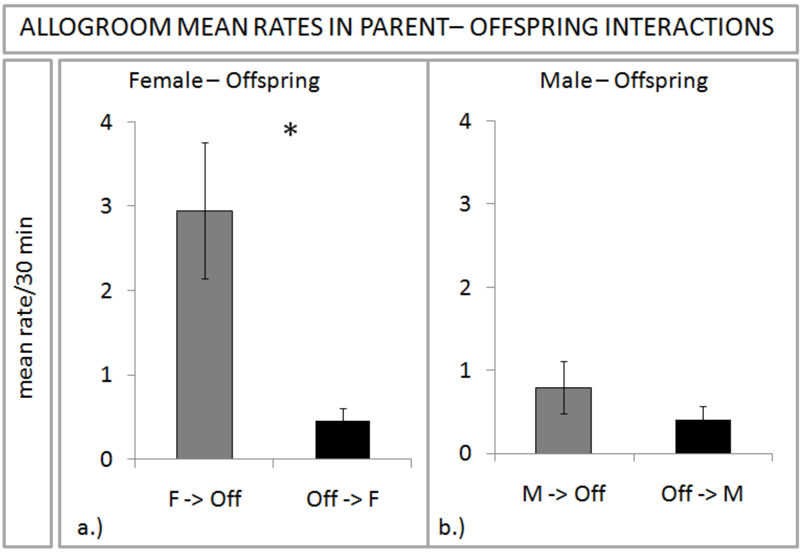

Fig. 14: Mean allogroom rates/30 min between adult female and offspring (**a**) (N = 3) and between adult male and offspring (**b**) (N = 3) in the lar group."F" = adult female, "M" = adult male, "Off" = Offspring (juvenile and infantile female). Interaction initiator and recipient roles are represented by arrows. T-test for equality of means (*$p < 0.05$), bars indicate the standard error of the mean.

In allogrooming behaviour context, significant differences are found in adult female – offspring interactions in terms of initiator and recipient roles (Fig. 14a), whereas adult female initiated grooming session are significantly more often observed (2.95±0.81 rates/30 min) than offspring initiated (0.45±0.15 rates/30 min; Levene's test for equality of variances: F = 22.914, $p < 0.001$; T-test for equality of means: df = 43.955, p = 0.004). No significant differences are obvious between rates in adult male and offspring inititiated grooming behaviour (14b).

Further, adult female initiated allogrooming sessions last significantly longer (8.37±2.06 sec/30 min) than offspring initiated (1.76±0.57 sec/30 min; Levene's test for equality of variances: F = 19.659, $p < 0.001$; T-test for equality of means: df = 47.355, p = 0.003). Allogrooming in adult male – offspring interactions lasts also significantly longer, when the adult male initiated it (4.31±1.52 sec/30 min) compared to the offspring initiating it (1.07±0.40 sec/30 min; Levene's test for equality of variances: F = 21.664, $p < 0.001$; T-test for equality of means: df = 43.166, p = 0.045).

COMPARED INTERACTION PAIRS	MEAN RATE/30’	MEAN DURATION/30’
ad F + inf F	0.82±0.32	3.60±1.04
ad F + juv F	2.33±0.85	4.60±1.35
T-TEST (SIGN.)	**n.s.**	**n.s.**

Tab. 21: Mean allogrooming rate and duration per 30 min observation units ± standard error of the mean in adult female - infantile female interactions in comparison to adult female - juvenile female interactions in the lar group. N = 4; T-test for equality of means (*p < 0.05).

In allogrooming comparison, no significant differences are found, neither in rates (Levene’s test for equality of variances: F = 8.293, p = 0.005; T-test for equality of means: df = 49.255, p = 0.109) nor in durations (Levene’s test for equality of variances: F = 0.976, p = 0.326; T-test for equality of means: df = 73.399, p = 0.559) between adult female – infantile female and adult female – juvenile female grooming encounters (Tab. 21).

ad M → juv F vs. *ad F → juv F*

No significant differences are obvious, neither in rates (Levene’s test for equality of variances: F = 0.912, p = 0.342; T-test for equality of means: df = 64.671, p = 0.462) nor in durations (Levene’s test for equality of variances: F = 2.223, p = 0.140; T-test for equality of means: df = 68.976, p = 0.824) between the adult male initiating grooming sessions with the juvenile female and the adult female initiating grooming with the juvenile female.

COMPARED INTERACTION PAIRS	MEAN RATE/30’	MEAN DURATION/30’
ad M + juv F	0.38±0.20	1.33±0.64
ad M + inf F	0.00±0.00	0.00±0.00
T-TEST (SIGN.)	**n.s.**	*****

Tab. 22: Mean allogrooming rate and duration per 30 min observation units ± standard error of the mean in adult male - juvenile female interactions in comparison to adult male - infantile female interactions in the lar group. N = 4; T-test for equality of means (*p < 0.05).

In adult male – offspring grooming interactions, no significant difference is obvious in rates between adult male – juvenile female and adult male – infantile female sessions (Levene’s test for equality of variances: F = 15.940, p < 0.001; T-test for equality of means: df = 39.000, p = 0.062), whereas grooming lasts significantly longer in adult male – juvenile female encounters, than in adult male – infantile female encounters (Levene's test for equality of variances: F = 20.388, p < 0.001; T-test for equality of means: df = 39.000, p = 0.043; Tab. 22).

2.2.4. CONTACT

<u>*ad F + inf F*</u> *vs.* <u>*ad F + juv F*</u>

In adult female – infantile female interactions contacting is significantly more often observed (0.92±0.27 rates/30 min) than in adult female – juvenile female encounters (0.00±0.00 rates/30 min; Levene's test for equality of variances: F = 35.837, p < 0.001; T-test for equality of means: df = 39.000, p = 0.001). Differences are also significant in longer contacting sessions among adult female and infantile female (3.80±1.17 sec/30 min) than among adult female and juvenile female (0.00±0.00 sec/30 min; Levene's test for equality of variances: F = 35.578, p < 0.001; T-test for equality of means: df = 39.000, p = 0.003).

<u>*ad M + inf F*</u> *vs.* <u>*ad M + juv F*</u>

No significant differences are found neither in contacting rates between the adult male and the infantile female (0.22±0.13 rates/30 min) in comparison to in adult male and juvenile female interactions (0.17±0.12 rates/30 min; Levene's test for equality of variances: F = 0.302, p = 0.586; T-test for equality of means: df = 33.863, p = 0.756), nor in contacting durations between adult male - infantile female (0.89±0.77 sec/30 min) and adult male - juvenile female encounters (0.72±0.67 sec/30 min; Levene's test for equality of variances: F = 0.48, p = 0.828; T-test for equality of means: df = 33.243, p = 0.871).

2.3. SPECIES COMPARISON

In order to find out if there are species-specific differences regarding parental role behaviour, allogrooming between the adult females and the infants, as well as play behaviour between the adult males and juvenile females in both study groups are compared at the siamang and lar infant's age of 10th, 11th, 19th and 20th week. For analysis, Levene's Test for equality of variances and T-test for equality of means is applied to compare averaged data of both study groups.

2.3.1. GROOM

COMPARED INTERACTION PAIRS (10^{th}+11^{th})	**MEAN RATE/30'**	**MEAN DURATION/30'**
ad F + inf F (siamang)	0.15±0.06	1.52.±1.00
ad F + inf F (lar)	0.29±0.12	1.23±0.39
T-TEST (SIGN.)	**n.s.**	**n.s.**

Tab. 23: Mean allogrooming rate and duration per 30 min observation units ± standard error of the mean in adult female - infantile female interactions in the siamang and the lar group in 10th and 11th development week of both infants. N = 4; T-test for equality of means (*p < 0.05).

No significant difference is found in rates of adult female - infantile female grooming sessions in the siamang group and adult female - infantile infant grooming sessions in the lar group (Levene's test for equality of variances: F = 1.837, p = 0.185; T-test for equality of means: df = 27.609, p = 0.321), as it is in duration (Levene's test for equality of variances: F = 0.467, p = 0.500; T-test for equality of means: df = 13.106, p = 0.866; Tab. 23).

COMPARED INTERACTION PAIRS (19^{th}+20^{th})	**MEAN RATE/30'**	**MEAN DURATION/30'**
ad F + inf F (siamang)	0.39±0.20	1.62.±0.92
ad F + inf F (lar)	0.06±0.03	0.18±0.13
T-TEST (SIGN.)	**n.s.**	**n.s.**

Tab. 24: Mean allogrooming rate and duration per 30 min observation units ± standard error of the mean in adult female - infantile female interactions in the siamang and the lar group in 19th and 20th development week of both infants. N = 4; T-test for equality of means (*p < 0.05).

No significant difference is found neither in grooming rates between adult female - infantile female interactions of the siamang group and adult female – infantile female interactions of the lar group (Levene's test for equality of variances: F = 18.657, p < 0.001; T-test for equality of means: df = 3.168, p = 0.190) nor in grooming durations at the infants' age of 19th and 20th week (Levene's test for equality of variances: F = 9.992, p = 0.005; T-test for equality of means: df = 3.118, p = 0.218; Tab. 24).

2.3.2. PLAY

COMPARED INTERACTION PAIRS (10^{th}+11^{th})	MEAN RATE/30’	MEAN DURATION/30’
ad M + juv F (siamang)	1.37±0.54	1.40.±0.46
ad M + juv F (lar)	0.52±0.22	0.88±0.36
T-TEST (SIGN.)	**n.s.**	**n.s.**

Tab. 25: Mean playing rate and duration per 30 min observation units ± standard error of the mean in adult male - juvenile female interactions in the siamang and the lar group in 10^{th} and 11^{th} development week of both infants. N = 4; T-test for equality of means (*$p < 0.05$).

At the infants’ age of 10^{th} and 11^{th} week no significant difference is obvious in playing rates between the adult male and juvenile female of the siamang group compared to with the adult male and the juvenile female of the lar group (Levene’s test for equality of variances: $F = 7.543$, $p = 0.010$; T-test for equality of means: $df = 14.685$, $p = 0.167$; Tab. 25). Differences are also not significant concerning playing duration (Levene’s test for equality of variances: $F = 0.051$, $p = 0.824$; T-test for equality of means: $df = 23.562$, $p = 0.381$).

COMPARED INTERACTION PAIRS (19^{th}+20^{th})	MEAN RATE/30’	MEAN DURATION/30’
ad M + juv F (siamang)	0.29±0.17	0.69.±0.37
ad M + juv F (lar)	0.36±0.14	0.51±0.18
T-TEST (SIGN.)	**n.s.**	**n.s.**

Tab. 26: Mean playing rate and duration per 30 min observation units ± standard error of the mean in adult male - juvenile female interactions in the siamang and the lar group in 19^{th} and 20^{th} development week of both infants. N = 4; T-test for equality of means (*$p < 0.05$).

No significant differences at the infants’ age of 19^{th} and 20^{th} week is found, neither in playing rates (Levene’s test for equality of variances: $F = 0.611$, $p = 0.442$; T-test for equality of means: $df = 11.989$, $p = 0.741$) nor in playing durations (Levene’s test for equality of variances: $F = 0.075$, $p = 0.787$; T-test for equality of means: $df = 7.678$, $p = 0.684$; Tab. 26).

3. INFANT'S DEVELOPMENT

In the following chapter, the siamang infant's behaviour is investigated in order to find out more about the physical and behavioural development over the total observation time. Alterations in behavioural requirements are expected to be reflected in changes of spatial relations and in terms of social and non-social behaviour of the infant with other family members. Comparison between the siamang and the lar gibbon infant's development at the age of the 10th, 11th, 19th and 20th week of age is also conducted to investigate species-specific differences during ontogenesis.

3.1. SPATIAL RELATIONS

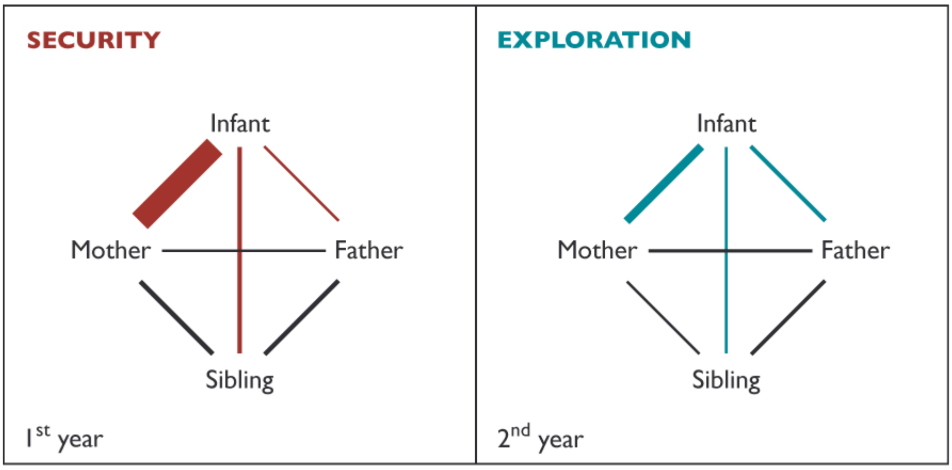

Fig. 15: Scheme on security and exploration proportion in parent-infant's relationship as measured by time spent in body contact in percentage of time [%] within the 1st year (data of early infancy) and the 2nd year (data of late infancy. Scheme: by Marion Fruhmann.

In the infant's first year, body contact between adult female and infant amounts 99.7 %, but decreases significantly to 36.7 % (X^2 - test: 294.750, df = 3, p < 0.001; Fig. 15). Adult male – infantile female body contact increases significantly from 11.8 % to 19.4 % (X^2 - test: 25.453, df = 3, p < 0.001). Juvenile female – infantile female body contact amount decreases significantly from 21.3 % in the first year to 12.7 % in the second year (X^2 - test: 16.887, df = 3, p = 0.001). Adult female – adult male body contact amount increases from 11.8 % to 15.3 % and adult male – juvenile female body contact amount decreases from 21.1 % to 16.1

% (no significant difference). Adult female - juvenile female body contact amount decreases significantly from 21.9 % to 11.3 %.

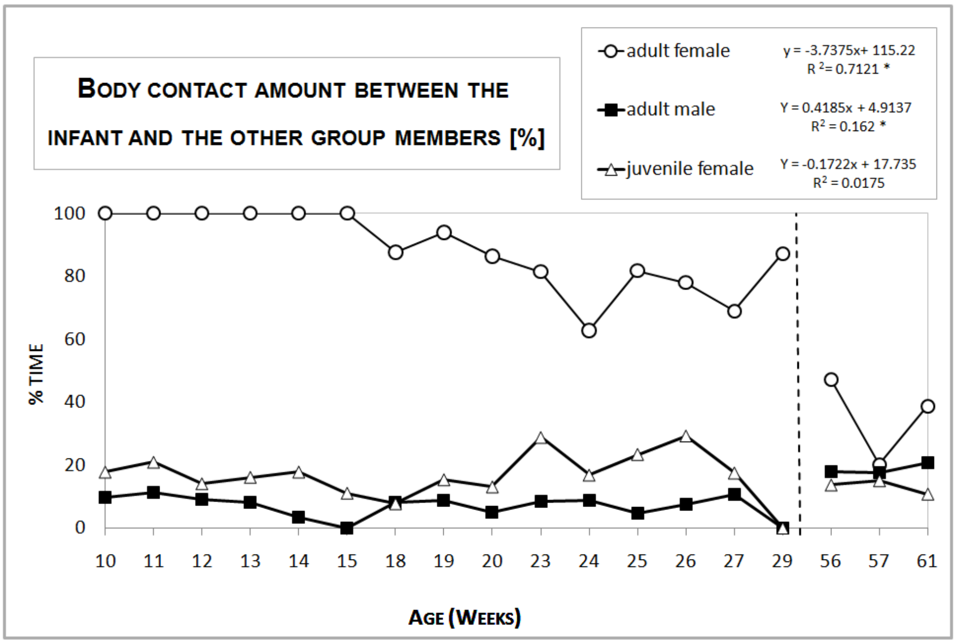

Fig. 16: Body contact amount between the siamang infant and the other group members longitudinally from the infant's age of 10 weeks onwards, expressed in percentage of time [%]. During data collection body contact with other family members at the same time was recorded and is not presented cumulative. Analysis is done for each pair combination. N = 3, Spearman rank correlation coefficients (* $p < 0.01$).

A significant decrease in the amount of time the adult female – infantile female pair spent in body contact with increasing age is found ($r_s = -0.160$, $p < 0.001$; Fig. 16). Up to the age of 18 weeks the infant spends 100 % of time in body contact with the adult female with a decrease in the following weeks. The lowest point up to the age of 29 weeks is reached in week 24, when body contact to the female amounts to 62.8 %. At the infant's age of about one year, body contact with the adult female ranges between 47.3 % and 20.3 %. A significant increase with age is also obvious in adult male - infantile female body contact amount ($r_s = 0.274$, $p < 0.001$), which remains under 12 % of time until the age of 29 weeks with an increase up to 20.7 % at the end of the study. No significant correlation is found in juvenile female – infantile female body contact according to the infant's age ($r_s = 0.124$, $p = 0.005$).

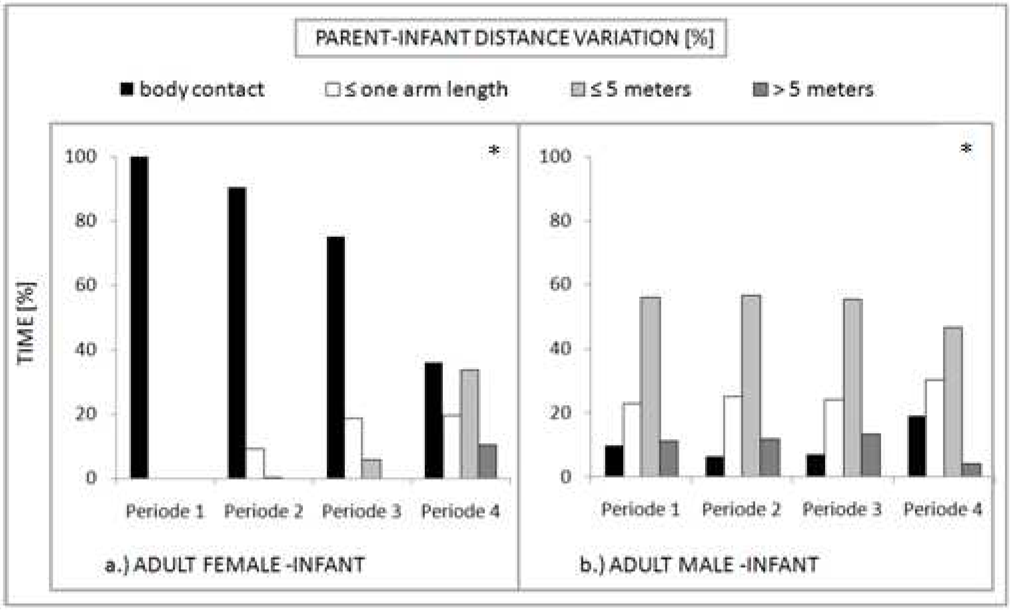

Fig. 17: Parent-infant distance variation in the siamang group in spatial relations according to the observation periods, expressed in percentage of time spent in different distance classes [%]. Data for period 1 to period 3: focal infant data, Data for period 4: scan data of activity budget in late infancy. X^2 – test (*p < 0.05); **(a)** N = 2, **(b)** N =2.

According to Fig. 17a, adult female – infantile female body contact is significantly higher in period 1 and period 2 in comparison to the other periods and time spent less than one arm length away from each other is significantly less in period 1 than in period 3 und 4. The adult female and the infant spend significantly more time less than five meters away from each other in period 4 compared to the amount of period 1 and period 2. In period 4 the amount of time spent in more than five meters distance is significantly higher than in the previous three periods (X^2 - test: 608.989, df = 9, p < 0.001).

In respect to the spatial relation of the adult male – infantile female pair a significant difference is found in time spent in body contact. Amount in period 4 is significantly higher compared to period 2 (Fig. 17b). No significant difference is found in less than one arm length and less than five meters proximity categories. Time spent more than five meters away from each other decreases significantly in period 4 (X^2 - test: 49.855, df = 9, p < 0.001).

3.2. INFANT’S NON-SOCIAL BEHAVIOUR

The dependence of the infant’s behaviour on its age is analyzed from infant focal data by means of ANOVA (Analysis of variance). Dunnett’s Post Hoc test T3 investigates the significance of differences of data between each period.

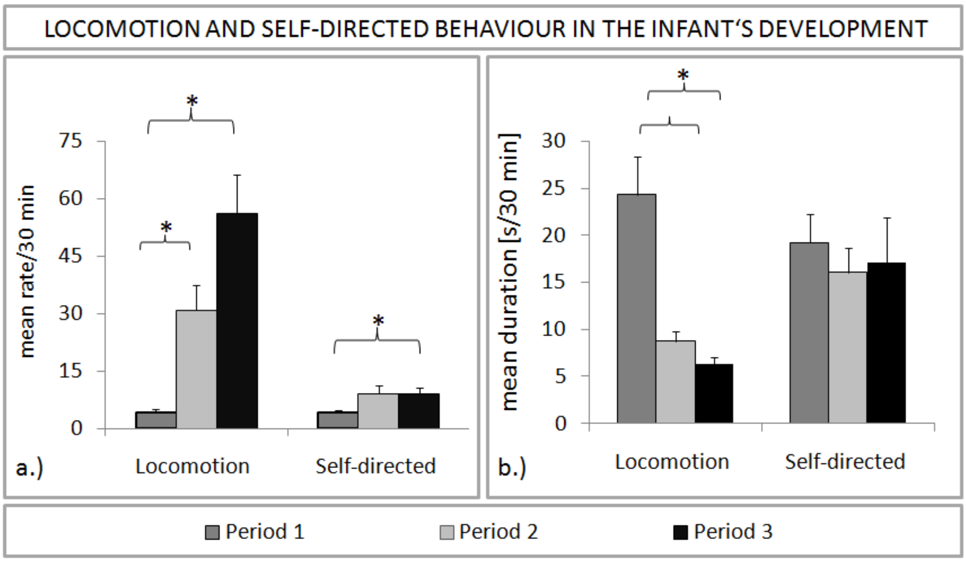

Fig. 18: Mean rate ± standard error of the mean **(a)** and duration ± standard error of the mean **(b)** per 30 min observation units of the siamang infant’s locomotion and self-directed behaviour over all three periods of focal infant data sampling. N = 1. Post Hoc Dunnett’s T3 (*$p < 0.05$).

Locomotion rate increases significantly from period 1 (4.26±0.82 rates/30 min) to period 2 (30.83±6.47 rate/30 min; Dunnett’s T3: $p = 0.001$), as well as from period 1 (4.26±0.82 rates/30 min) to period 3 (56.25±10.01 rates/30 min; Dunnett’s T3: $p < 0.001$; ANOVA: $F = 20.234$, $p < 0.001$; Fig. 18a). In respect to self-directed behaviour, differences are obvious in a significant increase from the first (4.18±0.65 rates/30 min) to the third period (9.16±1.54 rates/30 min; Dunnett’s T3: $p = 0.016$; ANOVA: $F = 4.732$, $p = 0.011$). Locomotion duration decreases significantly from period 1 (24.92±3.97 sec/30 min) to period 2 (8.74±1.02 sec/30 min; Dunnett’s T3: $p < 0.001$), as well as from period 1 (24.92±3.97 sec/30 min) to period 3 (6.28±0.76 sec/30 min; Dunnett’s T3: $p < 0.001$; ANOVA: $F = 11.496$, $p = 0.001$; Fig. 18b). No significant differences are obvious in duration of self-directed behaviour during the infant’s development (ANOVA: $F = 0.257$, $p = 0.774$, Dunnett’s T3: n.s.).

Further, the mean rate of object-play (in category self-directed behaviour) increases significantly from period 1 (0.00±0.00 rates/30 min) to period 3 (2.79±0.72 rates/30 min; Dunnett's T3: $p < 0.002$; ANOVA: $F = 8.317$, $p < 0.001$; Fig. 4). Mean duration also increases significantly from period 1 (0.00±0.00 sec/30 min) to period 3 (6.16±1.43 sec/30 min; Dunnett's T3: $p < 0.001$), as well as from period 2 (1.27±0.73 sec/30 min) to 3 (6.16±1.43 sec/30 min; Dunnett's T3: $p < 0.013$; ANOVA: $F = 16.731$, $p < 0.001$).

For more results on the infant's behavioural development see Table 38 in Appendix.

3.3. INFANT'S SOCIAL BEHAVIOUR

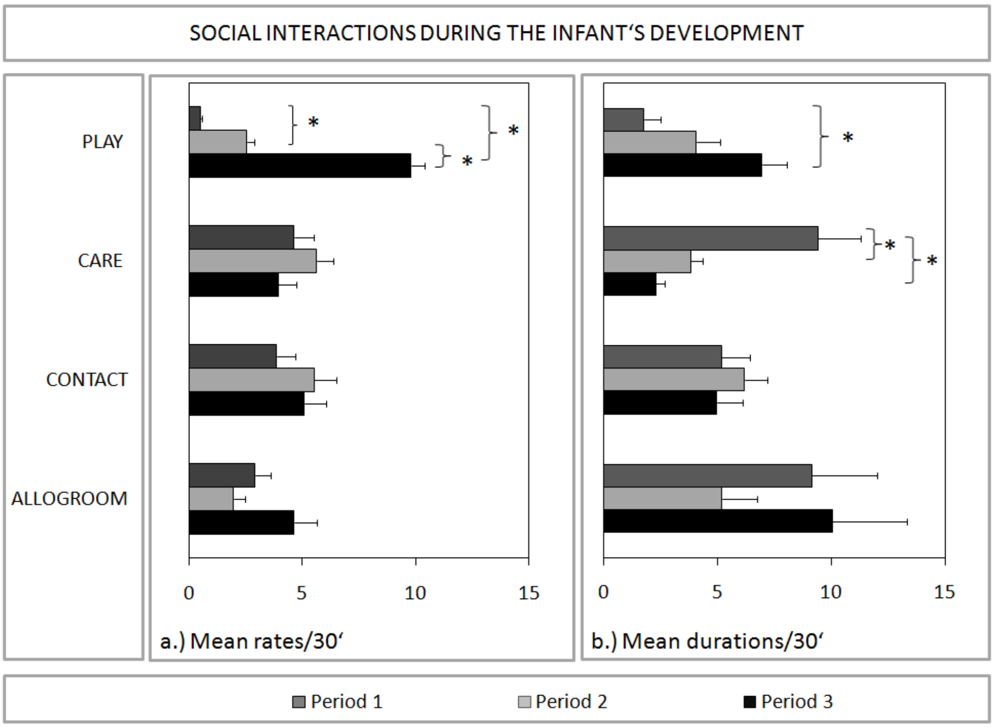

Fig. 19: Mean rate ± standard error of the mean **(a)** and duration ± standard error of the mean **(b)** per 30 min observation units of the siamang infant's social interactions over all three periods of focal data sampling. N = 4. Post Hoc Dunnett's T3 (*$p < 0.05$).

Play rate increases significantly from period 1 (0.49±0.21 rates/30 min) to period 2 (2.55±0.80 rates/30 min; Dunnett's T3: $p = 0.051$), as well as from period 1 (0.49±0.21 rates/30 min) to period 3 (9.75±2.18 rates/30 min; Dunnett's T3: $p = 0.001$) and between period 2 (2.55±0.80 rates/30 min) and 3 (9.75±2.18 rates/30 min; Dunnett's T3: $p = 0.013$;

ANOVA: F = 18.265, p < 0.001; Fig. 19a). No significant differences are obvious in caring, contacting and allogrooming rates.

Play duration increases significanty from period 1 (1.76±0.73 sec/30 min) to period 3 (6.95±1.10 sec/30 min; Dunnett's T3: p = 0.001; ANOVA: F = 7.544, p = 0.001; Fig. 19b). In respect to the duration of caring behaviour, a significant decrease is found from period 1 (9.40±1.89 sec/30 min) to period 2 (3.83±0.53 sec/30 min; Dunnett's T3: p = 0.020), as well as from period 1 (9.40±1.89 sec/30 min) to period 3 (2.28±0.40 sec/30 min; Dunnett's T3: p = 0.002; ANOVA: F = 7.323, p < 0.001). No significant differences are obvious in contacting and allogrooming duration during the infant's development.

In the following passage the infant's social behaviour collected in the three observation periods is analyzed regarding initiator and recipient roles, in order to find out if inter-individual social interactions change over the time in terms of rate and duration.

CARE		PERIODS			Analysis of variances between periods		Period to period analysis of variances		
Interaction Pair	mean rate (R) and duration (D)				ANOVA		Dunnett's T3		
		P1	P2	P3			P1 vs. P2	P2 vs. P3	P1 vs. P3
					F	Sign.	Sign.	Sign.	Sign.
ADULT FEMALE → INFANT	R	4.44±0.83	4.83±0.72	3.42±0.70	0.716	n.s.	n.s.	n.s.	n.s.
	D	9.69±1.80	3.60±0.50	2.22±0.37	9.027	*	*	n.s.	*

Tab. 27: Mean rate and duration ± standard error of the mean of caring behaviour between the adult female and the infant in the three observation periods. Interaction initiator and recipient roles are represented by arrows. N = 2, ANOVA (*p < 0.05) and Post Hoc Dunnett's T3 (*p < 0.05).

No significant difference is found between the adult female's caring frequency and the infant's age (ANOVA: 0.491.; Dunnett's T3: n.s.; Tab. 27). In terms of duration, a significant difference is obvious for the adult female's caring investment over the observation periods (ANOVA: p < 0.001). The post hoc test reveals that the differences of period 1 to 2 and 1 to 3 are responsible for this result, as a significant decrease is found between period 1 and 2 (Dunnett's T3: p = 0.007) and between period 1 and 3 (Dunnett's T3: p = 0.001).

PLAY		PERIODS			Analysis of variances between periods		Period to period analysis of variances		
Interaction Pair	mean rate (R) and duration (D)				ANOVA		Dunnett's T3		
		P1	P2	P3			P1 vs. P2	P2 vs. P3	P1 vs. P3
					F	Sign.	Sign.	Sign.	Sign.
ADULT FEMALE → INFANT	R	0.00±0.00	0.21±0.62	0.29±0.81	2.502	n.s.	n.s.	n.s.	n.s.
	D	0.00±0.00	1.33±0.73	2.49±1.22	3.332	*	n.s.	n.s.	n.s.

Tab. 28: Mean rate and duration ± standard error of the mean of social play between the adult female and the infant in the three observation periods. Interaction initiator and recipient roles are represented by arrows. N = 2, ANOVA (*p < 0.05) and Post Hoc Dunnett's T3 (*p < 0.05).

In adult female initiated plays with the infant, no significant difference of play rate over the periods is found (ANOVA: p = 0.088.; Dunnett's T3: n.s.; Tab. 28). Analyzing playing duration, however, a significant increase over the three observation periods becomes evident (ANOVA: p = 0.040), whereas no significant difference is found between each period (Dunnett's T3: n.s.).

PLAY		PERIODS			Analysis of variances between periods		Period to period analysis of variances		
Interaction Pair	mean rate (R) and duration (D)				ANOVA		Dunnett's T3		
		P1	P2	P3			P1 vs. P2	P2 vs. P3	P1 vs. P3
					F	Sign.	Sign.	Sign.	Sign.
ADULT MALE → INFANT	R	0.00±0.00	0.28±0.19	0.71±0.29	4.438	*	n.s.	n.s	n.s
	D	0.00±0.00	0.77±0.43	3.11±1.28	6.226	*	n.s	n.s	n.s

Tab. 29: Mean rate and duration ± standard error of the mean of social play between the adult male and the infant in the three observation periods. Interaction initiator and recipient roles are represented by arrows. N = 2, ANOVA (*p < 0.05) and Post Hoc Dunnett's T3 (*p < 0.05).

A significant increase in playing rate between the adult male as initiator and the infant as recipient is found (ANOVA: p = 0.015), whereas no significant difference is evident between the periods (Dunnett's T3: n.s.; Tab. 29). In playing duration, a significant increase is also found (ANOVA: p = 0.003), but no significant difference is obvious between the periods (Dunnett's T3: n.s.).

PLAY		PERIODS			Analysis of variances between periods		Period to period analysis of variances		
Interaction Pair	mean rate (R) and duration (D)				ANOVA		Dunnett's T3		
		P1	P2	P3			P1 vs. P2	P2 vs. P3	P1 vs. P3
					F	Sign.	Sign.	Sign.	Sign.
JUVENILE FEMALE → INFANT	R	0.21±0.10	1.00±0.43	6.00±1.47	17.591	*	n.s.	*	*
	D	1.23±0.69	3.25±1.04	6.36±1.07	7.863	*	n.s.	n.s.	n.s.

Tab. 30: Mean rate and duration ± standard error of the mean of social play between the juvenile female and the infant in the three observation periods. Interaction initiator and recipient roles are represented by arrows. N = 2, ANOVA (*p < 0.05) and Post Hoc Dunnett's T3 (*p < 0.05).

Rate in juvenile female initiated plays with the infant is increasing with the periods (ANOVA: p < 0.001), significantly from period 2 to 3 (Dunnett's T3: p = 0.009) and from period 1 to 3 (Dunnett's T3: p = 0.002; Tab. 30). In terms of duration, significant difference is found within the observation periods (ANOVA: p = 0.001), in detail between period 1 and 3 (Dunnett's T3: p = 0.001).

CONTACT		PERIODS			Analysis of variances between periods		Period to period analysis of variances		
Interaction Pair	mean rate (R) and duration (D)				ANOVA		Dunnett's T3		
		P1	P2	P3			P1 vs. P2	P2 vs. P3	P1 vs. P3
					F	Sign.	Sign.	Sign.	Sign.
INFANT → ADULT MALE	R	0.18±0.08	0.90±0.27	1.63±0.44	7.986	*	*	0.416	*
	D	1.67±1.10	2.36±0.96	3.93±0.90	1.135	n.s.	n.s.	n.s.	n.s.

Tab. 31: Mean rate and duration ± standard error of the mean of contacting behaviour between the adult male and the infant in the three observation periods. Interaction initiator and recipient roles are represented by arrows. N = 2, ANOVA (*p < 0.05) and Post Hoc Dunnett's T3 (*p < 0.05).

Differences are obvious in the infant's contacting rates toward the adult male over the periods (ANOVA: p = 0.001), conditional on significant difference between period 1 and 2 (Dunnett's T3: p = 0.045) and between period 1 and 3 (Dunnett's T3: p = 0.011; Tab. 31).

Contacting duration is not changing over observation periods (ANOVA: p = 0.326., Dunnett’s T3: n.s.).

3.4. Species Comparison in Infants’ Behaviour

Of all social and non-social behavioural categories, three of them are sorted out for comparison between the siamang and the lar gibbon infant’s behaviour, reflecting the infant’s exploration demand. For analysis Levene’s test for equality of variances and T-test for equality of means is chosen.

		10th+11th Week			19th + 20th Week		
Behaviour	Rates (R) + Durations (D)	Siamang	Lar	T-test (Sig.)	Siamang	Lar	T-test (Sig.)
Self-directed	R	4.00±1.47	7.65±1.47	n.s.	9.38±4.83	10.95±1.96	n.s.
	D	18.18±6.21	23.55±3.32	n.s.	9.69±3.02	17.99±2.53	*
Locomotion	R	2.42±0.67	1.35±0.56	n.s.	27.13±7.63	25.70±5.88	n.s.
	D	22.69±7.94	11.49±5.64	n.s.	6.77±2.36	10.25±2.08	n.s.
Play	R	1.17±0.61	8.88±0.60	n.s.	1.00±1.00	3,75±1.10	*
	D	0.00±0.00	0.19±0.19	n.s.	1.50±1.00	4.74±1.04	*

Tab. 32: Comparison of mean rate and duration ± standard error of the mean of different behavioural aspects between the siamang and the lar gibbon infant of focal infant data of 10th and 11th week of age, and of 19th and 20th week of age. N = 2, T-test for equality of means (*p < 0.05).

No species differences are obvious in the infants’ rates of self-directed behaviour in the 10th and 11th week of age (Levene’s test for equality of variance: F = 4.120, p = 0.051; T-test for equality of means: df = 29.988, p = 0.059), as well as in duration (Levene’s test for equality of variance: F = 1.631, p = 0.211; T-test for equality of means: df = 30, p = 0.410; Tab. 34). Rates do not differ significantly in 19th and 20th week (Levene’s test for equality of variance: F = 0.643, p = 0.430; T-test for equality of means: df = 9.387, p = 0.769), whereas a significant difference is found in duration (Levene’s test for equality of variance: F = 0.760, p = 0.391; T-test for equality of means: df = 17.145, p = 0.050).

In terms of locomotion behaviour, no significant differences are found in rates and durations, neither in week 10 and 11 (mean rates: Levene’s test for equality of variance: F =

0.278, p = 0.602; T-test for equality of means: df = 30, p = 0.237; mean durations: Levene's test for equality of variance: F = 898, p = 0.351; T-test for equality of means: df = 30, p = 0.249), nor in week 19 and 20 (mean rates: Levene's test for equality of variance: F = 0.144, p = 0.738; T-test for equality of means: df = 26, p = 0.893; mean durations: Levene's test for equality of variance: F = 0.938, p = 0.342; T-test for equality of means: df = 26, p = 0.347).

DISCUSSION

Gibbons and siamangs differ from other primate species in terms of the males' participation in parental investment. Such a biparental investment evolved to increase reproductive fitness for each parent obviously when investment of one parent alone is not sufficient for the survival of offspring. A monogamous reproductive system as evolved in gibbons and siamangs moreover favours this tendency as the male can be quite sure to invest in its own direct fitness.

The main issue of this study was to study cooperation of a siamang and a lar gibbon pair in terms of shared parental duties. It was assumed that male and female investment is distributed according to the changing requirements of the infant. Thus, according to Bischof's model of social motivation (Bischof 1975) during ontogeny, the need for security within the first stage of life is displaced by the need for arousal and exploration to gain autonomy critical for individual survival and reproduction. In most mammals a close attachment to the mother evolved to ensure survival of the infant providing security. Disruption of this attachment bond during early infancy e.g. by separation from the mother during dependence leads to severe social and physical disorders of the infant even if nutrition is readily available (Harlow & Harlow 1972). The amount of parental investment can be regarded as a cost-benefit analysis. It is assumed that the parents will distribute their parental investment complementarily according to the needs for security and arousal of the offspring. Thus, the mother is expected to invest most in the first stage of infant life in terms of nutrition and attachment thus satisfying the security system. When this need for security is displaced by the need for arousal and exploration, the father takes over in parental investment which enables his female partner to prepare and save energy for the next reproductive period. This hypothesis of complementary parental investment was tested in this study.

Non-social Activity Budgets and Housing Conditions

Wild siamangs spend between 40 and 50 % per day feeding (Geissmann 2003), respectively 29 % resting and 10 % travelling (Raemaekers & Chivers 1980, as cited in Orgeldinger 1999). Nevertheless, differences are found throughout many studies depending on seasonal weather conditions causing variation in the daily amount of feeding and resting (Chivers & Raemaekers & Aldrich-Blake 1975). In captive populations food supply is abundant hence reducing the time needed for feeding. Thus, in this captive study the adult individuals of the siamang group were observed to spend most of the day resting, followed by time spent in locomotion and feeding. The adult lar gibbon pair also spend most of the day resting, followed by feeding and locomotion behaviour. Nevertheless, in wild populations more time is invested in travelling between food patches than in feeding (Geissmann 2003).

As arboreal species the siamang group spent significantly more time in the trees and on the ground which was not possible for the lar gibbon group which spent significantly more time in the indoor enclosure due to differing housing conditions. These differences obviously influence behavioural data in species comparison. The siamang group had not much range to brachiate in their indoor enclosure and thus spent much time sitting on the floor inside the house but also in the grass on the ground outside of the house. The adult female was less restrictive with the infant on the ground because her full attention was not necessary anymore, as falling risk is negligible. This obviously enhanced social contacts of the infant with other group members. Contrarily, the lar gibbon's house has been large and high enough to locomote sufficiently inside, but less space has been offered for more than one gibbon to sit on platforms, therefore contact sitting was mainly possible on the, not often haunted, floor. In the beginning of observation, the lar gibbon mother prohibited its infant to leave her in the house, possibly due to the fact that she preferably sat on the elevated platforms. For this reason the location preference of both groups can not be rated as species and more as housing differences. Activity budgets of adults and juvenile offspring differed obviously from each other. While the adult lar as well as siamang pair rested significantly more in comparison to the juvenile female the latter spent significantly more time locomoting or with other behavioural patterns. In the lar group, the adult pair's behaviour was quite synchronized according to similar activity budgets.

Social Behaviour

Siamang and lar gibbons are claimed to differ in terms of intra-group cohesion, whereas observation on the siamang's social life indicate enhanced harmony and obliging integration, compared to the lar gibbon (Chivers 1976, reviewed in Palombit 1995). According to past studies (Fischer & Geissmann 1990) the hypothesis of the siamang's stronger coherence compared to the lar gibbon is affirmed. This assumption though never compared directly, is supported by data from this study. A direct comparison of the two captive groups with similar age and sex composition though slightly differed housing conditions shows that members of the siamang group interacted more often in social context than the lar group which spent significantly more time resting instead. Moreover, social tolerance among individuals is investigated in relaxed as well as in “competitive”, i.e. feeding context separately reflected in inter-individual distances, whereas a lower inter-individual proximity while resting and feeding was found in lar gibbons in contrast to siamangs.

According to Orgeldinger (1999) captive siamang groups spend about 31 % per day with social interactions, 14.2 % is invested in pair bonding behaviour and 69 % in non-social behavioural patterns.

In the wild, higher rates of the siamang’s affinitive interactions compared to the lar gibbon’s amount are observed, obvious in close inter-individual proximity, not only in social interaction e.g. embracing, but also in relaxed body contact sitting without social performance. Moreover the same sleeping tree is shared (Palombit 1995). Anyway, it is suggested that species differences in terms of social behaviour display may originate from increased intraspecific food competition in the frugivorous lar gibbons in comparison to the more folivorous siamangs (Palombit 1995).

Inter-individual differences have also been investigated, as reflecting relationship qualities among group members. In terms of time spent in body contact the juvenile female still spent almost as much time in body contact with the adult male as with the adult female. This can be explained by the juvenile female’s high interest in the infant clinching on the mother’s stomach and its frequent “visits” and playing attempts. In the siamang and the lar gibbon group, the adult females spent most of the time in body contact with their infants and the adult males with their juvenile offspring. Nevertheless, in contrast to the siamang juvenile, the juvenile lar female spent much more time in body contact with her mother than with her father which is probably caused by generally lower playing rates in adult male – juvenile female social interactions in the lar study group. Comparing inter-individual distance between the infants and the other family members of both study groups, it becomes clear that the siamang infant spent significantly more time in body contact and in less than one arm length with both, the adult male and the juvenile female than the lar gibbon infant did. According to these results, a species difference in terms of less motivation for close social association is already obvious in the offspring.

Another aspect reflecting strong group cohesion among a siamang family is the strict maintenance of sleeping partners. In this study the group members were never observed to deviate from their usual sleeping place, nor from the choice of preferred sleeping partners. Hence, the siamang adult female was observed to sleep with the infant and the adult male with the juvenile female, which is quite consistent with results of Chivers (1974) and Orgeldinger (1997). In contrast, in the lar group individuals varied the sleeping places and never slept in close proximity to each other, except the mother with the infant. According to Chivers (1972) and Ellefson (1974) lar group members are usually scattered when entering the sleeping tree, whereas only the lar gibbon infant sleeps in body contact with its mother until the age of about 2 years. Sometimes even several sleeping trees are sought out (Reichard 1998). Bartlett (2003) assumes that the lar gibbon's social behaviour might have been underestimated in past studies, as he points at observations of social grooming even between neighboured groups at Khao Yai National Park in Thailand. Therefore flexibility among individual groups must be taken into account a seen in recent gibbon studies. Nevertheless, results of this study support Palombit's (1995) findings of siamang group members spending significantly more time in close proximity than lar gibbon group members.

Differences in Male/Female Behaviour and Parental Investment

If the hypothesis of complementary parental investment is valid it was expected that the activity budget of the mother and the father differs significantly within siamangs and gibbons. Data from time budgets support this hypothesis for siamangs. The siamang male invested significantly more time playing with the offspring than the female whereas the latter spent significantly more time with caring behaviour. When comparing interaction pairs, adult male – juvenile female plays were observed to occur significantly more often and longer than adult female – juvenile female playing sessions, which is consistent with Orgeldinger's (1999) results. The father initiated also significantly more often play with the juvenile female than the adult female did and he initiated slightly more often play with the juvenile than vice versa which further supports the hypothesis of the siamang male to be an intensive caretaker (Whitten 1987).

Expectedly, the adult female on the other hand spent significantly more time with the infant in caring behaviour than the adult male and she also invested more time in caring for the infant than for the juvenile female. Grooming behaviour was also significantly more frequent between mother and infant than between father and juvenile. The infant was not yet able to reciprocate grooming but in the father-juvenile pair, the grooming rate was exchanged equally though the adult male groomed the offspring significantly longer than the offspring did in return. However, the mother still groomed her juvenile daughter more than the father did, i.e. she still invested in her juvenile daughter in terms of providing security whereas the father invested more in play, i.e. providing arousal and excitement. Though contacts with the infant were more frequently initiated by the mother than by the father, i.e. the mother often had to support the infant's climbing attempts or had to pick it up somewhere, the adult male contacted the infant significantly more than the juvenile. The father showed intense interest in his infant, e.g. obvious in frequently helping when the infant was trying to climb and tolerating the infant's curiosity towards him. Thus, the adult male – infant relationship is, among other things, based on the adult male's high tolerance level towards the infant. Further, as Alberts (1987) points out, indeed great interest obvious in frequent contacts of the infant towards the adult male, might also play a key role in father-infant relationship, emerging independently from the adult female's caring behaviour.

In the lar gibbons, male – offspring play was also more frequent than female – offspring play, though here it is the offspring who significantly more often initiated play. Thus the lar father appears less motivated to take the initiative for play investment in his offspring. As in the siamang group the male's play investment is concentrated on the juvenile offspring, i.e. the adult male initiated play significantly more often and also played longer than the adult female did. Similar to the siamang mother, the lar gibbon mother was more often involved in caring behaviour with the offspring in comparison to the father and the adult female's investment in grooming did not vary between the juvenile and the infantile female. However, the results are influenced by the general low allogrooming rates in the lar group as well as a shorter observation period on the lar gibbon group in comparison to the siamangs. In terms of contacting behaviour, the male lar gibbon father was not more interested in contacting the infant than the juvenile as was the siamang father. Thus, the lar father simply appears to be less interested in contacting his infant in comparison to the siamang father. Similar to the siamangs, the adult female was more often contacting the infant than the juvenile.

Comparing both species directly, it becomes obvious that the siamang mother was generally more active in contrast to the lar mother who spent more time resting instead. This is probably related to differences in housing and environmental enrichment conditions between the groups. However, more time was spent by the siamang mother on infant related behaviours, i.e. caring and allogrooming, than by the lar gibbon mother. Concerning the fathers, the siamang was much more time involved in paternal care than the lar male thus reflecting an obvious species difference in respect to paternal investment. The species comparison of play and grooming rates and duration did not reveal differences.

These results support the assumption that siamang fathers show more paternal investment, than other gibbon fathers, mostly obvious in infant carrying (observed in captivity: Alberts 1987, in the wild: Chivers 1972, Chivers & Raemaekers 1980). According to former studies siamang fathers usually show interest in the infant by contacting the baby only a few weeks after birth, as it was already obvious in the 8th week of the siamang infant's age in the present study. As in most gibbon species male care seems to be rare and exceptional (*Hylobates lar*: Clemens & Merker & Ujhelyi 2008), siamang males are claimed to belong to the class of "intensive care takers", which means a large daily amount of infant related social interaction (Whitten 1987). However, in some siamang study groups male care has not been observed at all (Dal Pra & Geissmann 1994, Fox 1972, Orgeldinger 1999), due to the fact that most females just restricted access to the infant (Fischer & Geissmann 1990). As seen in a study concerning the behavioural development of a pileated gibbon (*Hylobates pileatus*), siblings can be very encouraged in helping behaviour and might also be influencing male behaviour (Braendle & Geissmann 1997). In a study male carrying has been observed extraordinary frequently, whereat twin offspring in that siamang group must be mentioned, which might have been enhancing helping behaviour, due to the fact that siamangs usually give birth to single offspring (Dielentheis et. al. 1991). However in another siamang group with twin offspring, the male was never observed to carry the infants (Dal Pra & Geissmann 1994).

Moreover, according to latest studies it has been observed that in a multimale siamang group (at Way Canguk research station in the Bukit Barisan Selatan National Park on Sumatra) most males exhibit infant carrying (Lappan 2005, as cited in Lappan 2007). Further Lappan (2007) assumes the possible relation between the size of the group and the maintenance to keep other groups off the nutritious food patches, as "larger siamang groups had higher mean numbers of figs in their home range and had significantly higher infant and juvenile survivorship than those of smaller groups" O'Brien et al. (2003, as cited in Lappan 2007).

In another study of Lappan (2008) at the Way Canguk research station, she found that in polyandrous groups all males exhibited infant caring, whereas in socially monogamous groups males provided considerably more care. One possible explanation could be the reduction of high energetic, female reproduction costs to shorten birth intervals. Afterwards the individual infant may also play an important role in male-infant relationship (Lappan

2008), as on the infant's side curiosity and on the male's side high tolerance level may affect direct male care.

Allman et al. (1998) proposes that under evolutionary aspects male care promises fitness advantage in tendency to live longer. For example female lar gibbons live significantly longer than the males, whereas in comparison male siamangs have an advantage in contrast to the female siamang survival. This result was also found in titi monkeys (*Callicebus sp.*) and owl monkeys (*Aotus sp.*), which supports the hypothesis that the strength of these male-offspring relations associated with the hormonal and neurochemical status, might have an influence on survival rate.

A great variety in individual paternal investment as seen in recent studies, both from wild and captive groups has to be taken into account when interpreting data of this study. Male care has been and is still observed rarely in free ranging gibbon groups, due to challenging observation conditions. The distribution of paternal time investment in the wild must also be considered where indirect care by territorial behaviour may be more relevant for his direct fitness than direct paternal caring behaviour.

Anyway, disregarding evolutionary aspects, presented results are consistent according to past gibbon studies in captivity, claiming the siamang's higher male care amount compared to other gibbon males' less investment (Alberts 1987).

Infant's Development

Due to slow physical development gibbon infants are totally dependent on the mother's carriage for more than one year of age, thus high amount of time is spent in body contact. In this study a decrease in the siamang infant's time spent in body contact with its mother and the simultaneous increase in contacting or being contacted by other family members during study period was observed. In this study a possibly point of changing demands of the infant became obvious at the age of 18 weeks, as body contact with the adult female did not amount 100 % of time anymore. Siamang research by Alberts (1987) found also a decline from 100 % body contact with the adult female already in the 13th week of the infant's age. In comparison, in a study about the behavioural development of a pileated gibbon (*Hylobates pileatus*), the infant was increasing its distance to its mother at the age of 14 to 18 weeks, but decreased again for about two weeks. Only until the age of about 3 months the infant spent 100 % of time in body contact with its mother (Braendle & Geissmann 1997). However, the siamang infant in this study was observed to spend constantly more time in body contact with the juvenile female, than with the adult male. This might be due to the high interest of the juvenile female, obvious in mainly constant contact and play attempt rates. Crucial change was obvious in results found at the infant's age of one year: Body contact with the adult male had overtopped time spent in body contact with the juvenile female, but did not reach the amount of adult female – infant body contact, as it was the case in Alberts' (1987) study, where the infant spent 29 % of time with its father at an age of 57 weeks. However, it can be discussed, whether results are caused by the presence of a sibling, which was not the case in Alberts' (1987) study, or because of the female's dedicated caring behaviour. According to Chivers (1972), changes are expected to be crucial in the second year of the infant's life and the infant-adult male relation is likely to strengthen, reflected in higher body contact amount.

Further, the infant's non-social behaviour was also analyzed as a function of age to find indications on exploration display. One behavioural aspect is obvious in locomotion amount, whereat frequency changed in a constant significant increase with age, though duration decreased. This might be irritating, but can be explained by the enhanced, obviously exhausting movements the infant performed, while practising crawling, climbing and walking, resulting in a high frequency of short recovering phases. Moreover, the amount of self-directed behaviour as e.g. object-play also increased significantly with age.

In terms of social behaviour, mother initiated caring amount expectedly decreased significantly by the time. When considering helping behaviour obvious in infant-carrying, the adult male carried the infant, albeit very rare, whereas the juvenile female was never observed to do so, which is quite consistent with most of past studies. Although research by Dielentheis et al. (1991) found that in a siamang group with twin infants at Berlin Zoo, both the adult male and the juvenile sibling were observed to conduct carrying behaviour. Thus, it was assumed that helping behaviour is even more likely to occur in groups with twins, which is indeed rare. Nevertheless, in another study with twin offspring at Zürich Zoo, neither the adult male nor the sibling carried the infants. Although Braendle & Geissmann (1997) report even on a juvenile pileated gibbon (*Hylobates pileatus*), carrying its 29 weeks old sister, more family groups emphasising helping behaviour must be studied.

Nevertheless, play behaviour increased successive, whereas no significant change related to age was found in playing amount of both, mother – infant and father – infant social interactions. Play behaviour increased significantly between the infant and its older sister. Thus, in this study the juvenile female's high interest in the infant not only restraint in contacting behaviour, but also was quite clear to see in playing behaviour. This supports results from other studies, as the juvenile family member became the preferred playing partner (Chivers 1974, Fox 1972), as well as it was the case in a study of a pileated gibbon (*Hylobates pileatus*) infant (Braendle & Geissmann 1997). Taking into account the adult female could be the crucial factor on the amount of early infant social play (Dal Pra & Geissmann 1994). The more "severe" she acts and further restricts rough play, the less the infant has the opportunity to play. Thus, in the present study, the juvenile female had obvious learned to keep back its temper whenever the mother was in the near, otherwise she would take the infant and act agonistic towards her. Consequently, peering was always observed from the juvenile to the adult female, as if noting whenever play turned out rough.

Results on behavioural development between the siamang and lar gibbon infant concerning exploration display revealed no differences at the early age of 10 and 11 weeks. Significant differences became obvious in week 19 and 20 in an increased social playing amount of the lar gibbon infant compared to the siamang infant, as well as in longer sessions spent in self-directed behavioural patterns. Results support Dal Pra & Geissmann (1994) maintaining the hypothesis that members of the *lar* group exhibit a faster development than siamangs.

Development marker		*lar* group	*H. pileatus*	*H. syndactylus*[1]	*H. syndactylus (twins)*	*S. syndactylus*[2]
1.) Partial independence from mother (hangs on cage bars in contact with her)	Mean	9	11	9	≤8	8
	Range	9			≤8	
	Sample size	2	1	1	2	1
2.) Complete lack of contact with mother	Mean	15	12	16	14	10
	Range	6-22		13-22	12-16	
	Sample size	10	1	7	2	1
3.) Suspension by one arm	Mean	22	17	24	21	21
	Range	13-30			20-22	
	Sample size	3	1	1	2	1
4.) Bimanual brachiation	Mean	21	17	35	30	>29
	Range	10-39			30	
	Sample size	12	1	1	2	1
5.) Bipedal locomotion	Mean	39	27	43	$32<x<50$	>29
	Range	24-65			$32<x<50$	
	Sample size	9	1	1	2	1
6.) Feeding on solid food	Mean	19	25	12	16	10 (natural)/ 18 (prepared food)
	Range	10-35		9-15	16	
	Sample size	17	1	4	2	1
7.) Play with siblings	Mean	23	27	29	12 (between twins) 14 (with older sibling)	11 (with older sibling)
	Range	16-30		15-43		
	Sample size	2	1	2	2	1
8.) Being groomed by siblings	Mean	9	42	13	≤8	8
	Range			4-22	≤8	
	Sample size	1	1	2	2	1
9.) Grooming (allogrooming)	Mean	26	>52	45	>50	>29
	Range			36-54	>50	
	Sample size	1	1	2	2	1
10.) Infant calling	Mean	-	>52	32	12	>29
	Range			23-39	12	
	Sample size		1	3	2	1

Tab. 33: During behavioural observation developmental markers were recorded at individual stage of age (in weeks), in members of the *lar* group and in siamang infants (adapted from Braendle & Geissmann 1997). [1]Former used controversial siamang species name. [2]Data from the siamang infant observed in the present study added.

According to the fact that seven out of nine behavioural markers have been observed earlier in gibbons (column "*lar* group") than in siamangs (column "*Hylobates syndactylus*") support Dal Pra & Geissmanns (1994) assumption (Tab. 33). Contrarily, in the present siamang infant study some development markers were observed even earlier than in former studies, whereas others are missing as research was finished before. E.g. data from both, the *lar* group and the pileated gibbon (*Hylobates pileatus*) observations support the assumption of an accelerated development in comparison to the siamang infants' studies. Nevertheless, great difference is found in playing behaviour point of time, as social play between siamang siblings (*Hylobates syndactylus*) occur between the infant's age of 15 to 43 weeks according to past research, whereat in the presented study the siamang infant (*Symphalangus syndactylus*) was already actively playing in the 11th week (development marker 7). Moreover, a broad variety is also obvious in physical changes, because the siamang infant (*Symphalangus syndactylus*) was already completely independent to its mother (development marker 2) at the age of 10 weeks, whereas the siamang infants (*Hylobates syndactylus*) observed in the past were observed to do so at the mean age of 16 weeks and the lar gibbon infants at the age of 15 weeks. Therefore, results do not support Dal Pra & Geissmann's (1994) hypothesis, as in the present siamang study 6 out of 10 developmental markers were observed earlier than in the *lar* gibbon group. It can be assumed an underestimated broad flexibility in terms of infant development, primary depending on the individual necessity of time to develop, but also on social influences as e.g. group cohesion obvious in social interactions integrating the infant and even housing conditions, which might facilitate the infant's independence to its mother, as many cage bars, ropes and platforms motivate the exploration behaviour.

CONCLUSION

Hypothesis 1 is confirmed as higher amount of maternal investment in comparison to paternal investment during the infant's first year is found in both species. Results support the assumption on the adult male to spend more time in contact with the juvenile female, than with the infant and Hypothesis 2 is confirmed. Explanation is found in the high social play amount between the adult male and the juvenile female, compared to the amount in adult female – juvenile female amount, in both study groups. Further a significant correlation between the siamang infant's decreasing body contact amount with the adult female and increasing body contact amount with the adult male was determined, reflecting its integration process into social interactions among the group, thus Hypothesis 3 is confirmed. Finally mother prevention and protection behaviour dispose of infant contact amount to other family members as well, which might not only be species-, but also even group-specific. Concerning species comparison of paternal care, predictions are partly confirmed (Hypothesis 4). No difference in species playing amount of adult male – juvenile female was found and assumption on the siamang adult male's higher male investment can only be confirmed in general paternal behaviour, containing play, contact and caring behaviour. Moreover infant-carrying was observed in the siamang male and not in the lar male, supporting the hypothesis of the siamang male's outstanding contribution in parental role-behaviour in gibbons. Nevertheless, species differences were found in significantly lower rates of body contact respectively social interactions among the lar gibbon group, confirming the assumption of the siamang's more cohesive nature of the onset in differing intraspecific level of food competition.

To sum up, complementary parental investment attuned to infant development is apparent in siamangs and lar gibbons. Maternal investment is higher during the first stages of life when attachment and care to provide security is the primary need of the infant. However, siamang as well as lar gibbon mothers spend more time with caring behaviour not only for the infant but also for the juvenile offspring than the fathers. In later stages of life when arousal and exploration are more important for development the father takes over and provides paternal care in terms of play behaviour but also in terms of allogrooming. Beside this similarity among siamangs and lar gibbons, significant more social behaviour and less spatial proximity in siamangs supports assumptions that group cohesion is stronger and within group competition lower in siamangs in comparison to lar gibbons.

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APPENDIX

PHOTOS

(by Manuela Lembeck)

Fig. 20: Siamang group; adult male, infant (57th week), adult female, juvenile female (from left to right).

Fig. 21: Siamang group; adult male and adult female (from left to right).

Fig. 23: Siamang group; juvenile female.

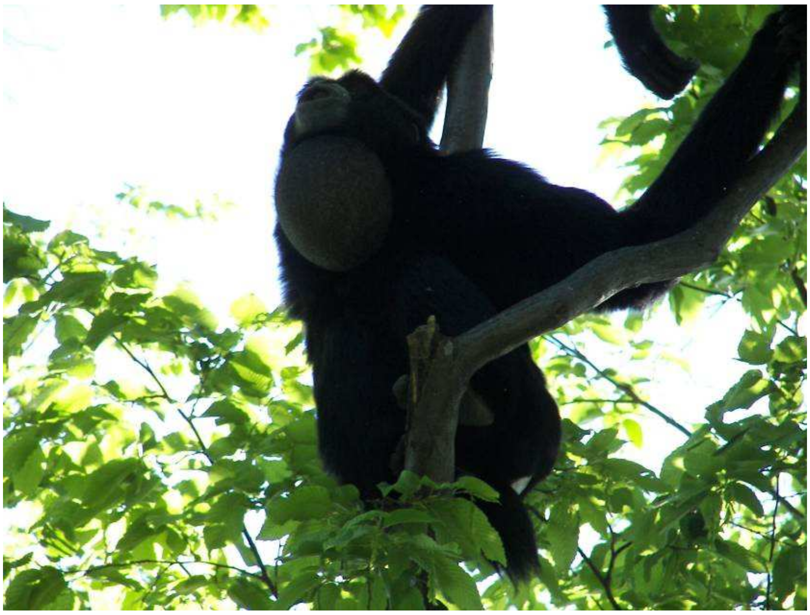

Fig. 24: Siamang group; adult male singing (with inflated throat sac).

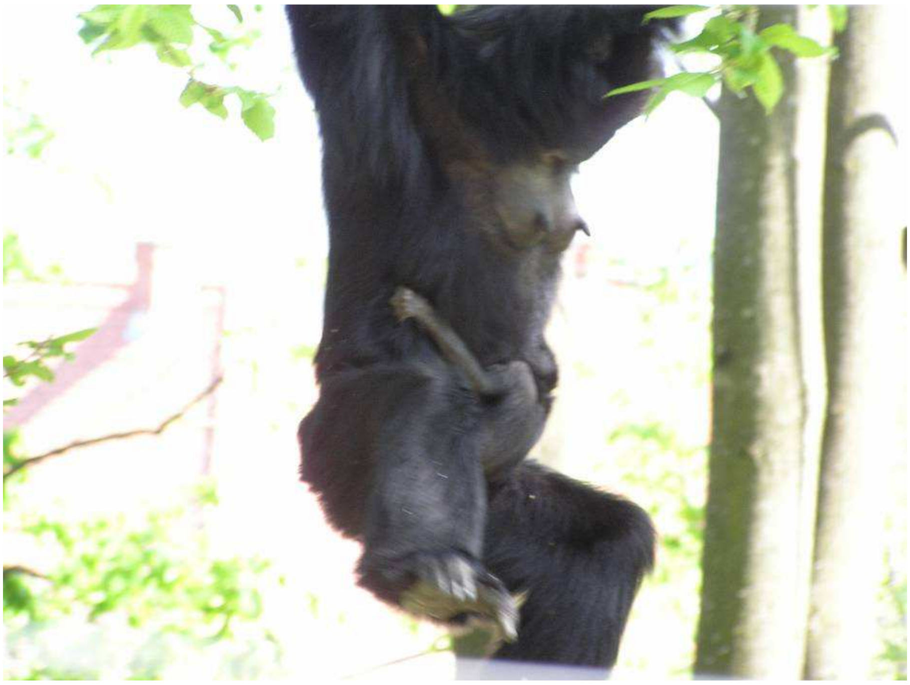

Fig. 25: Siamang group; adult female carrying the infant (age: 2 weeks).

Fig. 26: Siamang group; adult female and suckling infant age: (2 weeks).

Fig. 27: Siamang group; adult female and infant (age: 3 weeks).

Fig. 28: Siamang group; infant suckling (age: 3 weeks).

Fig. 29: Siamang group; infant (age: 11 weeks).

Fig. 30: Siamang group; infant exploration behaviour (age: 21 weeks).

Fig. 31: Siamang group; infant suckling (age: 25 weeks).

Fig. 32: Siamang group; adult male and adult female (behind, from left to right), infant in the front (age: 29 weeks).

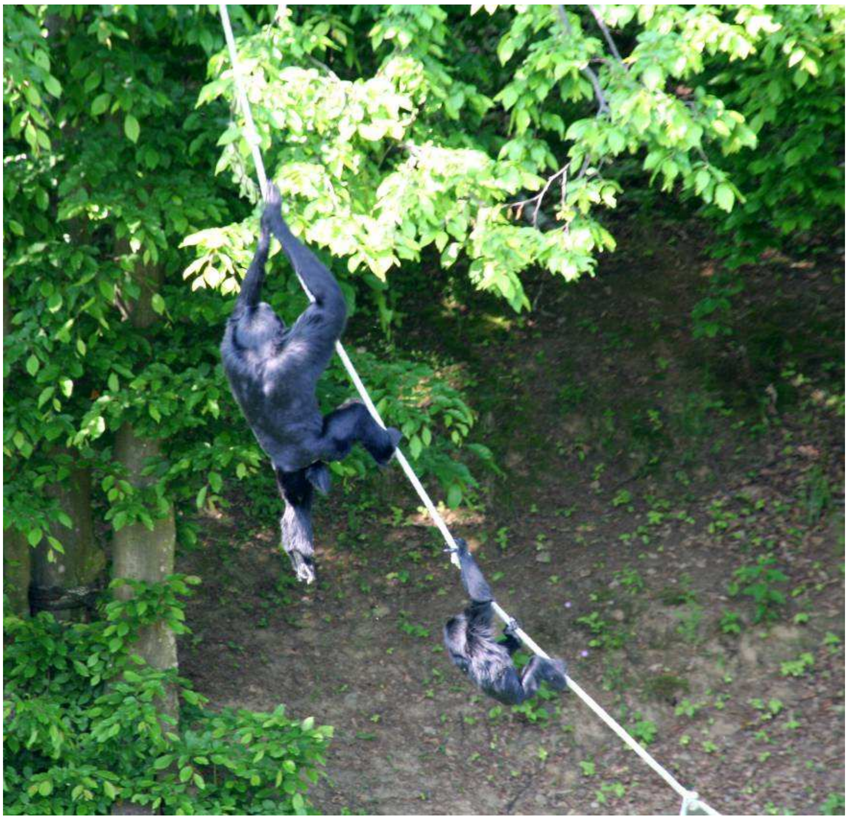

Fig. 33: Siamang group; adult male and infant (age: 57 weeks).

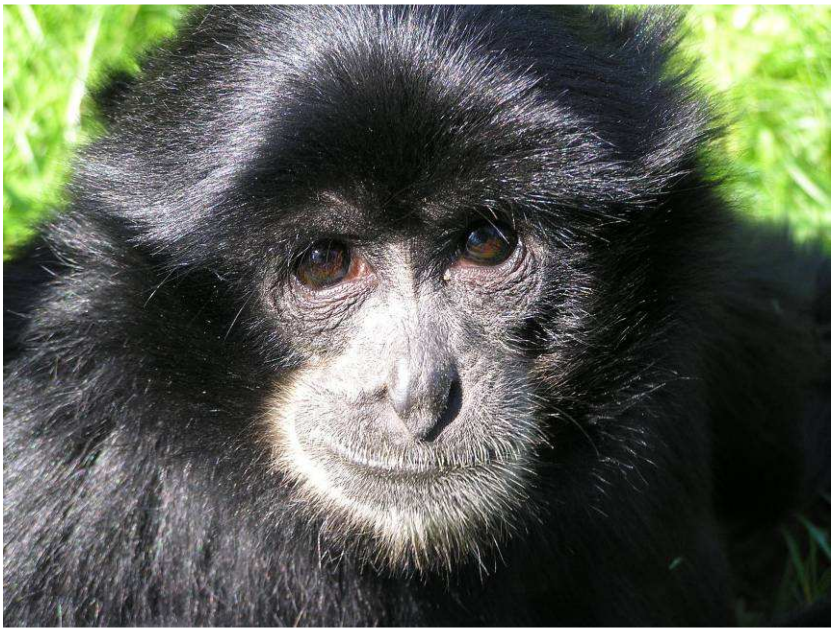

Fig. 34: Siamang group; juvenile female.

Fig. 35: Lar gibbon group; adult male.

Fig. 36: Lar gibbon group; adult female with infant (age: 8 weeks).

Fig. 37: Lar gibbon group; juvenile female.

Fig. 38: Lar gibbon group; adult female with infant (age: 8 weeks)

Fig. 39: Lar gibbon group; adult female with infant (age: 30 weeks).

ETHOGRAM

ST = STATES EV = EVENTS

LOCOMOTION

- *walk bipedal* *(st)*

  Describes a movement forward-turned on two legs. This action can be performed on the ground, on a rope or on a branch. Additionally, if the focal animal is leading or following someone, it is noted.

  (add: lead/follow)

- *brachiate* *(st)*

  Defined a swingeing movement performed, the typical movement of gibbon locomotion. Climbing movements are included. Additionally, if the focal animal is leading or following someone, it is noted.

  (add: lead/follow)

- *totter* *(st)*

  The infant's wag to and fro movement without changing the position, always while clinching to someone.

- *practise climb* *(st)*

  Infant tries to pull itself up along an object, e.g. a rope.

  (add: move to someone)
  (add: hold on to whom)

- *practise walk* *(st)*

  Infant tries to move forward on two legs.

  (add: move to someone)
  (add: hold on to whom)

RESTING

- *sit* *(st)*

  To rest without doing anything else but watching. A note is made when monitoring of other family members occurs (social monitoring) or something or someone from outside attracts attention (vigilance).

  (add: vigilance yes/no)
  (add: social monitoring yes/no)
  (add: if yes: who is being watched)

- *lay* *(st)*

  To rest dorsal, ventral or lateral. A note is made when monitoring of other family members occurs (social monitoring) or something or someone from outside attracts attention (vigilance).

  (add: social monitoring yes/no)
  (add: if yes: who)
  (add: vigilance yes/no)

- *sit / lay with closed eyes* *(st)*

  The individual rests with closed eyes.

FEEDING

- *feed natural* *(st)*

  To feed material from the natural environment like seeds, leaves, grass, insects, but also contains drinking display.

- *feed prepared* *(st)*

  To consume prepared food from the keeper, e.g. fruits or vegetables.

- *forage* *(st)*

  To search for food, but without changing the place by e.g. plucking grass, leaves from the branches.

- *nibble* *(st)*

  To chew something.

ALLOGROOMING

- *groom (sender)* *(st)*

  Manipulation of the fur of conspecifics in order to remove detritus or parasites by using the fingers.

- *groom (recipient)* *(st)*

  The individual is scanning its own coat for foreign material.

(add: body part)	E.g. face, head, front side (including chest and stomach), back (including shoulder), limb (including hand and finger, foot and toe), side (including armpit) and buttock.
(add: who approaches)	An individual is coming up to another one in order to dispense, receive or exchange affiliative gestures.
(add: offer body part yes/no)	An unmistakable display to signalize the wish to be groomed by a conspecific.
(add: if yes: unresponsiveness)	The other individual doesn’t start grooming.
(add: if yes: passive acceptance)	One individual accepts being groomed, but often does something else like feeding at the same time and does not show any attendance of being groomed.
(add: if yes: active acceptance)	When being groomed, the individual offers one body part or just changes the position to ease the grooming.
(add: who stops grooming)	

PLAY

- *play with someone (no body contact)* *(st)*

  To perform social play. An open mouth display (playing face) is visual. Chase – flight plays without body contact.

- *play with someone (body contact)* *(st)*

  Social play including behavioural patterns like wrestling, pull, push, slap, kick.

(add: with whom)	Playing partner’s name.

(add: who initiates play)	E.g. teasing an individual by jumping forward, slap and draw back or by performing an inhibited bite.
(add: accept/refuse invitation)	Start to play after being invited / refuse play invitation by showing agonistic display or ignorance behaviour,
(add: who chases/flights)	Definition of chase and flight playing role.
(add: where do they play)	Defines play court, e.g. ground, tree or house.
(add: in which play context)	E.g. before / after feeding.
(add: high intensity, low intensity)	High intensity games are characterized by high velocity and powerful, precise movements. Low intensity games are performed with less willingness, apparent by moving slowly and less responding.
(add: who stops playing)	Who discontinued the play.

CARE

- *clinch* *(st)*

  To hold on to someone by using all extremities.

  (add: to whom)

- *carry baby* *(st)*

  The infant is being carried, further it is recorded in which position.

  (add: front/back/side)

- *inspect baby* *(st)*

  To stare at the baby and touch it gentle, by holding e.g. one hand.

  (add: active/passive)

- *nipple contact* *(ev)*

  Describes holding the mother's nipple in the mouth.

- *lick* *(ev)*

  Tongue-contact.

- *take someone* *(st)*

  To pick someone to change location, e.g. the mother takes the infant when moving somewhere.

  (add: active/passive)

- *retrieve* *(st)*

  Keep back someone, or being held back.

  (add: active/passive)

  (add: who keeps back/is held back)

- *sit/lay and hold on to someone/* *(st)*

  To sit/lay independently, while not using all extremities to hold on something.

  (add: to whom/which object)

  (add: social monitoring whom)

  (add: explore someone whom)

  (add: explore something)

  (add: how many extremities)

- *embrace* *(st)*

  To hug someone by reaching at least the arms around the other individuals front side.

  (add: active/passive)

CONTACTING

- *place hand* *(st)*

  To place at least one hand on another individual.

  (add: on whom)

- *pull infant's limbs* *(st)*

  The attempt to move the infant away from the mother.

- *explore someone* *(st)*

  To nibble on the other individual's fingers or toes or run its fingers on the other's face.

- *grab at someone* *(st)*

  To reach for someone to find physical stability.

AGONISTIC / SUBMISSIVE BEHAVIOUR

- *open mouth-threat* *(ev)*

  To open the mouth and display the canines. The threat is combined with a staring gaze, including a movement forward-turned.

- *ignore warning* *(ev)*

  The recipient does not react to the open mouth threat.

- *side step from someone* *(ev)*

  To adopt a submissive position and places away from someone, after being threaten.

- *inhibited bite* *(ev)*

  To bite someone, but very softly, without injuring.

- *pull or push aside arm* *(ev)*

  Someone's arm is pulled or pushed aside.

- *turn away from someone* *(ev)*

  To disappear from someone's sight who is sitting in the near, without changing the position.

- *displace* *(ev)*

  Make someone move away from its position by turning forward, occupying the other's place.

  (add: active/passive)

SELF-DIRECTED

- *play alone* *(st)*

  Play alone while performing movements like rolling, to walk around in circles, somersault, object-play. Objects are: e.g. branches, hay, prepared food, soft toy.

  (add: with/without object)

  (add: which object)

- *autogroom* *(st)*

  To search through the own coat for foreign material.

- *self-directed orality* *(st)*

  Thumb-, finger-, or toe-sucking.

- *explore something* *(st)*

  To manipulate an object with fingers or toes, maybe nibble or suck on it.

OTHERS

- *shake* *(ev)*

  To agitate and move all body parts at the same time.

- *duet song* *(st)*

  Species-specific song performed by all group individuals.

- *alarm call* *(ev)*

  It is defined as a call without the great call sequences of a duet song.

- *beg for food* *(st)*

  Approaching close to a conspecific, who is feeding, and then sitting close to it, staring at the food and sometimes even whining is performed.

- *grab at someone's food* *(st)*

  The attempt to steal food while someone else is feeding,

  (add: access / deny)

- *shy away from something* *(st)*

  To avoid something and draw back from the source, e.g. an unfamiliar noise.

- *scratch* *(ev)*
- *yawn* *(ev)*
- *exterior influence* *(ev)*

  E.g. the keeper's car stops at the house and causes an approach of the individuals.

OUT OF SIGHT *(st)*

The focal animal is not visible.

TABLES

FOCAL ANIMAL DATA IN THE SIAMANG GROUP

GROOM			PLAY		
COMPARED INTERACTION PAIRS	MEAN RATE/30′	MEAN DURATION/30′		MEAN RATE/30′	MEAN DURATION/30′
ad M + juv F	1.63±0.40	5.10±0.83		5.38±1.34	5.43±0.81
ad F + juv F	3.75±0.60	8.74±1.11		0.15±0.07	1.94±0.91
T-TEST (SIGN.)	0.004*	0.010*	T-TEST (SIGN.)	0.000*	0.005*
ad F + inf F	2.00±0.34	6.48±1.43		0.39±0.11	1.38±0.40
ad F + juv F	3.03±0.55	7.04±0.99		0.19±0.13	0.89±0.42
T-TEST (SIGN.)	0.114	0.748	T-TEST (SIGN.)	0.280	0.402
ad M + inf F	0.05±0.04	0.35±0.27		0.36±0.12	1.34±0.42
juv F + inf F	0.16±0.05	0.42±0.16		2.71±0.62	2.88±0.51
T-TEST (SIGN.)	0.096	0.829	T-TEST (SIGN.)	0.000*	0.020*
ad M + inf F	0.05±0.02	0.43±0.18		0.14±0.07	2.23±1.36
ad F + juv F	3.75±0.60	8.73±1.11		0.15±0.07	1.94±0.91
T-TEST (SIGN.)	0.000*	0.000*	T-TEST (SIGN.)	0.926	0.860
ad F + ad M	0.64±0.13	4.53±0.95		0.00±0.00	0.00±0.00
inf F + juv F	0.16±0.05	0.42±0.16		2.71±0.62	2.88±0.51
T-TEST (SIGN.)	0.001*	0.000*	T-TEST (SIGN.)	0.000*	0.000*
ad F + ad M	0.64±0.13	4.53±0.95		0.00±0.00	0.00±0.00
ad F + juv F	3.03±0.55	7.04±1.00		0.19±0.13	0.88±0.42
T-TEST (SIGN.)	0.000*	0.069	T-TEST (SIGN.)	0.143	0.040*
ad F + inf F	2.00±0.34	6.48±1.43		0.39±0.11	1.37±0.40
ad M + inf F	0.05±0.04	0.35±0.27		0.36±0.12	1.34±0.42
T-TEST (SIGN.)	0.000*	0.000*	T-TEST (SIGN.)	0.866	0.954
ad F + inf F	2.00±0.34	6.48±1.43		0.39±1.14	1.38±0.40
juv F + inf F	0.16±0.05	0.41±0.16		2.71±0.62	2.88±0.51
T-TEST (SIGN.)	0.000*	0.000*	T-TEST (SIGN.)	0.000*	0.021*
ad F + inf F	2.00±0.34	6.48±1.43		2.00±0.34	6.48±1.43
ad F + juv F	3.03±0.55	7.04±1.00		3.03±0.55	7.04±0.99
T-TEST (SIGN.)	0.114	0.748	T-TEST (SIGN.)	0.114	0.748
ad F + juv F	3.03±0.55	7.04±0.99		0.19±0.13	0.89±0.42
juv F + inf F	0.16±0.05	0.42±0.16		2.71±0.62	2.88±0.51
T-TEST (SIGN.)	0.000***	0.000***	T-TEST (SIGN.)	0.000*	0.003*
ad F + ad M	0.64±0.13	4.53±0.96		0.00±0.00	0.00±0.00
juv F + inf F	0.16±0.05	0.42±0.16		2.71±0.62	2.89±4.92
T-TEST (SIGN.)	0.001*	0.000*	T-TEST (SIGN.)	0.000***	0.000*
ad M + inf F	0.05±0.02	4.43±0.18		0.14±0.07	2.23±1.36
ad F + ad M	1.14±0.30	5.39±0.93		0.00±0.00	0.00±0.00
T-TEST (SIGN.)	0.001*	0.000*	T-TEST (SIGN.)	0.037*	0.106
ad M + juv F	1.63±0.40	5.10±0.83		5.38±1.34	5.43±0.81
ad M + inf F	0.05±0.02	0.43±0.18		0.14±0.07	2.23±1.36
T-TEST (SIGN.)	0.000*	0.000*	T-TEST (SIGN.)	0.000*	0.046*
ad M + juv F	1.63±0.40	5.10±0.83		5.38±1.34	5.43±0.81
ad M + ad F	1.14±0.30	5.84±0.93		0.00±0.00	0.00±0.00
T-TEST (SIGN.)	0.337	0.818	T-TEST (SIGN.)	0.000*	0.000*
ad M + juv F	1.63±0.40	5.10±0.83		5.38±1.34	5.43±0.81
juv F + inf F	0.15±0.05	1.21±0.38		2.00±0.35	3.22±0.47
T-TEST (SIGN.)	0.001*	0.000*	T-TEST (SIGN.)	0.017*	0.020*
ad F + inf F	2.00±0.34	6.48±1.43		0.39±0.11	1.38±0.40
ad F + ad M	0.64±0.13	4.53±0.95		0.00±0.00	0.00±0.00
T-TEST (SIGN.)	0.000*	0.256	T-TEST (SIGN.)	0.001*	0.001*

Tab. 34: Mean grooming and playing rate and duration per 30 min observation units ± standard error of the mean (SEM) of different compared interaction pairs, N = 4; Levene's test for equality of variances (*$p < 0.05$).

Care			Contact		
Compared Interaction Pairs	mean rate/30′	mean duration/30′		mean rate/30′	mean duration/30′
ad M + juv F	0.00±0.00	0.00±0.00		0.10±0.03	0.50±0.33
ad F + juv F	0.00±0.00	0.00±0.00		0.12±0.04	0.20±0.15
T-Test (sign.)	-	-	T-Test (sign.)	0.692	0.410
ad F + inf F	3.06±0.36	3.41±0.54		0.94±0.19	3.21±0.62
ad F + juv F	0.02±0.02	0.01±0.01		0.02±0.01	0.05±0.04
T-Test (sign.)	0.000*	0.000*	T-Test (sign.)	0.000*	0.000*
ad M + inf F	0.18±0.05	1.15±0.40		0.85±0.17	2.13±0.39
juv F + inf F	0.08±0.04	0.16±0.08		2.28±0.38	2.59±0.48
T-Test (sign.)	0.134	0.018*	T-Test (sign.)	0.001*	0.463
ad M + inf F	0.00±0.00	0.00±0.00		0.93±0.25	4.06±1.00
ad F + juv F	0.00±0.00	0.00±0.00		0.12±0.04	0.200±0.15
T-Test (sign.)	-	-	T-Test (sign.)	0.002*	0.000*
ad F + ad M	0.02±0.01	0.06±0.06		0.05±0.26	2.67±2.51
inf F + juv F	0.08±0.04	0.16±0.08		2.28±0.38	2.59±0.48
T-Test (sign.)	0.119	0.254	T-Test (sign.)	0.000*	0.976
ad F + ad M	0.02±0.01	0.06±0.06		0.05±0.26	2.67±2.51
ad F + juv F	0.02±0.02	0.01±0.01		0.02±0.01	0.05±0.04
T-Test (sign.)	0.960	0.412	T-Test (sign.)	0.301	0.300
ad F + inf F	3.06±0.36	3.41±0.54		0.94±0.19	3.21±0.62
ad M + inf F	0.18±0.05	1.15±0.41		0.85±0.17	2.13±0.39
T-Test (sign.)	0.000*	0.001*	T-Test (sign.)	0.734	0.144
ad F + inf F	3.06±0.36	3.41±0.54		0.94±0.19	3.21±0.62
juv F + inf F	0.08±0.04	0.16±0.08		2.28±0.38	2.59±0.48
T-Test (sign.)	0.000*	0.000*	T-Test (sign.)	0.002*	0.432
ad F + inf F	3.06±0.36	3.41±0.54		0.94±0.19	3.21±0.62
ad F + juv F	0.02±0.02	0.01±0.01		0.02±0.01	0.05±0.04
T-Test (sign.)	0.000*	0.000*	T-Test (sign.)	0.000*	0.000*
ad F + juv F	0.02±0.02	0.01±0.01		0.02±0.01	0.06±0.04
juv F + inf F	0.08±0.04	0.16±0.75		2.28±3.67	2.59±0.48
T-Test (sign.)	0.049*	0.000*	T-Test (sign.)	0.000*	0.000*
ad F + ad M	0.02±0.01	0.06±0.06		0.05±0.03	2.67±2.51
juv F + inf F	0.08±0.04	0.16±0.08		2.28±0.38	2.59±0.48
T-Test (sign.)	0.119	0.254	T-Test (sign.)	0.000*	0.975
ad M + inf F	0.00±0.00	0.00±0.00		0.93±0.25	4.06±1.00
ad F + ad M	0.00±0.00	0.00±0.00		0.05±0.02	0.07±0.05
T-Test (sign.)	-	-	T-Test (sign.)	0.001*	0.000*
ad M + juv F	0.00±0.00	0.00±0.00		0.09±0.03	0.50±0.33
ad M + inf F	0.00±0.00	0.00±0.00		0.93±0.25	4.06±1.00
T-Test (sign.)	-	-	T-Test (sign.)	0.001*	0.001*
ad M + juv F	0.00±0.00	0.00±0.00		0.10±0.03	0.50±0.33
ad M + ad F	0.00±0.00	0.00±0.00		0.05±0.02	0.08±0.05
T-Test (sign.)	-	-	T-Test (sign.)	0.319	0.207
ad M + juv F	0.00±0.00	0.00±0.00		0.10±0.03	0.50±0.33
juv F + inf F	0.00±0.00	0.00±0.00		0.12±0.04	0.20±0.15
T-Test (sign.)	-	-	T-Test (sign.)	0.692	0.410
ad F + inf F	3.06±0.36	3.31±0.54		0.94±0.19	3.21±0.62
ad F + ad M	0.02±0.01	0.06±0.06		0.05±0.03	2.67±2.51
T-Test (sign.)	0.000*	0.000*	T-Test (sign.)	0.000*	0.834

Tab. 35: Mean caring and contacting rate and duration per 30 min observation units ± standard error of the mean (SEM) of different compared interaction pairs, N = 4; Levene's test for equality of variances (*$p < 0.05$).

Groom			Play		
Compared Interaction Pairs	mean rate/30′	mean duration/30′		mean rate/30′	mean duration/30′
ad M + juv F	0.38±0.20	1.33±0.64		1.23±0.33	2.01±0.53
ad F + juv F	2.25±0.73	4.70±1.12		0.03±0.03	4.40±0.40
T-Test (sign.)	0.017*	0.011*	T-Test (sign.)	0.001*	0.018*
ad F + inf F	0.82±0.32	3.59±1.05		0.22±0.17	0.23±0.13
ad F + juv F	2.32±0.86	4.60±1.35		0.00±0.00	0.00±0.00
T-Test (sign.)	0.109	0.559	T-Test (sign.)	0.211	0.084
ad M + inf F	0.00±0.00	0.00±0.00		0.00±0.00	0.00±0.00
ad F + inf F	0.82±0.32	3.59±1.05		0.22±0.17	0.23±0.13
T-Test (sign.)	0.013*	0.001*	T-Test (sign.)	0.211	0.084
ad M + inf F	0.00±0.00	0.00±0.00		0.00±0.00	0.00±0.00
juv F + inf F	0.05±0.03	0.29±0.21		1.79±0.61	2.24±0.63
T-Test (sign.)	0.160	0.183	T-Test (sign.)	0.006*	0.001*
ad M + inf F	0.00±0.00	0.00±0.00		0.00±0.00	0.00±0.00
ad F + juv F	2.32±0.86	4.60±1.35		0.00±0.00	0.00±0.00
T-Test (sign.)	0.010*	0.002*	T-Test (sign.)	-	-
ad F + ad M	0.60±0.35	2.94±1.23		0.00±0.00	0.00±0.00
inf F + juv F	0.12±0.05	1.47±0.97		0.53±0.29	1.34±0.63
T-Test (sign.)	0.182	0.386	T-Test (sign.)	0.072	0.038*
ad F + ad M	0.60±0.35	2.84±1.23		0.00±0.00	0.00±0.00
ad F + juv F	2.25±0.73	4.70±1.12		0.03±0.03	0.40±0.40
T-Test (sign.)	0.046*	0.264	T-Test (sign.)	0.323	0.323
ad F + inf F	0.82±0.32	3.59±1.05		0.22±0.17	0.23±0.13
juv F + inf F	0.05±0.03	0.29±0.21		1.79±0.61	2.24±0.63
T-Test (sign.)	0.020*	0.003*	T-Test (sign.)	0.017*	0.003*
ad F + inf F	0.82±0.32	3.59±1.05		0.21±0.17	0.23±0.13
ad F + juv F	2.33±0.86	4.60±1.35		0.00±0.00	0.00±0.00
T-Test (sign.)	0.109	0.559	T-Test (sign.)	0.211	0.084
ad F + juv F	2.33±0.86	4.60±1.35		0.00±0.00	0.00±0.00
juv F + inf F	0.05±0.03	0.29±0.21		1.79±0.61	2.24±0.63
T-Test (sign.)	0.012*	0.003*	T-Test (sign.)	0.006*	0.001*
ad M + juv F	0.38±0.20	1.33±0.64		1.23±0.33	2.01±0.53
ad M + ad F	0.60±0.35	2.84±1.23		0.00±0.00	0.00±0.00
T-Test (sign.)	0.575	0.282	T-Test (sign.)	0.001*	0.001*
ad M + juv F	0.38±0.20	1.33±0.64		1.23±0.33	2.01±0.53
ad M + inf F	0.00±0.00	0.00±0.00		0.00±0.00	0.00±0.00
T-Test (sign.)	0.062	0.043*	T-Test (sign.)	0.001*	0.001*
ad M + ad F	0.60±0.35	2.84±1.23		0.00±0.00	0.00±0.00
ad M +inf F	0.00±0.00	0.00±0.00		0.00±0.00	0.00±0.00
T-Test (sign.)	0.093	0.024*	T-Test (sign.)	-	-
ad F + inf F	0.82±0.32	3.59±1.05		0.22±0.17	0.23±0.13
ad F + ad M	0.48±0.28	1.98±0.98		0.00±0.00	0.00±0.00
T-Test (sign.)	0.416	0.263	T-Test (sign.)	0.211	0.084
ad M + juv F	0.38±0.20	1.33±0.64		1.23±0.33	2.01±0.53
juv F + inf F	0.12±0.05	1.47±0.97		0.53±0.29	1.34±0.63
T-Test (sign.)	0.215	0.905	T-Test (sign.)	0.119	0.418

Tab. 36: Mean grooming and playing rate and duration per 30 min observation units ± standard error of the mean (SEM) of different compared interaction pairs, N = 4; Levene’s test for equality of variances (*p < 0.05).

Care			Contact		
Compared Interaction Pairs	mean rate/30′	mean duration/30′		mean rate/30′	mean duration/30′
ad M + juv F	0.00±0.00	0.00±0.00		0.05±0.03	0.35±0.30
ad F + juv F	0.00±0.00	0.00±0.00		0.00±0.00	0.00±0.00
T-Test (sign.)	-	-	T-Test (sign.)	0.160	0.255
ad F + inf F	4.15±0.68	2.30±0.35		1.84±0.42	6.30±1.43
ad F + juv F	0.00±0.00	0.00±0.00		0.00±0.00	0.00±0.00
T-Test (sign.)	0.000*	0.000*	T-Test (sign.)	0.000*	0.000*
ad M + inf F	0.00±0.00	0.00±0.00		0.19±0.13	0.59±0.35
ad F + inf F	4.15±0.68	4.15±0.68		1.84±0.42	1.84±0.42
T-Test (sign.)	0.000*	0.000*	T-Test (sign.)	0.001*	0.000*
ad M + inf F	0.00±0.00	0.00±0.00		0.19±0.13	0.59±0.35
juv F + inf F	0.16±0.05	0.41±0.16		1.40±0.35	2.23±0.49
T-Test (sign.)	0.070	0.058	T-Test (sign.)	0.002**	0.008*
ad M + inf F	0.00±0.00	0.00±0.00		0.19±0.13	0.59±0.35
ad F + juv F	0.00±0.00	0.00±0.00		0.00±0.00	0.00±0.00
T-Test (sign.)	-	-	T-Test (sign.)	0.146	0.102
ad F + ad M	0.00±0.00	0.00±0.00		0.00±0.00	0.00±0.00
inf F + juv F	0.10±0.06	0.39±0.22		0.97±0.25	1.26±0.33
T-Test (sign.)	0.103	0.088	T-Test (sign.)	0.000*	0.000*
ad F + ad M	0.00±0.00	0.00±0.00		0.00±0.00	0.00±0.00
ad F + juv F	0.00±0.00	0.00±0.00		0.00±0.00	0.00±0.00
T-Test (sign.)	-	-	T-Test (sign.)	-	-
ad F + inf F	4.15±0.68	2.30±0.35		1.84±0.42	6.30±1.34
juv F + inf F	0.16±0.05	0.41±0.16		1.40±0.35	2.23±0.49
T-Test (sign.)	0.000*	0.000*	T-Test (sign.)	0.428	0.006*
ad F + inf F	4.15±0.68	2.30±0.35		1.84±0.42	6.30±1.34
ad F + juv F	0.00±0.00	0.00±0.00		0.00±0.00	0.00±0.00
T-Test (sign.)	0.000*	0.000*	T-Test (sign.)	0.000*	0.000*
ad F + juv F	0.00±0.00	0.00±0.00		0.00±0.00	0.00±0.00
juv F + inf F	0.16±0.05	0.41±0.16		0.40±2.20	2.23±0.49
T-Test (sign.)	0.070	0.058	T-Test (sign.)	0.000*	0.000*
ad M + juv F	0.00±0.00	0.00±0.00		0.05±0.03	0.35±0.30
ad M + ad F	0.00±0.00	0.00±0.00		0.10±0.06	0.48±0.36
T-Test (sign.)	-	-	T-Test (sign.)	0.486	0.776
ad M + juv F	0.00±0.00	0.00±0.00		0.05±0.03	0.35±0.30
ad M + inf F	0.00±0.00	0.00±0.00		0.00±0.00	0.00±0.00
T-Test (sign.)	-	-	T-Test (sign.)	0.160	0.255
ad M + ad F	0.00±0.00	0.00±0.00		0.00±0.00	0.00±0.00
ad M +inf F	0.00±0.00	0.00±0.00		0.10±0.06	0.48±0.36
T-Test (sign.)	-	-	T-Test (sign.)	0.102	0.182
ad F + inf F	4.15±0.68	2.30±0.35		1.84±0.42	6.30±1.34
ad F + ad M	0.00±0.00	0.00±0.00		0.00±0.00	0.00±0.00
T-Test (sign.)	0.000*	0.000*	T-Test (sign.)	0.000*	0.000*
ad M + juv F	0.00±0.00	0.00±0.00		0.05±0.03	0.35±0.30
juv F + inf F	0.10±0.06	0.39±0.22		0.97±0.25	1.26±0.33
T-Test (sign.)	0.103	0.088	T-Test (sign.)	0.001*	0.046*

Tab. 37: Mean caring and contacting rate and duration per 30 min observation units ± standard error of the mean (SEM) of different compared interaction pairs, N = 4; Levene's test for equality of variances (*p < 0.05).

	Mean rate ± SEM (R) and duration ± SEM (D)				Analysis of variances between periods				
		PERIODS			ANOVA		Dunnett T3 (Sign.)		
BEHAVIOUR		P1	P2	P3	F	Sign.	P1 vs. P2	P2 vs. P3	P1 vs. P3
Rest	R	16.36±2.09	30.38.±3.72	39.54±5.32	11.370	*	*	n.s.	*
	D	64.11±15.40	91.85±61.54	106.84±74.38	0.204	n.s.	n.s.	n.s.	n.s.
Feed	R	3.56±0.73	7.59.±1.07	13.79±3.21	6.864	*	*	n.s.	*
	D	9.91±3.07	17.05±3.37	16.32±4.54	1.351	n.s.	n.s.	n.s.	n.s.
Locomotion	R	4.26±0.82	30.83.±6.47	56.25±10.01	20.234	*	*	n.s.	*
	D	24.32±3.97	8.74±1.02	6.28±0.76	11.496	*	*	n.s.	*
Self-directed	R	4.18±0.65	9.17.±2.02	9.17±1.54	4.732	*	n.s.	n.s.	*
	D	19.24±2.95	16.05±2.66	17.11±4.75	0.257	n.s.	n.s.	n.s.	n.s.
Allogroom	R	2.90±0.68	1.97.±0.51	4.63±1.01	2.909	n.s.	n.s.	n.s.	n.s
	D	9.14±2.86	5.19±1.55	10.05±3.27	0.842	n.s.	n.s.	n.s.	n.s.
Play	R	0.49±0.21	2.55±0.80	9.75±2.18	18.265	*	*	*	*
	D	1.76±0.73	4.07±1.06	6.95±1.10	7.544	*	n.s.	n.s.	*
Care	R	4.64±0.86	5.62.±0.76	3.92±0.81	0.910	n.s.	n.s.	n.s.	n.s
	D	9.40±1.88	3.83±0.53	2.28±0.40	7.323	*	*	n.s.	*
Contact	R	3.85±0.82	5.52.±0.97	5.08±0.96	1.012	n.s.	n.s.	n.s.	n.s
	D	5.18±1.23	6.19±1.02	4.97±1.15	0.281	n.s.	n.s.	n.s.	n.s.

Tab. 38: Mean contacting rates and durations ± standard error of the mean per 30 min observation units of the siamang infant's social and non-social behaviour of all observation periods. N = 1; ANOVA (*$p < 0.05$).